Public Water Agencies

Interior Delta Flows and Related Stressors

During the April 16 and 17, 2014, workshop, the Panel primarily considered issues related to the effects of water project operations, particularly the use of OMR to avoid entrainment and relationships between CVP-SWP project operations and salmon survival (e.g., export-inflow ratio and Delta Cross Channel Gate operation). The issue of interior flows and related stressors is certainly broader than just the potential effects of CVP-SWP operations. To completely address the questions posed to the Panel would require identification of the function of flows under the conditions within which native species evolved, and an identification of what is achievable in restoring natural flow functions using a range of available tools. Believing this is the appropriate approach, the water contractors have been working with UCD and SFEI to develop such an analysis for future restoration efforts.

Acknowledging the narrow scope of much of the material presented to the Panel, the Public Water Agencies observe that the CVP-SWP is already heavily regulated. The fundamental tension that the Panel must therefore grapple with is: 1.) whether adopting more of the same regulations will result in measureable increases in species health and abundance, and 2.) if there are non-regulatory actions that are likely to improve species health and survival. How the Water Board uses its authority to balance competing beneficial uses, including improvements in species health and survival, is a policy decision. Ultimately, the Water Board may acknowledge that fixing the Delta is best accomplished through multiagency efforts like the BDCP; because to be effective, a solution needs to be multifaceted and comprehensive and therefore may not be under the authority of any single government agency.

Summary of questions relevant to CVP-SWP operations:

1. Will amending the Water Quality Control Plan ("Delta Plan") E:I ratio provide a measureable benefit to out-migrating salmon?

   No. The literature does not support a conclusion that water project operations are having a significant negative effect on the survival of out-migrating San Joaquin River salmon.

   a. "…[A]ssociations between water export levels and survival probabilities were weak to negligible," (Newman 2008, p. 4).

   b. "…[S]ubstantial uncertainties remain regarding the effects of water operations on the survival and behavior of out-migrating salmonid smolts," (Anderson *et al.* 2012, p. 28).

   c. "…Characterizations of survival in terms of river km or mean flow are inadequate because of rapid travel time and complex routing of fish through different reaches cannot be explained by these mean measures. The IRP suggests the

travel, routing and survival of fish through the system needs to account for migrant behavior and the behaviors of the predators in response to the strong tidal influences in the Delta," (Anderson *et al.* 2012, p. 21).

d. In any case, substantial uncertainties remain regarding the effects of water operations on the survival and behavior of out-migrating salmonid smolts. Conflicting findings of different studies and methodological issues associated with the approaches used to evaluate survival and routing behavior of out-migrating salmonid smolts have not yet provided a clear path to suggest that fine-tuning water operations will provide a successful means of maintaining or restoring salmonid populations that migrate through the southern Delta," (Anderson *et al.* 2012, p. 28).

e. "The [NAS] committee concludes that the rational for increasing San Joaquin River flows has a stronger foundation than the prescribed action of concurrently managing inflows and exports," (NAS 2010, p. 60).

2. Will amending the Delta Plan to require Head of Old River Barrier (HORB) provide a measureable benefit to out-migrating Chinook salmon?

   No. The literature does not support a conclusion that installation of the HORB measurably improves survival of out-migrating San Joaquin River salmon.

   a. "The decision to install a rock barrier at Head of Old River (HORB) was based upon an assumption that it would not enhance predation on salmonid smolts; a previously tested non-physical barrier (bubble curtain) was shown to enhance the risk of predation mortality on smolts, which was the primary reason given for not using that approach," (Anderson *et al.* 2012, p. 14).

   b. "…findings of the 2011 VAMP acoustic tag study…found that the highest survival rate through the Delta was via Old River. Most (64%) of the tagged smolts surviving to Chipps Island did so via artificial transport from the CVP holding tank…data presented by the VAMP study showed that forcing smolts through the Delta by blocking the entrance to Old River decreased survival, presumably due to predation through the central Delta region," (Anderson *et al.* 2012, pp. 14-15).

   c. "...it suggests that the use of rock and/or other barriers at the head of Old River on the San Joaquin River that force smelts into the Delta interior where survival is less than 2% should be reconsidered. Indeed, it seems plausible from findings of recent acoustic tagging studies that higher smolt survival will be achieved through encouraging migration down Old River and towards the CVP tank," (Anderson *et al*., 2012 pp. 26-27).

3. Will amending the Delta Plan to require increased closure of the Delta Cross Channel provide a measureable benefit to out-migrating Sacramento River Chinook salmon?

Perhaps, but any increase would be quite small and likely have a negative effect on water quality.

a. "Eliminating entrainment into the interior Delta is expected to result in a 2-7 percentage point increase in overall survival," (Perry *et al.* 2012, p. 9).

b. "…the small absolute increase in survival is also due to low survival probabilities observed in all routes. Route specific survival for all routes was <0.5 for most release groups," (Perry *et al*. 2012, p.9).

c. "The effect of eliminating entrainment into the interior Delta at any particular junction depends, in part, on the fraction of the population passing the junction as there are multiple points of entry," (Perry *et al*. 2012, p. 9).

4. Will amending the Delta Plan to include OMR limitations provide a measureable benefit to delta smelt?

No. The 2008 FWS BiOp already includes highly restrictive OMR limitations even though the population level effect of entrainment is currently unknown.

a. "…[C]urrently published analyses of long-term associations between delta smelt salvage and subsequent abundance do not support the hypothesis that entrainment is driving population dynamics year in and year out (Bennett 2005; Manly and Chotkowski 2006; Kimmerer 2008; Maunder and Deriso 2011)," (DOI at 14).

b. "In conclusion, the scientific evidence available to the Service is inconclusive about the long-term population level importance of adult entrainment," (DOI at 16).

c. "The Service recognizes that the upstream migration path leads them into Old and Middle Rivers regardless of South Delta exports because adult delta smelt salvage has occurred at all OMR flows less than 0 cfs and even when OMR was positive," (DOI at 20).

d. "…There clearly is a relationship between OMR flows and salvage rates, but the available data do not permit a confident identification of the threshold values to use in the action, and they do not permit a confident assessment of the benefits to the population of the action," (NAS 2010, p. 51).

e. The various life cycle models identify entrainment as a weak covariate (Maunder and Deriso 2011, Maunder and Deriso 2012, *unpub*., Miller *et al*. 2012, Thomson *et al.* 2010, MacNally *et al*. 2010). Kimmerer 2008 found similarly, "…no effect of

export flow on subsequent midwater trawl abundance is evident."

f. "…the historical distribution of smelt on which the relationship with OMR flows was established no longer exists. Delta smelt are now sparsely distributed in the central and southern delta [cite omit], and pump salvage also has been extremely low, less than four percent of the 50-year average index," (NAS 2010, p. 50).

g. Technical reviews of the FWS' 2008 BiOp analysis relating OMR flows to total salvage have raised questions.

    i. FWS analysis contains inappropriate use of raw salvage numbers (Deriso 2009, Doc. 396, pp. 16-21 and Doc. 401, pp. 9-11, 16-20).

    ii. Salvage and OMR flows do not have a statistically significant effect on the population growth rate (Deriso 2009, Doc. 396, p. 21-26 and Doc. 401, pp. 11, 21-26 and Doc. 508, pp. 2-13).

    iii. Turbidity and OMR can be used to construct a normalized salvage model predicting winter salvage rates (Deriso 2011, Doc. 772, pp. 2-9; See also, Nobriga Interior Flows and Other Stressors Workshop presentation.)

h. "…The Fall Midwater Trawl was not designed to collect delta smelt and any assumed relationship between the abundance index based on those collections and the actual size of the smelt population is questionable at best," (Anderson *et al.* 2013, p. 26).

5. Will amending the Delta Plan to include OMR limitations provide a measureable benefit to Chinook salmon and steelhead?

   No. OMR does not appear to be a strong predictor of entrainment. Regardless, take has been very low for about a decade (starting prior to the current BiOp), being less than 1% or 2% of the population (Chinook winter-run and Chinook spring-run respectively).

   a. "The [NAS] committee concludes that the strategy of limiting net tidal flows toward the pump facilities is sound, but the support for the specific flow targets is less certain. In the near-term telemetry-based smolt migration and survival studies (e.g., Perry and Skakski, 2009) should be used to improve our understanding of smolt responses to OMR flow levels. Reliance on salvage indices or the PTM results alone is not sufficient," (NAS (2010), p. 58).

   b. "Additionally, there is little direct evidence to support the position that this [OMR] action alone will benefit the San Joaquin salmon….," (NAS (2010, p. 58).

c. Technical reviews of NMFS' 2009 BiOp analysis relating OMR flows to total salvage have raised questions. Review concluded that it is inappropriate to use raw salvage because the analysis must consider the proportion of the population lost to salvage. If the data is properly normalized, the result is that there is no statistically significant relationship between the take index and OMR flows (Deriso 2010, Doc. 271, pp. 2-9).

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Report of the 2013 Independent Review Panel (IRP) on the Long-term Operations Biological Opinions (LOBO) Annual Review

Prepared for: **Delta Science Program**

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Scope and Intent of Review: This report represents findings and opinions of the Independent Review Panel (IRP) assembled by the Delta Science Program to inform the National Marine Fisheries Service (NMFS) and the U.S. Fish & Wildlife Service (USFWS) as to the efficacy of water operations and certain regulatory actions prescribed by their respective Long-term Operations Biological Opinions' (LOBO) Reasonable and Prudent Alternative Actions (RPAs) as applied from October 1, 2012 through September 30, 2013 (Water Year 2013).

This year's annual review focused primarily on: (1) implementation of NMFS's RPAs for Shasta Operations in connection with the activities of the Sacramento River Temperature Task Group (RPA Actions I.2.1 – I.2.4), (2) new approaches to loss estimation of Chinook salmon, steelhead and green sturgeon at the Skinner Delta Fish Protective Facility and Tracy Fish Collection Facility (NMFS Opinion Term and Condition 2a), and (3) the USFWS RPAs related to Water Operations in connection with protection of delta smelt from December through June of the 2013 Water Year (RPA Action 1).

The federal government shutdown in early October 2013 affected the timely provision to the IRP of an official written report on Water Operations related to protection of delta smelt, and so comments and recommendations on this aspect of the original charge to the panel was amended to be at the discretion of the IRP; the IRP included comments and recommendations on delta smelt in its 2013 report.

After reviewing a required set of written documents (Appendix 1), the IRP convened at a public workshop in Sacramento, CA on 6-7 November 2013. The first day of the 2-day workshop provided a forum for the IRP to consider information on water operations, activities and findings related to RPA Actions related to Shasta Operations and effects on aspects of the early life history of winter-run Chinook salmon in the Sacramento River, the development of loss equations for listed anadromous fishes associated with Delta Water Operations, and a retrospective consideration of Delta Water Operations as related to delta smelt protective actions early in the 2013 Water Year (WY). On the second day the IRP deliberated in a private session beginning at 8:30 a.m. in order to prepare and present their initial findings at the public workshop at 2:00 p.m., after which there was an opportunity for agency representatives, members of the public and the IRP members to comment and otherwise exchange impressions and information. Subsequent IRP communication and deliberations were conducted via email and conference calls in the course of drafting this final report.

EXECUTIVE SUMMARY

The review panel recognizes the unique challenges and constraints faced by all of the agencies attempting to balance existing commitments and mandated coequal goals of (1) providing a reliable water supply for California and (2) protecting, restoring and enhancing the Delta environment and associated Central Valley ecosystems. The agencies charged with this daunting task continue to cooperate and integrate activities, at least to some degree, but polarity of focus remains evident. Perhaps this is to be expected in an environment where so much is at stake, socio-economic pressure is intense, and so little is precisely predictable.

The dry 2013 water year (WY) presented an even greater challenge to achieving specific RPA targets than was the case in 2012 and confirmed concerns expressed in previous IRP reports (Anderson et al. 2010, 2011, 2012) that some physical targets may not be routinely achievable. After four years of operating under the RPA actions, observations are available for a small sampling of both wet and dry years. The 2013 WY began with the promise of a wet or normal year but ended dry with low reservoir storage due largely to a sparse snowpack and one of the driest January-May periods in the past 90 years.

Although it still remains too early to make definitive assessments of long-term effects on listed species populations, signs linking specific RPA actions to improved conditions remain elusive. A science review panel is not required to confirm or refute that prescribed physical/numerical targets such as temperature compliance points and incidental take are met in any given year. Rather, as noted by all of the previous OCAP/LOO IRPs, the current LOBO IRP emphasizes the continued need to explicitly link the success or failure of meeting physical targets prescribed in the RPA Actions to the biological/ecological responses of the listed species. This is the only way that the intended goals (e.g., protection of listed species) of RPA Actions can be assessed in a scientific context.

The IRP was encouraged by a perceived continued movement toward research aimed at linking the survival and behavior of fishes to water operations on the Sacramento River as well as at the Delta Pumping Facilities. Inclusion of more ecological and behavioral responses of the fish populations or life stages targeted by the RPA actions continues to be recommended as multiple years of observations become available to support a more comprehensive evaluation of the co-equal goals. Despite recent efforts to improve loss estimates from water operations in the Delta, the IRP remains concerned with the assumptions and statistical approaches applied in the evaluation of

listed fish species loss estimates associated with the pumping facilities. In particular, direct and indirect losses due to entrainment into the pumping facilities and the variance estimates associated with those losses may be substantially underestimated, and are not well-connected to population size estimates. Given that loss estimates are essential for establishing levels of incidental take, accurate estimates of losses relative to the size of the at-risk populations would certainly be worth the effort required to obtain them.

As noted in previous years, the regular evaluation of realistic goals and objectives is as much a part of an adaptive management strategy as are decisions to alter actions when justified by novel observations and response data that deviate from expectations. The dry 2013 WY provided another opportunity to consider how it is not too soon to step back and consider whether the intentions of habitat restoration efforts are tracking toward expected outcomes. If effects of water operations and protective actions on populations of listed species are not detectable following a series of either “good” or “bad” water years in the future, concerns about whether or not fine-tuning of water operations can contribute substantively to the survival of native species will persist.

The IRP again appreciated the opportunity to concentrate on a focal subset of RPA actions this year but noted some concerns about progress, biological responses and consequences in applying the many other prescribed actions within the watersheds. Promised improvements intended to reduce fish losses at the pumps, expand spawning and rearing habitat, preserve cool water reservoir storage and advance temperature model development are reportedly progressing but remain behind schedule.

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INTRODUCTION

Historically, the challenge of meeting water needs for much of California's growing human population has been met by engineering water storage and delivery systems that have profoundly changed the landscape and flow regimes of riverine and deltaic ecosystems associated with California's Central Valley. These and other anthropogenic alterations over time have been accompanied by profound changes in aquatic flora and fauna, including a persistent decline in native fishes. Consequently, some species have been afforded protection under the Endangered Species Act (ESA) and government agencies have been charged with developing ways of protecting these populations from further jeopardy associated directly or indirectly with water operation projects in the region.

Recent formal legislative recognition that water and other habitats should be managed to restore and enhance the ecosystem as a coequal goal with providing a reliable water supply to California (Delta Reform Act) provided an ambitious and novel conceptual approach to water management within the region. Ultimately, the ability to meet this mandate appears to rest largely on adjusting existing water operations within the context and constraints of a system developed and engineered to primarily achieve one of these goals – a reliable water supply in a region where precipitation is highly variable in both space and time. This constrains the options for meeting the aforementioned co-equal goals largely to modifications in water operations that amount to frequent serial adjustments in reservoir releases and export pumping from the system so as to avoid jeopardizing protected fish populations while continuing to ensure the availability of water for other human uses.

***Background on the LOBO RPA review process*:** NOAA's National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (USFWS) have each issued Biological Opinions on long-term operations of the Central Valley Project (CVP) and State Water Project (SWP, hereinafter CVP/SWP; Long-term Operations Biological Opinions) that include Reasonable and Prudent Alternatives (RPA) designed to alleviate jeopardy to listed species and adverse modification of critical habitat. NMFS' Opinion requires the U.S. Bureau of Reclamation (USBR) and NMFS to host a workshop no later than November 30 of each year to review the prior water year's operations and to determine whether any measures prescribed in the RPA should be altered in light of new information (NMFS' OCAP Opinion, section 11.2.1.2, starting on page 583). Amendments to the RPA must be consistent with the underlying analysis and conclusions of the Biological Opinions and must not limit the effectiveness of the RPA in avoiding jeopardy to the ESA listed species or result in adverse modification of critical habitat.

The purpose of this annual review of the Long-term Operations Biological Opinions (LOBO) is to inform NMFS and USFWS as to the effectiveness of operations and regulatory actions prescribed by their respective RPAs in the 2013 Water Year.

Since the Long-term Operations Opinions were issued, NMFS, USFWS, USBR, U.S. Geological Survey (USGS), California Department of Fish and Wildlife (CDFW) and the Department of Water Resources (DWR) have been performing scientific research and monitoring in concordance with the implementation of the RPAs. Technical teams and/or working groups, including the geographic divisions specified in the NMFS' Long-term Operations Opinion, have summarized their data and results following implementation of the RPA Actions within technical reports. The data and summary of findings related to the implementation of the RPAs provide the context for scientific review regarding the effectiveness of the RPA Actions for minimizing the effects of water operations on ESA listed species and critical habitat related to the operations of the CVP/SWP. A subset of these technical reports was presented for consideration by the 2013 LOBO IRP (see Appendix 1).

General charge and scope for the 2013 LOBO IRP: Annual reviews prior to 2012 considered all of the RPA Actions but in 2013, as in the previous year, the panel's charge focused on a subset of the operations and RPAs.

This year's annual review included:

(1) Temperature management opportunities and constraints in WY 2013 as assessed by the Sacramento River Temperature Task Group (SRTTG);

(2) Proposed modifications to Term and Condition 2a of the NMFS Long-term Operations BiOp, which required USBR to develop alternative methods for the quantification of incidental take of listed salmonid species and green sturgeon at the Federal and State export facilities;

(3) A retrospective analysis of water operations and delta smelt protective actions taken in WY 2013.

The specific scope of the 2013 LOBO review was defined by questions posed to the 2013 IRP by the technical teams/task groups that presented materials for review. This IRP report addresses each of the questions posed from a scientific perspective, and provides additional observations, opinions and recommendations where, in the panel's opinion, they seemed potentially useful to agency staff for consideration in real-time decision making.

***Acknowledgements*:** The members of the IRP appreciate and acknowledge the efforts of the agency and technical team representatives and contractors who prepared the written materials and delivered the workshop presentations on which this report is based. Each year we are cognizant that much of the material has to be compiled, analyzed and organized in a relatively short time, and that this year the federal government shutdown in October 2013 was a particularly difficult challenge for the federal agencies involved. Despite the many competing demands on the workshop participants, the materials were presented professionally, concisely, and largely on schedule. The panel wishes to express a special thanks to the Delta Science Program management and the entire staff for providing the organization and logistical support to facilitate our task. In particular, Lindsay Correa (Senior Environmental Scientist), as usual, expertly attended to a wide variety of technical and provisional details in support of the IRP's efforts before, during and following the workshop. Similarly, George Isaac ably assisted us through a number of administrative issues.

LOBO IRP COMMENTS ON RPA ACTIONS IN WATER YEAR 2013

General comments and observations

The IRP begins this annual review with a familiar mantra to encourage the development of scientifically defensible connections between satisfying the conditions of specific physical or numerical targets prescribed in the RPAs and ecological responses in the listed species populations. Meeting prescribed targets such as temperature control points within specific river reaches and prescribed levels of incidental take is not the same as succeeding in the intended overarching purpose of the RPAs. An annual science panel is not required to confirm whether or not prescribed targets are achieved but rather if achieving those targets can reasonably be expected to address the intended purpose of reducing or eliminating jeopardy to listed species associated with annual water operations. This requires a demonstrable connection between biological responses of the protected species and the RPAs. The 2013 panel's intent is not to suggest that previous IRP statements to the same effect have gone unheeded, but rather as a reminder to encourage the continued movement we have seen in this direction.

At the workshop in Sacramento, the panel was presented with a brochure that briefly described the California Data Exchange Center and Flood Emergency Response Program. Presumably, this was offered in response to previous IRP recommendations (Anderson et al., 2011, 2012) to develop of a web-based collaborative tool that encouraged multidisciplinary collaboration and a centralized data source for real-time management of water resources as applied to the LOBO objectives. The purpose of the program is to provide reservoir operations staff secure and rapid access to data from

remote sensors and instrumentation that feeds into forecasting models intended to coordinate reservoir operations prior to and during flood emergencies. It was not surprising that such a system is in place, but it is unclear how easily it could be adapted to the purposes the previous IRPs envisioned.

Hydrologic summary of the 2013 Water Year (WY)

The 2013 WY presented a forecasting challenge for water operations in that precipitation early in the year held out a false promise of water availability later in the year. The early season precipitation was followed by the driest January to May period on record for the past 90 years. Although total precipitation for the WY was nominally less than 10% below average, it was the distribution of precipitation that presented the challenge for water management. Snowpack in the mountains did not persist much beyond April and there were early demands for irrigation water from some users with senior water rights.

Given the wealth of annual flow records available to various technical groups, it is important to have and use the results of a comprehensive analysis of rainfall patterns coupled to regional and global climatic patterns. Such an analysis should identify precipitation-related conditions under which regional aquatic biota have evolved and which also help to identify reservoir release patterns that can be used as part of an adaptive management strategy favoring the survival of those species [see, for example, recent studies conducted in the eastern United States; Maxwell et al. 2013, Sheldon and Burd 2013, and Sherwood and Greening 2013]. One requirement for restoring or maintaining habitat quality will be to recreate or simulate previously existing hydrographic cues important to the survival of listed species. A first step is to establish a relevant benchmark that characterizes important cyclic phenomena. These cycles may not be apparent simply by looking at random blocks of a certain number of years, but rather by viewing historical running averages of various lengths in order to detect predictable cycles of wet/dry periods. With increasing observations of linkage between long-term oscillations in oceanic temperature and/or changes in climatic trends (e.g., Werritty 2002, Hannaford and Marsh 2006, and Maurer *et al.* 2004), it is increasingly important to understand regional runoff patterns (Kelly and Gore 2008). Maurer (2007) and Cayan *et al.* (2008) have done extensive modeling of potential climate change scenarios and could offer insights into changes in runoff that might affect management decisions.

The IRP suggests that a review of annual flow records to detect any predictable patterns influenced by the Pacific Decadal Oscillation (PDO) as well as consideration of proposed scenarios for climate change in California will be useful exercises to “fine-tune” future management options. This objective can be easily accomplished [and may

have already been completed] through analysis of running averages of monthly flow records over 10, 20, 30 and 50 year periods in order to detect oscillations that drive long-term forecasts of water availability. It is likely, for example, that 10-year oscillations will parallel the PDO and longer oscillations may reflect more complex phenomena but will allow the development of wet-period and dry-period forecasting and management strategies.

The very dry 2013 hydrologic year, particularly following on the heels of a previously dry year in 2012, is an opportunity to refine long-term forecasting and management strategies, as the inclusion of these years will result in a downward trend in estimates of available water and a more realistic expectation of achieving the co-equal goals of water supply and resource protection under less than optimal conditions.

The analysis of data describing physical habitat characteristics important in sustaining populations of ESA target species in this very dry year also presents an excellent opportunity to identify marginal habitats that may be limiting the successful recovery of these species, and how the characteristics of those habitats are affected by RPA actions.

Sacramento River Temperature Task Group 2013 Technical Report for the Long-Term Operations BiOps

As in previous dry years, when temperature compliance points (TCP) could not be met downstream, they were moved upstream. This year was no exception and the TCP of 56º F was moved upstream to Airport Road Bridge, where there is no temperature monitoring station to verify that the TCP is even being met. A surrogate station at Balls Ferry is used to estimate water temperature at Airport Road. Riverine temperatures are monitored in one dimension longitudinally at discrete points, which does not account for spatial variation in temperature along a cross-section of the river, with depth, or due to springs (hyporheic flows from the streambed or adjacent upland) or various levels of shade provided by riparian vegetation in off channel habitats. Monitoring the spatial variation in water temperature could provide useful, even essential, information for water management aimed at maintaining or improving survival of salmonid early life stages. Given the apparent difficulty with achieving TCPs between Balls Ferry and Bend Bridge, there appears to be a need to reconsider requirements for TCPs farther downriver of Clear Creek, particularly where there is little overlap with the location of salmonid spawning sites and early life stages. The fact that the vast majority of salmon redds are located upriver of Balls Ferry only serves to support a focus on what can be accomplished in terms of water operations to maintain suitable spawning and early

rearing habitat in areas that are being used by fish. Cold water storage that is conserved rather than released in unsuccessful attempts to extend TCPs farther down river than necessary to insure survival of developing embryos and alevins where redds are located, can be used to improve survival of juveniles during the summer months by reducing both temperature stress and the risk of stranding; that is, it may be a useful exercise to determine the location of the TCP by the downstream extent of a predetermined majority of potentially successful redds in both main-stem and secondary channels. See Appendix 3 for details of a heuristic model that should help to demonstrate this point.

The IRP suggests that the question of changing compliance points from a daily average temperature to a 7-day average daily maximum (7DADM) needs to be evaluated in the context of how it affects the location of the TCP as well as survival of salmonid early life stages. The current management scheme, based on daily average temperature, is potentially suboptimal because the location of the TCP is too far downstream, which then reduces the water available to address other mortality processes, e.g. redd dewatering and juvenile stranding (See Appendix 3). If the 7DADM metric effectively moves the TCP farther downstream (relative to the current average temperature location) and so requiring additional water, then the standard could be detrimental to both total fish survival and flexibility of Shasta operations. Alternatively, if the TCPs are allowed to change locations based on the availability of cold water resources, changing them from a daily average temperature to a 7DADM could even result in the TCP moving upstream. Therefore, until a model is developed and applied to consider tradeoffs in water allocations the IPR believes the effects of the temperature standard on fish is uncertain.

As noted by previous OCAP and LOO panels, decisions to augment or constrain water releases need to consider the coupling of hydrology and biology, including spatio-temporal impacts on adult selection of redd locations as well as survival of egg through early juvenile life stages. Some of these relevant issues are discussed in Appendix 5.

The Effect of TCD Hydraulic Operational Criteria on Storage of Cold Water

Constraints on Shasta operations that affected the use of the cold water resource within the reservoir were evident in WY 2013. According to the technical report:

"Because of the low storage and elevation at Shasta Reservoir this water year, Shasta Temperature Control Device (TCD) operational criteria limited Reclamation's flexibility with the TCD gate configurations. This reduced the temperature operation efficiency for a period in June 2013. In June, Reclamation was required to open all the middle shutters sooner than desired to meet hydraulic operational criteria. This was based on

the Shasta TCD operation manual, which states at water surface elevation 1010 feet, all middle gates are to be open to maintain proper submergence of the penstock intakes."

We note that operations to meet temperature criteria in June of 2013 (page 9) could not be optimized because of these operational restrictions. It may be useful to evaluate the likelihood of critical depletions more than 30 days in advance so that water deliveries can be scheduled over a longer time period and hence avoid the hydraulic operational criteria that have the net effect of forcing the inefficient use of cold water storage. In this recommendation, we assume that the need to invoke this operational criteria decreases with reductions in powerhouse discharge.

Use of HEC-5Q for Long Term Temperature Forecasts

The IRP understands that the quantity of cold water storage primarily in Shasta Reservoir, but also in Trinity and Whiskeytown Reservoirs determines the downstream extent of Sacramento River habitat that meets the temperature requirements of early life history stages of fall and winter-run Chinook salmon. Effective use of the cold water resource over an annual operational cycle to maximize survival benefits for fish requires accurate predictions and monitoring of: (a) reservoir stratification dynamics, (b) selective withdrawal characteristics of the reservoir outlets, and (c) water temperature dynamics of the upper river. The IRP was informed at the LOBO workshop that HEC-5Q was used to develop water flow and temperature management scenarios for consideration. HEC-5Q is a standard modeling tool developed by the Corps of Engineers to evaluate alternative operational plans. It can be used for short-term optimization (optimum blending of water from different reservoir strata to meet an immediate downstream temperature target) when combined with selective withdrawal capability. It can also be used for long-term optimization (i.e., determine release quantity and water temperatures to optimize reservoir storage) to meet long-term downstream temperature criteria. We have several comments related to the use of HEC-5Q to support water temperature management in the Sacramento River.

First, as with all models, there are tradeoffs between model accuracy and run-time. Models useful for optimization must be relatively simple to minimize the time required for multiple runs to converge on an optimal operation given a specific optimization function. We assume that the need for reduced run-time factored into the decision to use this model. However, some of the attributes of HEC-5Q that make it useful for long term operational optimization also increase the error of its predictions. While calibration details for the modeling were not provided, based on experience and expertise represented on the IRP, there are multiple sources of uncertainty that may affect the accuracy of the forecasts by as much as 2-3º C. Increased error in model forecasts increase the risk that incorrect water management decisions may be made. In the case

of the HEC-5Q application, we note three attributes of the HEC-5Q application that likely affect forecast accuracy:

- The model was updated with meteorological conditions at 6-hour time-steps instead of 1-hr or even 3-hr updates. While longer time periods between updates will likely not affect prediction accuracy of reservoir stratification, they will likely affect the accuracy of river temperature predictions, particularly at lower flows or during high temperatures when salmon early life stages are most susceptible to temperature effects.

- The reservoir dynamics were simulated with a 1-D representation (vertical) whereas stratification and water quality dynamics within reservoirs are typically 2-D (longitudinal and vertical) although situations may occur were a full 3-D representation may be required. As a consequence, calibration parameters in a 1-D model must be adjusted to ranges outside of values that have physical meaning to "force" the 1-D model to calibrate to reality that is usually at least 2-D, if not 3-D. The amount of error associated with use of a 1-D model to simulate a reservoir depends upon the extent to which the 1-D assumption is violated.

- The river was simulated with a 1-D representation (longitudinal). This is likely the smallest source of error and may be negligible depending upon how the temperature calibration was performed. For example, if the riverine part of the HEC-5Q model was calibrated to accurately simulate low flow, summer time conditions then the simulations may be of acceptable accuracy. However, if the model was calibrated to minimize residuals (i.e., differences between predicted and observed water temperatures) over an annual cycle then the simulation accuracy may be reduced for the time periods that are most critical to salmon early life stages. In addition, the report mentions a number of ungaged and unmonitored tributaries downstream of Keswick Dam that may seasonally affect water temperature. The methods used to synthesize tributary flow and temperature should be reviewed to optimize forecast accuracy.

Next, while there is nothing inherently wrong with HEC-5Q we note that it is an older legacy model that, to our knowledge has not been updated for more than a decade. For purposes addressed in this review, a more current model such as CE-QUAL-W2 or a dedicated temperature model that can be run to support real-time operations (CE-QUAL-W2 can also be used for this purpose) may be more appropriate. Interestingly, CE-QUAL-W2 has been applied to Shasta Dam and the IRP wondered why it was not used to support management decisions that are based on downstream temperature and stage dynamics.

There seems to be suboptimal communication between field survey teams monitoring redd dewatering and juvenile stranding and group members who simulate water temperatures. Model selection and calibration should be coordinated within the SRTTG such that future temperature modeling and forecasting are configured, calibrated and optimized to accurately predict temperatures at TCPs located at different distances downstream of Keswick dam during critical salmon early life stages or alternatively to identify a TCP based on the distributions of redds.

Temperature modelers may wish to calibrate to extreme values/conditions in the Sacramento River instead of using standard methods to reduce deviations (differences between measurements versus predictions) over an annual cycle. That is, the ability to simulate temperatures around 40° F is less important than the ability to accurately simulate temperatures around 55° F. This can be done easily during calibration by weighting more heavily (e.g., doubling them) residuals associated with critical time periods when temperatures approach detrimental levels.

Another question of interest is also affected by the details of model calibration. The LOBO workshop presentation by Brycen Swart (NOAA Fisheries) included temperature measurements summarized as average daily water temperature versus a seven day running average of daily maximums (7DADM). There is typically about a 2^{O} F difference between the two temperature statistics which is likely consistent with the expected error in the river water temperature predictions from HEC-5Q. The selection of an acceptable maximum temperature measure that avoids deleterious effects on early salmon life stages, while minimizing demands on water resources, should include input from river water temperature modelers to ensure model accuracy during the months and flow conditions considered to be most critical to salmon survival.

The IRP noted that the extensive water temperature data collected by the California Department of Fish and Wildlife (CDFW) in connection with monitoring salmon redds did not appear to be integrated into the temperature modeling studies conducted by the BoR. It would have been useful to compare the measured temperatures obtained by the CDFW during redd dewatering/stranding studies to the predictions made by HEC-5Q to get a better idea of the differences between predicted and observed water temperatures.

NMFS seemed most interested in how water releases affected seasonal variation in water depth as it pertains to redd dewatering and juvenile stranding. HEC-5Q (or a future model) can output both stage and depth. The IRP considered ways that the output of both stage and discharge estimates could be coupled to survival of early life

stages associated with dewatering/stranding of redds and juveniles (see Appendix 3 of this report).

Better Integrating Long-term Forecast Simulations with Real-Time Operations

Reservoir operations currently appear to be based on relatively long-term simulations derived from data and hydrologic models from the U.S. Army Corps of Engineers Hydrologic Engineering Center (HEC) but many of the issues addressed by the Sacramento River Temperature Task Group (SRTTG) require short-term remedies using real-time operations at Shasta, Trinity, and Whiskeytown Reservoirs. The SRTTG seems to be largely operating in a reactive adjustment mode as a means of meeting RPA targets. For example, TCPs in any given year are reset depending on the availability of cold water storage in reservoirs, but ultimately are expected to meet 10-year running average expectations at multiple riverine locations (Clear Creek, Balls Ferry, Jelly's Ferry and Bend Bridge). In WY 2013, a 56º F TCP was set at Airport Road Bridge, where there is no RPA requirement to meet any 10-year running average success criterion. The SRTTG annually recommends a TCP point that, given available cold water storage, is feasible for the longest river reach that could provide salmonid spawning habitat regardless of where active spawning is occurring. Long-term forecast simulations were apparently inadequate to support more strategic use of the cold water resource during the dry 2013 WY, if in fact there even were a more effective way of managing reservoir operations. Inter-annual variability in the seasonal amount and spatial distribution of precipitation in the region presents a serious forecasting challenge.

It appears that the real-time operations needs of the SRTTG and the long-term forecasting of USBR are not well interfaced, and perhaps there is an opportunity here to collaborate on development of an integrated long-term forecasting and real-time operations capability. For example, the present *ad hoc* temperature monitoring system does not include a station at Airport Road Bridge. This could easily be remedied and such collaboration would increase the accuracy of temperature forecasts and provide increased lead time prior to water crisis situations thereby potentially increasing the efficiency with which the cold water resource can be managed to enhance survival of salmonids as suggested in Appendix 3 of this report.

Critical elements of an improved real-time monitoring system would include at least: (a) one or more automatic temperature profilers within Shasta Reservoir to describe temperature stratification patterns near the dam; (b) real-time temperature reporting sondes located at points within the Sacramento River channel and significant tributary mouths; (c) real-time calibrated reporting stage monitors, and (d) a dedicated high

resolution temperature forecasting model that can be used in near-real time to forecast and evaluate downstream temperatures, stages, and discharges based on different scenarios of dam releases, release temperatures, and range of anticipated meteorological conditions. The real time model, coupled with reporting temperature and stage monitors, will help ensure that the cold water resource within the three reservoirs is used as efficiently as possible to protect fish and allow flexibility in water operations.

Establishing a real-time modeling capability requires additional information. For example, transects of channel and flood plain morphology at key locations at known spawning habitats should be surveyed if such information does not presently exist. Annually collected low flow light detection and ranging (Lidar) data for the reaches below Keswick dam to Red Bluff diversion dam (see Fig. 1 in Revnak and Killam 2013) could be used to develop a Digital Elevation Model (DEM) to feed into existing hydraulic models. The DEM in conjunction with stage-discharge and temperature relationships could be used to evaluate the likelihood of stranding and dewatering over all discharge regimes and as spatial distribution of spawning and rearing change from year to year.

In addition, the IRP supports continued and expanded monitoring of redd dewatering and juvenile stranding and suggests that the teams place temperature/water level sensors in redds and important juvenile rearing habitats. This will allow a retrospective analysis of modeling and application of water flows intended to benefit the species of interest over their riverine life cycle stages. Then the important question of how many fish benefit from the water management can be addressed so that informed decisions can be made to maximize protection of salmon redds and low flow juvenile salmon habitat. With this type of assessment informed decisions about moving TCP can be made in keeping with RPAs, which are aimed at protecting fish not simply meeting TCP goals.

Consideration of River Water Temperature Dynamics

In general, the SRTTG seems to consider river water temperatures in a simplistic way as though water temperatures are laterally and vertically homogeneous within the river corridor. It would be desirable to measure the spatial variability of temperature and water level relative to critical spawning and rearing habitat, including secondary channels (see Appendix 5). Future temperature dynamics studies within the river corridor should include monitoring temperatures in the main channel, secondary channels, hyporheic (within the gravel) zones, secondary channels, and tributaries.

Loss Estimation for Listed Anadromous Species

The technical team (TT) uses Jahn's (2011) simple model to estimate fish loss*:*

$$K = G\text{-}H = H/S\text{-}H$$

where K =loss, G=entrainment, S=survival proportion, and H=salvage.

Given that entrainment cannot be measured directly, there appears to be no other means of estimating loss except from observed (expanded) salvage and an assumed survival rate, even though this may compromise the accuracy of the total loss estimate if entrainment (or losses associated with it) are large or highly variable. Setting the entrainment issue aside for now, the IRP also had several concerns with the implementation of the loss model and with estimates of its uncertainty:

a) characterizing S as a fixed parameter leads to underestimates of total loss,

b) characterizing the uncertainty of *S, H, G, and K* by standard errors understates their true variability,

c) Equations 8 and 9 of Jahn's (2011) error propagation method are incorrect, and

d) Jahn's (2011) model fails to account for probable losses associated with zero salvage, further negatively biasing its loss estimates.

See Appendix 2 for a more detailed explanation of the concerns and some recommendations for resolving these issues. Appendix 2 includes several suggested ways to reduce the bias of the loss estimates and increase the realism of their uncertainties, including: a) modeling S to realistically vary over short time scales (daily, weekly), b) estimating annual loss as the sum of daily losses, c) treating G and K as random variables whose uncertainties are estimated via Monte Carlo simulation rather than closed-form error propagation, and d) using a Bayesian method to estimate the probable losses associated with zero salvage. Finally, we suggest statistical strategies for making RPA-triggering decisions based on daily loss estimates, in the face of high uncertainties in those estimates.

Delta Water Operations and Delta Smelt Protective Actions

The seasonal distribution of precipitation in the Central Valley watersheds in WY 2013 resulted in a distinct “first flush” event, which has not been as discretely discernible in previous years. The Smelt Working Group (SWG) thus had some information to alert them to a potential trigger for spawning migration that could place some portion of the pre-spawn adult delta smelt population in a location that would make them susceptible to entrainment into the pumping facilities. By mid-December delta smelt were appearing in salvage and the USFWS determined that OMR flows should be constrained under RPA Action 1. This was the first time that Action 1 had been applied to protect pre-spawn delta smelt and when negative OMR flows were reduced, the number of salvaged delta smelt declined, totaling 86 between December 12 and January 1. The continued presence of delta smelt in the central and south Delta led to the implementation of continued – albeit more relaxed - constraints under subsequent RPA Action 2 in January, which was associated with another 146 delta smelt in expanded salvage, for a total of 232 by February 2, 2013. This level of take remained below the revised allowable incidental take value of 362 for WY 2013.

Recent efforts to understand the population dynamics of delta smelt using an individual-based modeling approach (Rose et al. 2013a, b) have suggested that multiple factors (e.g., temperature, stage-dependent growth rates, entrainment into water operations, etc.) are important in determining the inter-annual abundance of this species in the estuary but the importance of key factors may vary among years (i.e., wet versus dry). However, Rose et al. 2013a also cautioned that their model was not designed to forecast future delta smelt population abundance.

The IRP continues to believe that discerning behavioral responses of delta smelt to tidal oscillations (e.g., Feyrer et al. 2013) and perhaps associated turbidity changes is crucial for understanding delta smelt movements and spatial dispersion, which has potential consequences for affecting the level of fish entrainment at the Delta pumping facilities. Reliance on salvage to estimate delta smelt mortality associated with water operations remains a concern of the IRP. New information about potential losses associated with entrainment at the pumping facilities (e.g., Castillo et al. 2012) suggest that the determination of allowable incidental take even from extended salvage estimates may underestimate actual facility impacts on this species.

The IRP also continues to believe that the use of particle tracking models may not adequately capture the behavioral responses of delta smelt to important migration cues. Reliance on turbidity measures associated with discrete “first flush” events to predict delta smelt migration is risky because these events vary in intensity and annual

occurrence. Furthermore, delta smelt tend to be distributed within the water column during incoming tides and move to the bottom and shallow channel edges during ebb tides (Feyrer et al. 2013) as a means of maintaining their position within the estuary.

Lacking convincing evidence to the contrary, it seems counter-intuitive that an annual species such as the delta smelt would have evolved to depend for its survival on temporally unreliable environmental cues to trigger migrations associated with crucial life cycle events such as spawning or selection of nursery locations. Perhaps turbidity cues are more obvious to the smelt than to human observers, but the smelt are not making decisions about water operations.

See Appendix 4 for a discussion of delta smelt behavior and a potential approach for developing preemptive actions to reduce entrainment.

IRP RESPONSESTO QUESTIONS DEFININGTHE SCOPE OF THE 2013 LOBO ANNUAL REVIEW

Responses to questions regarding Sacramento River Temperature Task Group 2013 specific questions

1) **How well did implementation of the RPA actions meet the intended purpose of the actions?**

When the intended purpose of an RPA action is to meet a very discrete objective, it is relatively easy to decide if the intended purpose is met. For example, Action I.2.2.A requires USBR to convene a group to consider a range of fall actions if the end of September storage is 2.4 MAF or above. This was the case in WY 2013, so this action met its intended purpose in WY 2013. Other examples are not so clear, especially when only certain portions of the intended purpose are either met or not achieved. For instance, part of Action 1.2.4, which deals with the development and implementation of a Keswick release schedule, requires that USBR fund an independent modeler to report on temperature management and recommend refinements by March 2010. This has yet to occur, so the intended purpose of this portion of Action 1.2.4 has not been met.

Determining the successful implementation of other aspects of Action 1.2.4 may depend on whether one perceives the intended purpose of the actions as meeting a physical target or having a desirable biological effect on salmonid populations. It continues to be difficult, if not impossible in dry years (such as WY 2013), to meet TCPs as one moves farther downriver, but based on modeling water temperatures and using a surrogate monitoring station at Balls Ferry, it appears that an average daily temperature of 56º F

can be maintained at Airport Road Bridge. However, this has yet to be demonstrated with *in situ* measurements.

TCPs are also intended to be measured on the basis of a 10-year running average at multiple locations, but this is only the fourth year they have been in place. Thus, it is not possible to determine if TCPs are even meeting their intended site-specific targets. One complication with using Airport Road Bridge is that it was not one of the original locations specified in the RPAs and there is no temperature monitoring station at that location, which will make it difficult to include in a 10-year running average. Finally, the link between RPA actions and survival of salmonid early life stages remains elusive, but see Appendix 3 of this report.

Aspects of other RPA actions (e.g. I.2.3.A) were clearly the result of compromises that seemed to favor water operations over the requirements of the fish populations, at least as viewed by the fish agencies. While the fish agencies expressed a desire to maintain Keswick releases at 4500 cfs to avoid dewatering redds and stranding juvenile Chinook salmon, releases were ramped down from December through mid-February to 3800 cfs. While this was 550 cfs higher than desired by USBR, it was 1250 cfs lower than what the fish agencies considered necessary for salmonid protection. In such an instance, it is impossible to make an assessment as to whether or not the intended purpose of an RPA action was met.

2) **How effective was the process for coordinating real-time operations with the technical team's analyses and input as presented in the NMFS' Long-term Operations BiOps?**

Six meetings were convened to discuss cold water reserves that could be allotted to maintain TCPs and desirable river stage levels in the Sacramento River. However, there is little evidence to suggest any of the operations had a significant positive or detrimental effect on Sacramento Chinook populations (dewatering of some redds notwithstanding), nor was any evidence presented on how water transfers from Trinity to Shasta Lakes might be affecting salmonids in the Trinity River. Consequently, the IRP was unable to provide an objective answer to this question. Meetings were held, technical teams provided input and USBR made water operation decisions that were affected by considerations extrinsic to those that were part of the process to which the question pertains.

3) **Were the scientific indicators, study designs, methods and implementation procedures used appropriate for evaluating the effectiveness of the RPA actions? Are there other approaches that may be more appropriate to use?**

No. Spatial variation in water temperature and river stage needs to be better addressed within the context of impacts on salmonid spawning habitat and early life stage impacts of water operations. Deployment of water level loggers and temperature probes in spatial arrangements that are relevant for addressing the question of how flow regulation impacts fish is seemingly a requisite first step. Modeling alone may not solve the problem without accurate on the ground measurements.

Currently the ability to meet the TCPs is a central measure of the effectiveness of the RPA Action I.2.1. The IRP postulates that a more effective measure might be developed by integrating information on the spatial/temporal distributions of salmon during critical freshwater life stages into the TCP decision. Instead of meeting a TCP, consider a model-derived estimate of salmonid freshwater survival. As demonstrated in Appendix 3, such a measure might improve fish survival and flexibility in storage water operations. The IRP understands moving away from the current TCP measure would affect reservoir operations. Given the implications, the IRP suggests that NOAA form a working group to consider this issue.

4) **How can implementation of RPA actions I.2.1. – I.2.4. be adjusted to more effectively meet their objectives?**

Aquatic biota key to local geophysical dynamics and geospatial complexity. These factors are not reflected in the RPA actions, with the result that the river corridor of the upper Sacramento River is treated as a homogeneous system. By default, management actions are restricted to adjusting flow and release rates in attempts to meet a TCP based on storage of cold water in the upstream reservoirs. Substantial opportunities for salmon recovery and conservation may be realized by considering geophysical dynamics and geospatial complexity. For example, 29 of 45 redds pictured in Revnak and Killam (2013, Appendix D) were located in secondary channels. Environmental conditions (particularly temperatures) in the secondary channels can be substantially different than those in the main channel. Also, substantial numbers of juvenile Chinook were either stranded or in jeopardy of stranding in secondary channels and marginal riverine habitats. Although total juvenile abundance was not monitored, these shallow marginal habitats and secondary channels are certainly used by juvenile salmon. NMFS should consider adjusting RPA actions 1.2.1 - 1.2.4 so that redd location and juvenile abundance are better related to temporal and spatial patterns in habitat quality (e.g., water temperature, depth, and velocity pattern) at the scale salmon life stages respond to their environments (see Appendix 5).

In the SRTTG report and presentation at the LOBO workshop in Sacramento, there was a proposal to change the nature of the temperature compliance points from daily

average values to 7DADM. There may be good biological justification for considering this depending on how sensitive early life stages are to brief exposures to suboptimal, or even lethal, temperatures. There is some evidence that the 7DADM may better protect salmon early life stages from negative effects of temperature spikes than does an average daily temperature TCP. However, the specific temperature of a TCP based on daily maxima was not suggested. If the intent is to use the same value (56º F), the effect of using the 7DADM would be to move the current TCP (daily average temperature) downriver at considerable cost in cold water resources with little improvement in early life stage survival if the distribution of redds continues to remain upriver of Airport Road Bridge. Alternatively, if the intent is to set a higher temperature (i.e., > 56º F) for a daily maximum-based TCP, there may be little or no effect on location of the current TCP, or it could even move upstream. In any case, it is important to consider inter-annual variation in cold water storage and the trade-offs associated with adopting a 7DADM TCP (or a different duration of running average) as the preferred maximum thermal threshold for insuring survival of salmon early life stages. These trade-offs are considered by the IRP in Appendix 3 of this report.

Responses of 2013 IRP to questions regarding Chinook, steelhead and green sturgeon loss estimation at the Delta Pumping facilities

1) **Are the technical work team's proposed equations for estimating loss supported by current science?**

Mostly. However, the direct application of the equations to annual salvage creates a bias. Overlooking the losses associated with inserted zeros creates additional bias in the loss estimates. Additional modeling research may be needed to devise the most accurate (least biased) loss estimates.

2) **Are the technical work team's proposed equations for estimating annual loss confidence intervals scientifically appropriate?**

No. Uncertainty has been modeled in terms of standard errors (SE) of fixed parameters. This approach greatly understates the true uncertainty. Also, an error propagation method was used to estimate the SE of loss from the SEs of survival and salvage. Two of Jahn's (2011) equations (8 and 9) for this propagation are incorrect. The IRP proposes modeling salvage, survival, entrainment and loss as random variables, and estimating the mean and standard deviation of daily and annual losses via Monte Carlo simulation instead of closed-form error propagation.

3) **Which, if any, of the proposed terms in the technical work team's equations introduce the greatest uncertainty? How might these formulations be improved in the future?**

The greatest uncertainty is due to the survival proportion, and to the lack of direct measures of entrainment. The IRP suggests additional research to better characterize whole-facility survival, as a function of season, flow, temperature and other relevant factors. Appendix 2 of the present review report includes a Bayesian model for loss estimation which has the ability to incorporate independent knowledge about entrainment, if and when such knowledge becomes available.

4) **Which, if any, data inputs in the technical work team's equations are likely to reduce accuracy in their estimates?**

The current assumptions about zero data values for salvage leads to a negative bias in daily and annual loss estimation. Appendix 2 suggests a correction for this bias. The unrealistic assumption of a single, fixed value for survival creates an additional negative bias for annual loss.

5) **Are ongoing studies sufficient to gather data needed to calibrate coefficients and terms in the loss equations? What changes to ongoing studies or recommendations for future studies are needed to gather data to measure coefficients and values in the equations' terms?**

The concept of coefficients that can be calibrated, and of model parameters with standard errors, is not a realistic framework for modeling survival rate, entrainment, and loss. Realistically, these quantities vary widely and unpredictably over time. The IRP suggests viewing these quantities as random variables and modeling their distributions, as is done by Cramer Fish Sciences (2013). A careful synthesis of previous mark-recapture experiments that estimate whole-facility survival (e.g., Clark et al. 2009), along with additional novel experiments, may be the most effective path to estimate survival distributions and to model the effects of factors that control survival. In addition, research aimed at directly measuring entrainment is encouraged. Even if resulting measurements are crude, they can increase the accuracy of loss estimates via the Bayesian model described in Appendix 2.

6) **Given the importance of the hypothesized relationship between water velocity and facility efficiency for salmonid salvage, what scientific study designs and methods might be appropriate to investigate how this relationship could be incorporated into whole facility survival estimates?**

Given the limited potential to manipulate exports for the purposes of conducting controlled experiments aimed at establishing a relationship between water velocity and whole facility survival rates, controlled flume studies may provide a portion of the

answer. However, it will be difficult to simulate realistic conditions that capture all of the variables that determine whole facility survival. For example, the effects of predator fields associated with the facilities would be particularly difficult to simulate. In order to accurately determine whole facility survival rates, it is important to determine whether or not there is even a relationship between salmonid salvage and entrainment survival (mortality). Perhaps this could be addressed with carefully designed mark-recapture experiments conducted over multiple but relatively short-term periods of controlled water export pumping that would not interfere with total exports. For example, low and high water velocity runs could be alternated in experimental runs such that average weekly (or monthly) exports were unaffected while monitoring the recapture (in salvage and escapement – i.e., *sensu* fish overcoming the influence of entrainment flows and migrating out of the area) of marked fish released at the point where they would be initially entrained into the pumping facilities.

7) **What additional studies should be seasonally, annually, or semiannually completed to increase the accuracy of estimates of loss for green sturgeon?**

So little is known about the life-history of the green sturgeon that any studies shedding light on this species' responses to physical habitat variables (velocity, depth, substrate, cover, and complex hydraulics), particularly during its early life stages are likely to be useful.

8) **How well is the genetic information used in the technical work team's equation for estimating loss of winter run Chinook?**

With the information provided, it is difficult to determine the effectiveness of the genetic information.

9) **What sampling design provides the most accurate approach for characterizing the presence of genetic winter run Chinook salmon occurring inside and outside the Delta model winter-run size category?**

The IRP was not provided with alternative approaches to consider and is reluctant to suggest novel sampling designs at this time. However, the ability to separate cohorts associated with different salmon runs from overlapping size distributions seems to be at the core of this issue. There are algorithms and software packages that may assist in separating these cohorts with an assignable probability of goodness of fit (e.g., legacy software MIX Program v. 3.1, and the more current mixdist; for details see http://ms.mcmaster.ca/peter/mix/mix31.html and http://cran.r-project.org/web/packages/mixdist/mixdist.pdf). In practice, fitting mixed distributions can be more of an art than a science, but the more information that one has at the start, the better the chances of successfully distinguishing cohorts among mixed size

distributions. In this regard, the genetic information available on winter-run Chinook salmon could be applied in retrospective analyses to test the accuracy of this approach.

Responses to questions regarding the retrospective analysis of water operations and delta smelt protective actions taken during December – June of WY 2013

1) **How well did implementation of RPA Action 1 meet the intended purpose of the Action?**

The information necessary to answer this question is incomplete. The outcome in the absence of the Action cannot be determined. The answer also depends on the intended purpose of the Action.

If the intent was to prevent exceedence of the allowable incidental take of delta smelt, then the answer is a qualified "maybe" because incidental take was not exceeded. However, this conclusion should be viewed in light of observations from previous years when incidental take limits also were not exceeded even though Action 1 was not implemented. Take limits were not exceeded in any of the past four water years and Action 1 was not implemented in three of the four years. Consequently, there is no apparent association between the implementation of Action 1 and whether or not the calculated allowable incidental take is exceeded. What might have happened if Action 1 was not implemented in WY 2013 is simply conjecture.

If the intent of Action 1 is to protect the delta smelt population from impacts of water pumping operations, there is little on which to base a judgment. Incidental take is calculated from historical delta smelt salvage (Cumulative Salvage Index, CSI) and no clear relationship has been demonstrated between salvage and total mortality of pre-spawn adults attributable to pumping operations. For example, if recent studies (e.g., Castillo et al. 2012) are any indication, entrainment mortality may be substantially greater than previously envisioned. That is, salvaged delta smelt may represent a very small percentage of actual "take" (loss) associated with water operations. Also, allowable incidental take is calculated using a measure of estimated relative population size (i.e., the Fall Midwater Trawl Index) that may not be reliable. The Fall Midwater Trawl was not designed to collect delta smelt and any assumed relationship between the abundance index based on those collections and the actual size of the smelt population is questionable at best. This is interesting in light of the fact that larger salvage values in the past can determine the current allowable take limits. For example, this year the allowable take of adult delta smelt (not including losses other than extended salvage) was originally calculated as 305, but an error discovered in the value for salvage in the 2006 WY resulted in a revised allowable take value of 362, an

increase of nearly 20% based on a revised single value of salvage from seven years ago.

2) **How can implementation of RPA Action 1 be adjusted to more effectively meet its objectives?**

Without knowing the effectiveness of RPA Action 1 (see answer to the previous question) it is difficult to suggest a means of improving effectiveness. At the LOBO Workshop in Sacramento this year, earlier implementation of Action 1 was proposed as a means of providing preemptive protection for delta smelt while at the same time allowing for greater subsequent water exports; essentially, the proposal was to increase efficiency of delta smelt protection. The IRP agrees, in concept, that a more aggressive and preemptive implementation of Action 1 is worth developing. See Appendix 4 for a discussion of delta smelt behavior and movements that the IRP offers as straw-man guidance in the development of an improved implementation procedure for Action 1 that may provide more preemptive protection for pre-spawning adults.

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APPENDIX 1 – Materials for 2013 IRP Review

Review Materials Available to the 2013 LOBO Independent Review Panel

I. The following documents were provided in electronic format as required reading by the IRP prior to the 2-day workshop in Sacramento, CA on 6-7 November 2013:

1) Sacramento River Temperature Task Group 2013 Technical Report for the Long-Term Operations BiOps Annual Science Review

2) Chinook, Steelhead, and Green Sturgeon Loss Estimation for Skinner Delta Fish Protective Facility and Tracy Fish

II. The following document was provided to the IRP with a delay resulting from the federal government shutdown in early October 2013 and, as a consequence, it was left to the discretion of the 2013 IRP to address in the annual review:

1) Retrospective Analysis of Water Operations and Delta Smelt Protective Actions Taken in Early Water Year 2013

III. ***The following additional reports were made available in electronic format for supplemental use in providing historical context for the IRP***:

- Jahn, A. 2011. An Alternative Technique to Quantify the Incidental Take of Listed Anadromous Fishes at the Federal and State Water Export Facilities in the San Francisco Bay-Delta Estuary. Kier Associates, Ukiah California. Prepared for National Marine Fisheries Service, Central Valley Office. (http://www.kierassociates.net/Kier%20Assoc_OIA%20TO%203062_Incidental%20take%20at%20the%20Delta%20pumps_final.pdf)
- American River Group (ARG) Annual Report of Activities
- Stanislaus Operations Group (SOG) Annual Report of Activities
- Delta Operations for Salmonids and Sturgeon Group (DOSS) Annual Report of Activities
- Interagency Fish Passage Steering Committee (IFPSC) Annual Report of Activities
- The Smelt Working Group (SWG) 2013 Annual Report of Activities

Additional background information from the Science Program website was also available, including the RPA Summary Matrix of the NMFS and USFWS Long-term Operations BiOps RPAs and reports for previous IRPs.

APPENDIX 2 – Accuracy and Precision of Loss Estimates for Chinook Salmon, Steelhead and Green Sturgeon at the Skinner and Tracy Fish Facilities

The draft (Sept. 30, 2013) of this loss estimation report (hereafter "LER") describes an approach for estimating annual loss, and its uncertainty, of anadromous fish species at the two pumping facilities.

To estimate annual loss and its uncertainty, LER used the general loss model of Jahn (2011), with some changes in values of model parameters. The IRP has several statistical concerns and suggestions related to the Jahn (2011) approach, as detailed below. As a result of these concerns we believe that the underlying statistical model for loss estimation requires further research and development.

Jahn's (2011) simplified model for estimating loss:

For a single species and one pumping facility, Jahn's (2011) loss model is:

$$K = G - H = H/S - H \qquad (1)$$

where:

K = Total number of fish lost over a time period.

H = Total expanded salvage over the period, equal to the sum of the 2-hourly expanded salvages within the period.

$G = H/S$ = Total number of fish entering the facility ("entrained"), whose survivors were salvaged during the period.

S = Survival proportion for the period, defined here as the proportion of entrained fish that navigate the facility and enter the holding tanks alive during the salvage period.

Comments on loss estimation:

1. **Equation 7 of Jahn (2011) has an unrealistic assumption**

Jahn's (2011) Equation 7 (hereafter Equation J-7) estimates the standard error of G (hereafter, SE(G)), as a function of S, H and their standard errors. Equation J-7 is an application of a widely-used error propagation method, often called the "delta method" (Rice 1988).

The IRP has two principal concerns about Jahn's (2011) interpretation of Equation J-7:

a) Equation J-7 gives an approximate, not an exact, estimate of SE(*G*). The approximation can be poor, especially for a highly nonlinear function like *G* = *H/S*, unless random values of *S* vary closely around their mean value.

b) Jahn (2011) assumes that the covariance between *H* and *S* is 0, hence his omission of the covariance term from Equation J-7. Jahn (2011) makes this assumption because there is no obvious way to estimate the covariance. However, salvage is the causal result of survival operating on entrainment, that is, *H*= *G***S*. Thus, there must be a sizeable, positive covariance between *H* and *S*. Setting this covariance to zero will result in the estimated SE(*G*) being too large, as Jahn (2011) notes. Although this strategy is conservative from a policy perspective, it is nevertheless unrealistic and merits further research.

2. **Equation J-8 is incorrect.**

The correct expression is (Rice 1988, p. 124):

$$SE(K) = \sqrt{\left(SE(G)\right)^2 + \left(SE(H)\right)^2 - 2COV(G,H)} \qquad (2)$$

Thus, the correct value of SE(*K*) is probably larger than the incorrect estimate given by Equation (J-8). Again, there is no estimate for the covariance, COV(G,H). However, since *G*= *H/S*, one would certainly expect *G* to covary positively with its numerator, H. Thus, it is unrealistic to assume that COV(*G,H*) = 0.

The unknown covariance in Equation 2 can be avoided by applying the error propagation method to the full loss expression, that is, to *K* = (*H/S* – *H*). From the formula for the approximate variance of any function of two random variables (Rice, 1988, p. 146), we can derive

$$SE(K) \approx \sqrt{\frac{(1-S)^2}{S^2}\left(SE(H)\right)^2 + \frac{H^2}{S^4}\left(SE(S)\right)^2 - 2\frac{H(1-S)}{S^3}COV(H,S)} \qquad (3)$$

Equation 3 replaces the incorrect, 2-step estimate of Equations J-7 and J-8. As the "≈" indicates, the error propagation method gives only an approximate estimate of SE(*K*).

Equation 3 still contains the unknown, and non-negligible, covariance, COV(*H,S*). However, as Jahn (2011) did with Equation J-7, setting this covariance equal to 0 gives a conservative (largest possible) estimate for SE(*K*). If the technical team continues

using the error propagation method to estimate SE(*K*), then it seems appropriate to abandon Equations J-7 and J-8, in favor of Equation 3, while making some reasonable assumption about the value of COV(*H,S*). Below, we suggest how to estimate the uncertainty of annual loss without using the error propagation method.

3. Equation J-9 is incorrect.

The correct formula is (Rice, 1988, p. 124):

$$SE(K_{total}) = \sqrt{\left(SE(K_1)\right)^2 + \left(SE(K_2)\right)^2 + 2COV(K_1, K_2)} \quad (4)$$

In this case, it may be reasonable to assume that COV(K_1,K_2) = 0, signifying that loss estimates from the two pumping facilities are mutually independent. Equation 4, rather than Equation J-9, should be used to calculate the SE of the total loss estimate. Below, we suggest an alternative approach for estimating K_{total} and its uncertainty.

4. Time scale for loss estimation.

Jahn's (2011) approach applies Equation 1 to estimate the total annual loss, and its uncertainty, as follows: First, accumulate daily (or 2-hour) estimates of expanded salvage over the year, to estimate total annual salvage (*H*). This *H* estimate, along with a single value of *S*, are inserted into Equation 1 to yield a point estimate of total annual loss. Jahn (2011) then uses Equations J-7 to J-9 to estimate the SE of annual loss, based on the point estimates of *H* and *S* and their SE's.

However, the technical team also applies Equation 1 to daily salvage, thus estimating daily loss in real time, as described in CFS (2013). The daily loss estimate can potentially trigger an RPA action.

As an alternative to Jahn's (2011) approach, daily loss estimates could be summed over the year to estimate annual loss. An annual sum of daily loss estimates will be more accurate than Jahn's approach, for two reasons. First, a daily loss estimate more accurately represents the loss "process" experienced by individual fish, which spend only a few days to a few weeks moving through a pumping facility (e.g., Clark et al. 2009, Table 16). Second, daily loss estimates enable one to model *S* more realistically, as a random variable with substantial variation over time. With the present LER approach, summed daily losses will exactly equal their annual loss estimate, because the daily and annual estimates use the same, single value of *S*. However, if *S* is more realistically assumed to vary on a daily basis, then the two approaches will generally yield quite different annual loss estimates.

To demonstrate this, we carried out a Monte Carlo simulation using the framework of CFS (2013), in which daily salvage and daily survival proportion are modeled as random variables:

A. Expanded salvage statistics from Table (J-12) were rescaled to model daily salvage as a negative binomial random variable, with mean and standard deviation (not standard error) of 0.94 and 2.51 fish, respectively. It was assumed that the Table (J-12) data extended over 180 days (the actual period length is unclear from the table).

B. Survival proportion for any week was modeled as a normally-distributed random variable, with mean = 0.33 (Jahn's (p.20) high estimate)) and standard deviation (not standard error) of 0.10 (Clark et al. 2009, Table 12).

C. We generated 100 data sets, each with 180 daily values of salvage and survival proportion, by taking independent random samples from the distributions in A and B.

D. For each data set, the total 180-day loss was estimated in two ways:

a) The 180 daily salvages were summed to estimate whole-period salvage. Then Equation 1 was applied, with *S* = sample mean of the 180 daily survival proportions. This simulates Jahn's (2011) approach, yielding an estimate of total loss over 180 days.

b) The 180 daily losses were estimated by applying Equation 1 to the random daily values of salvage and survival proportion. Daily losses were then summed over 180 days to estimate total loss.

Results: Figure A2.1 below plots the 100 pairs of estimates of the total 180-day loss. A single point on the plot shows 2 estimates (a and b) derived from exactly the same set of 180 daily salvage values and 180 daily survival proportions. The straight line is the 1-1 line.

As the plot suggests, the annual sum of daily losses usually exceeded the Jahn-model loss. In fact, this occurred for 93 of 100 synthetic data sets, and by a mean exceedance of 142 fish. The annual sum of daily losses also had greater variability (SD=323 fish) over the 100 data sets than did annual loss from the Jahn model (SD=68 fish).

For each data set, the total salvage (180-day sum of daily salvage) was identical for both estimation methods. Thus, the differences in Figure A2.1 are due entirely to the effect of allowing *S* to vary daily, rather than assume a single mean value of *S* for the 180-day period. The negative bias in the Jahn estimate, relative to the summed-daily-

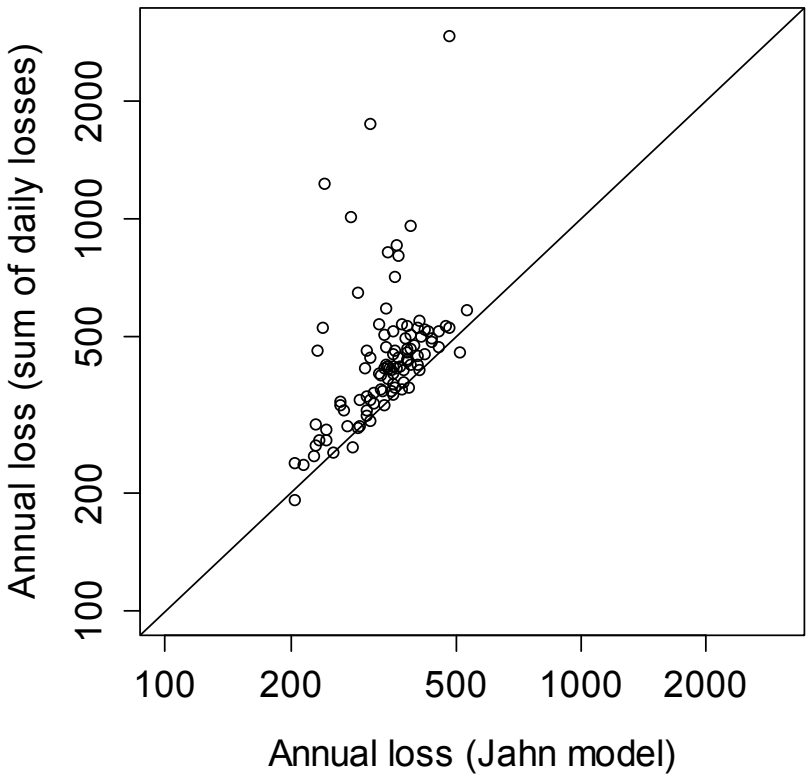

Figure A2.1. Plot of annual loss calculated as sum of daily loss estimates versus annual loss estimated from the Jahn model

loss estimate, can also be theoretically predicted from the nonlinear role of *S* in Equation 1 (Jensen inequality: Mood et al. 1974). Thus, a pattern somewhat like Figure A2.1 will be seen regardless of the particular distributions and the shorter time scale (daily, weekly, monthly) that is used to model survival and salvage.

Figure A2.1 does not reveal which of the annual loss estimates (Jahn model versus summed daily loss) is closest to the true annual loss. However, summed losses from shorter time periods (daily? weekly? biweekly?) should be more accurate than Jahn's whole-period loss estimate for the reasons given above.

5. **The Jahn (2011) model does not account for probable losses associated with zero observed salvage.**

Jahn (2011, p.8-9) inserts zero-count values of salvage into the raw 2-hour-sample data set for selected 2-hr sampling periods, during which fish might well have entered the

facility, based on factors like season, flow, and recent nonzero salvage. This seems to be a sensible approach. However, Jahn assumes that these inserted zeros do not contribute to the annual or daily loss estimates. We believe that this approach overlooks the probable fish loss that is associated with zero observed salvage, resulting in underestimates of loss.

Suppose a particular 2-hr sampling period has zero salvage (H=0). According to Equation 1, $G = H/S$. Thus, the Jahn (2011) approach also assumes that a zero salvage estimate for the period is the result of zero entrainment (G=0) associated with that period. And, it is true that if G=0, then H must be 0. However, it is also possible that some small, nonzero number of fish could have been entrained (G>0), and all of them were ultimately lost, resulting in H=0 for the period.

For example suppose G = 3 fish are entrained, and assume that S = 0.20, that is, 20% of entrained fish survive. For a small number of fish, S is more accurately interpreted as a survival probability, that is, each entrained fish has a 20% probability of surviving. Assuming independence of individual fish, the probability that none of the 3 fish survives is equal to the probability that all 3 are lost, which is given by:

$$\text{Prob (0 survivors)} = (1-S)^3 = 0.8^3 = 0.51 \qquad (5)$$

In other words, there is about a 50% chance that all 3 entrained fish will be lost, resulting in a salvage of 0 fish. Jahn's model fails to account for this possible loss.

One might argue that Jahn (2011) accounts for the zero-salvage probable losses by allowing them to contribute to an increased standard error in annual salvage, and hence to an increased standard error of annual loss (SE(K)). However, Jahn (2011) uses SE(K) to construct a two-sided, symmetric confidence interval around the point estimate of K. But in reality, the zero-salvage probable losses create a one-sided bias -- their omission can only create an underestimate of annual and daily losses.

We can estimate the probable loss associated with zero salvage. Equation 5 is an example of calculating Pr(H=0 | G=3), the conditional probability of obtaining zero salvage, given that 3 fish were entrained. However, we now need to calculate the conditional probability that 3 fish were entrained, given that the observed salvage was zero, that is, Pr(G=3 | H=0). From Bayes Theorem, we get:

$$Pr(G = m \mid H = 0) = \frac{Pr(H=0|G=m)Pr(G=m)}{\Sigma_j Pr(H=0|G=j)Pr(G=j)} \qquad (6)$$

These probabilities can be calculated for entrainment values of m = 0,1, 2, … fish . Then the probabilities can be used to calculate the mean and variance of the number of

entrained fish, given that zero salvage was observed. In Equation 6, Pr(H=0 | G=m) = $(1-S)^m$. In Equation 6, Pr(G = m) is the prior probability that m fish were entrained. Without a basis for estimating these priors, a standard approach is to assume they are equal. Under this assumption, Pr(G = m) = Pr(G=j), so these terms cancel out of the numerator and the denominator of Equation 6, leaving:

$$Pr(G = m \mid H = 0) = \frac{(1-S)^m}{\Sigma_j (1-S)^j} \qquad , m = 0,1,2\ldots \tag{7}$$

For m greater than about 30 fish, these probabilities are negligible, so we only calculate the first 31 probabilities (including that for m = 0).

Once the probabilities of Equation 7 are calculated, the expected number (mean) of entrained fish, given zero salvage, is calculated as:

$$\text{Mean}(G \mid H=0) = \Sigma_m\, m\, \Pr(G=m \mid H=0) \tag{8}$$

A similar equation can be written for the conditional variance of G, given that H=0.

Equations 7 and 8 were calculated using an assumed survival proportion (probability) of S = 0.1, then the calculation was repeated for S = 0.2, and again for S = 0.3. This yielded expected entrainments of 7.8, 4.0, and 2.3 fish, respectively. In other words, every 2-hr period of inserted-zero salvage results from an average of between 2.3 and 7.7 fish becoming entrained and then lost, assuming survival rates in the range 0.1 – 0.3.

These expected losses are not accounted for by the Jahn estimates, and they could add up to many fish on an annual basis. The IRP recommends that the mean value of this probable loss be calculated for all inserted-zero salvages in the data set, and added to daily and annual loss estimates.

Finally, we note that the Bayesian approach (Equations 6-8) can just as easily be used to estimate loss from nonzero salvage values. That is, one can use Equations 7 and 8 to calculate the mean and variance of entrainment, G, given any value for salvage. Then $K = G - H$. Replacing G=H/S with the probability calculations of Equations 6-8 avoids possible discretization errors, when H is a small number of fish. In addition, the Bayesian method allows for improved accuracy, if future research or monitoring can provide direct estimates of entrainment, that is, of Pr(G = m). The IRP suggests that the technical team explore the use of the Bayesian method, via Monte Carlo simulation (see below), to estimate all daily and annual losses, and their variances.

6. Statistical modeling framework for loss estimation

The IRP strongly suggests changing the statistical framework for estimating daily and annual loss. The current framework assumes that annual survival proportion, salvage, and loss can be modeled as single-valued parameters, with their uncertainties characterized by SE's. This framework may seriously understate the true uncertainty of estimated loss, because it understates the true uncertainty in survival proportions. Survival uncertainty is more accurately represented by Table 5, for example, in which Chinook survival proportions were observed to vary by a factor of 60 over 8 mark-recapture trials. In another experiment (Table J-6), Chinook survival rates through CVP louvers varied by a factor of 10 across replicate mark-recapture trials conducted within a two-week period. We believe that these magnitudes of variability, rather than the SE of mean survival, should be represented in the uncertainty of loss estimates. Moreover, in some cases, Jahn (2011) is driven to stating placeholder values, and /or guestimates (Table J-4; "high", "medium", "low"), for survival rates, because the true survival rates are so very uncertain. The assignment of SE's to such speculative survival rates is not credible, because the SE's do not represent the high uncertainty that prompted the speculation in the first place.

We suggest that survival proportion, and hence loss, instead be modeled on a short time scale (daily?) as random variables. The CFS (2013) report gives examples of how to model the probability distributions of these random variables. Daily loss, and hence annual loss estimated by the sum of daily losses, would also be random variables characterized by their estimated means and standard deviations. This strategy can incorporate the realistic variability of survival proportion that is observed in mark-recapture experiments. We believe that the random-variable framework would provide more accurate estimates of loss and its uncertainty.

7. Computing the annual loss and its uncertainty

If the technical team pursues these suggestions, then the computation of annual loss and its uncertainty is no longer so simple. For example, we have suggested that survival rates and loss be modeled on a daily basis, as random variables, with daily loss then summed over the year. In addition, loss-estimation factors such as prescreen and louver components of survival, cleaning adjustments, Chinook ESU classification, and serial correlation of salvage all have their own uncertainties to contribute. Finally, the probable zero-count losses should be added to daily and annual losses.

With these added complexities, it becomes impractical, and perhaps impossible, to estimate the standard deviation of loss using closed-form error propagation (e.g., Equation 3).

For this reason, the IRP suggests using Monte Carlo simulation to estimate daily and annual loss and its uncertainty. For a single day, the observed salvage could be taken at face value, as a number known without error. Then randomly select 100 values of S from its assumed probability distribution. For each *S*-value, calculate *G* from *G*=*H/S*, or else calculate the conditional mean of *G* from the Bayes equations. Next, add any zero-salvage corrections to the *G* values. Finally, inserting the 100 *G*-values into Equation 1 gives 100 estimates of daily loss, *K*. This yields a probability distribution of *K* for the day, whose mean and variance can be calculated. Summing the means and variances of loss for the year gives the statistics of the annual loss distribution. From such statistics, one can construct approximate confidence intervals or exceedance probabilities for daily and annual losses.

The above scheme assumes that daily expanded salvage is known without error. An option would be to obtain the daily salvage from a measurement error model, which would have the same intent as Jahn's Equations J-4 to J-6

A well-conceived and well-documented Monte Carlo script would offer a flexible computing environment for exploring a broad spectrum of quantitative scenarios about the numerous factors that contribute to fish losses. The script(s) developed for CFS (2013) would probably be a good starting point.

Finally, the major challenge of a Monte Carlo approach is how to represent the causal dependence of salvage on survival in a random-variable context, in other words, how to model the covariance between these two variables. This problem pervades the application of Equation 1 or of Equations 6-8, whether one uses closed-form estimates (Jahn 2011) or Monte Carlo estimates for uncertainty.

8. Making an RPA-triggering decision, based on highly-uncertain daily losses

During the Nov. 6-7 panel meetings, the technical team requested advice on interpreting higher, more-realistic variances of daily losses, such as those seen in CFS (2013) and in our simulation scenarios (Comment 4). Specifically, how can a highly-uncertain daily loss estimate be meaningfully compared to an RPA- triggering threshold?

To illustrate the problem, suppose that an RPA is supposed to be triggered if the daily loss exceeds 15 fish. And suppose that the expanded salvage on a certain day is 12 fish. Monte Carlo application of Equation 1 to this salvage value, using the random survival assumptions of Comment 4, yields an estimated loss distribution with a mean of 31 fish and standard deviation (SD) of 21 fish. This high SD, relative to the mean, is due to our assumption of high daily variability in the survival rate. Now, suppose that we

calculate a 2-sided, 90% confidence interval (CI) around the “best” point estimate of loss (the mean), yielding 31 ± 1.64*21 = [-3, 65] fish (assuming Normality). This CI extends far below the trigger level of 15 fish, indicating that the true loss might not have exceeded the trigger, even though the mean estimated loss (31 fish) is more than double the trigger level. With such a wide CI, it is very difficult to decide whether the trigger was exceeded.

Two possible strategies for making a sensible trigger-exceedance decision in the face of such high uncertainty are:

a) Make the trigger-exceedance decision based on a 7-day moving average of daily loss, rather than an individual daily loss. The 7-day moving average has a standard deviation equal to SD/√7, which implies that CI width will be reduced by a factor of √7 = 2.6. This increased precision may be adequate to develop a more useful CI for estimated loss. The moving average smooths out any apparent daily spikes in loss, but such spikes are highly questionable anyway, because of the high variance in estimated loss..

b) Use a one-sided (rather than two-sided) confidence interval, and relax the confidence level. As before, assume that a day’s loss is normally distributed with mean = 31 and SD= 21. The trigger decision depends only how small the true loss might be, not on how large it might be. Thus, we can construct a 1-sided, lower confidence bound for the true loss, and compare this bound to the trigger level. Reducing the confidence level will also help shrink the lower bound towards the mean. For example, a lower one-sided 75% confidence bound for loss is given by 31 – (0.67*21) = 17 fish. In other words, we can be 75% confident that the true loss was at least 17 fish. Because this exceeds the trigger of 15 fish, the RPA could be activated. The key strategic idea here is the need for managers to tolerate a reduced level of confidence (e.g., 75% rather than 90% or 95%) in decision rules, due to realistically high uncertainties.

APPENDIX 3 – Forecasting storage water release for temperature control and limit stranding and dewatering

The IRP was asked to answer the question, “What other tools are available to help forecast and manage storage and releases levels so we are not annually running into the issue of dewatering redds and stranding juveniles?” The short answer is that models are available or can be developed to predict the effect of storage water decisions on fish survival.

We suggest that both simple and detailed models are useful for management. Heuristic models that illustrate interactions of processes in terms non-dimensional parameters are useful for demonstrating the nature of the water allocation tradeoffs. Detailed models calibrated to the existing system and linked to physical models are needed to characterize the interaction of management actions and fish survival. The development of management models will involve considerable effort and require a team approach. However, a simple model that illustrates the processes can be relatively straightforward. Below we develop a simple or heuristic model to illustrate the system variables. Surprisingly, simple models may also have value in actual management as tools to inform managers that ultimately must make decisions based on judgments.

Heuristic Optimal Temperature Compliance Point Model (hOTCP)

This example model illustrates the approach of expressing the tradeoff storage water releases for cooling redds vs. releases for stage control to limit dewatering of eggs and stranding of juveniles. Currently the water storage is allocated to maintain a temperature control point in the Sacramento River during egg incubation stages. The model example illustrates the tradeoff of allocating storage water for egg and juvenile stages.

The model is intended to illustrate overall survival benefits that can be achieved during the egg vs. juvenile stages using available cold water storage in a trade-off to control temperature benefiting egg/embryo survival early on and later to reduce stranding during the juvenile stage. However, the concept is applicable for simultaneous actions involving temperature and stage controls to address redd dewatering as well as juvenile stranding.

For this illustration assume the effect of water releases on the survival of eggs and juveniles are independent. Then including a survival term for the background survival independent of reservoir operations, the total survival from egg through the juvenile stage is

$$S_{total} = S_{egg} S_{juv} S_{other} \tag{3.1}$$

Assume all redds upstream of the temperature compliance point (TCP) have 100% survival and redds below the TCP have 0% survival. This assumption is allowed because other mortality effects are captured in S_{other}. For a more realistic representation of temperature, the effect of temperature on mortality can be included but the essential dynamic should not be significantly different from eq. 3.1.

Assume the density of redds decreases exponentially with distance x from the face of Keswick Dam as

$$\rho(x) = \frac{1}{\lambda} \exp\left(-\lambda x\right) \tag{3.2}$$

where λ expresses the shape of the distribution of redds along the river. Note that the function fits well the observed distribution of redds. The survival of eggs in the river that depends on reservoir releases is a function of distance downstream as

$$S_{egg}(x) = \int_0^x \rho(x')dx' = 1 - \exp\left(-\lambda x\right) \tag{3.3}$$

where x is a distance equal to or less than the maximum temperature compliance point (TCP) defined as x_0. Typically x_0 is forecast prior to the beginning of the season and represents the maximum distance downstream at which temperature can be maintained below the critical maximum required to insure egg survival during incubation season.

Define the total preseason forecast of storage volume available for fish as v_0 and assume the maximum TCP location has a linear relationship with v_0 as

$$x_0 = \alpha v_0 \tag{3.4}$$

Here the relationship between TCP and volume is highly simplified but the form represents the basic property that more water is required to maintain a TCP further downstream. Because we assume the volume of water used and TCP location are linearly related in this model, the relationship between storage volume v_x and another TCP further upriver can be expressed as

$$x = \alpha v_x \,. \tag{3.5}$$

Having simplified egg survival as either 0 or 100% we can disregard egg incubation time and variations in storage water during incubation, so water storage after incubation can be described as

$$v_1 = v_0 - v_x = v_0\left(1 - \frac{x}{x_0}\right) \tag{3.6}$$

This remaining volume v_1 is thus available for other uses independent of temperature control. For our example, assume the remaining fish storage water is allocated for stage control to avoid juvenile stranding. The volume could also be allocated during the incubation period to minimize redd dewatering.

The more water available for river stage control, the less mortality from river stage effects. However, because of the nonlinear properties of flow and river elevation, the effect of storage volume decreases with volume amount. We can capture the general diminishing effect of additional flow on river elevation with an exponential function as

$$S_{juv} = 1 - \mu e^{-\beta v_1} \tag{3.7}$$

where μ is the maximum juvenile mortality if no storage water releases were available to target stranding and dewatering events and β characterizes the efficiency of water releases on reducing dewatering and stranding. Note that a brief analysis of the relationship between spawning and dewatering flows for fall-run Chinook salmon (Appendix B, Table B1 in Sacramento River Temperature Task Group 2013 Technical Report) indicates that an exponential relationship describes the impact of flow reduction on dewatering. Because both dewatering and stranding are processes driven by flow effects on river stage, we expect that eq. 3.7 is adequate for representing the effect of flow on stage-dependent mortality processes.

Combining the above equations the total survival over the two life stages is

$$S_{total}(x) = \left(1 - e^{-\lambda x}\right)\left(1 - \mu e^{-\beta v_0 (1 - x/x_0)}\right) S_{other} \tag{3.8}$$

where $x \le x_0$.

We simplify the equation first by normalizing the compliance point x to the distance of maximum temperature compliance x_0 giving

$$y = x/x_0 \tag{3.9}$$

such that y has the range $0 \le y \le 1$. Next, combine the parameters. The extent to which the available volume of storage water is capable of protecting the population of redds can be characterized as

$$a = \lambda \alpha v_0 . \tag{3.10}$$

That is, increasing the parameter *a* by an increase in any of the component terms increases the protection of the redds. For example, a larger λ implies the redd distribution is closer to Keswick dam so less storage water is required to cool the egg distribution. A larger v_0 implies more water is available to cool the redds. Note that *a* is a non-dimensional coefficient that can be estimated by fitting the distribution of redds scaled to the maximum temperature compliance point x_0. That is, in principle *a* can be estimated from the redd distribution, the amount of storage water available and the hydraulic properties of the system.

The second term defines the extent to which storage water can protect redds and juveniles from dewatering and stranding. It is defined as

$$b = \beta v_0 \,. \tag{3.11}$$

In principle *b* can be characterized from information on the hydraulic properties of the system and the location of redds and juveniles. An increase in *b* can be achieved by any combination of increased efficiency (β) and available coldwater storage (v_0). The IRP suggests that the efficiency term might be estimated from currently available information such as is illustrated in Appendix B, Table B1 in Sacramento River Temperature Task Group 2013 Technical Report.

With these non-dimensional parameters the total survival as a function of the TCP at distance *y* is

$$S_{total}(y) = S_{egg} S_{juv} = \left(1 - e^{-ay}\right)\left(1 - \mu e^{-b(1-y)}\right) S_{other} \tag{3.12}$$

Note that the value of S_{other} is not important because it does vary with storage reservoir operations.

The distance of the TCP that yields the optimum total survival is defined by $dS(y)/dy = 0$ giving

$$\frac{dS_{total}(y)}{dy} = \frac{ae^b}{\mu} - be^{(a+b)y_*} + \left(b - a\right)e^{by_*} = 0 \tag{3.13}$$

Note in Fig. A3.1 the total survival of eggs quickly approaches the asymptote of 100% survival and essentially tracks the cumulative distribution of redds downstream of Keswick Dam. Water not allocated for temperature control is allocated for stage control to reduce egg dewatering and juvenile stranding. Therefore S_{juv} is greatest when $y = 0$ and decreases progressively with increasing y because water not allocated to temperature control is allocated for stage control. The curvature of the total survival

curve to the right of the optimum depends on the effectiveness of storage water for stage control activities.

Eq. 3.13 may be useful for management if it identifies the optimal distance for the temperature control point that balances survival of eggs and the survival of juveniles. Furthermore, the optimum allocation of storage water for temperature control is

$$v^* = y^* v_0 . \tag{3.14}$$

The salient point is that the optimum TCP and volume of water allocated for temperature control is likely to be generally less than the volume of water that is used under the current RPA. Figure A3.1 illustrates this point by applying the model to WY 2013 in which the location of the TCP was set at Airport Road, which gives x_0 ~ river mile 17.

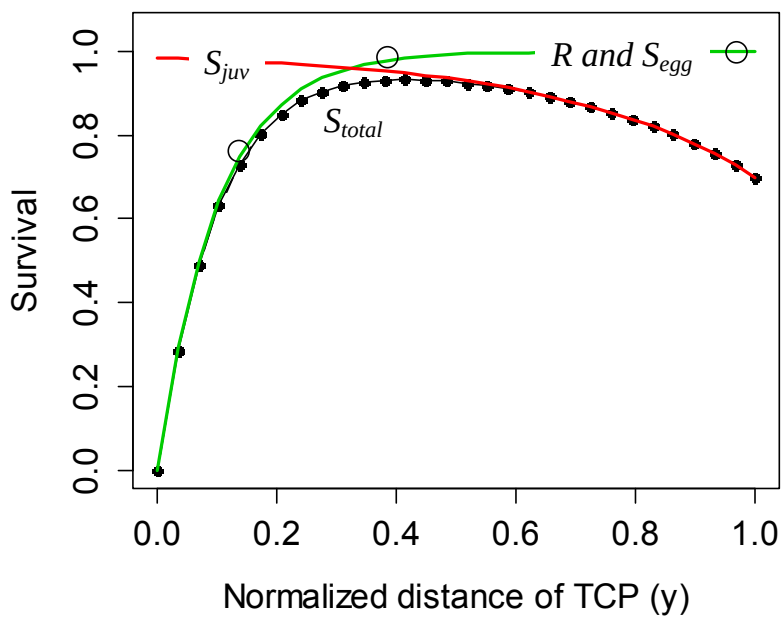

Fig. A3.1. Model output showing relationship between egg (S_{egg}), juvenile (S_{juv}) and total survival as a function of temperature compliance points (*y*) based on eq. 3.12. The large circles depict cumulative redd density *R* at the normalized TCP location. Optimum TCP is *y= 0.41 for this scenario.**

We estimated the parameter *a* using the redd density information for winter run Chinook from Table 2 in Sacramento River Temperature Task Group Annual Report of Activities 2013. From eq. (3.3) the cumulative distribution of percent redd vs. distance is

$$\mathrm{R}(y) = 1 - \exp(-ay) . \tag{3.14}$$

where $R(y)$ is the cumulative redd distribution as a function of normalized distance y. Knowing the distribution $R(y)$ we estimate the parameter giving a = 10 for WY 2013. We have no estimate of parameter b but in principle it is straightforward because its components can be estimated; v_0 is simply the total amount of storage water available for fish and β be estimated from river stage information and juvenile distributions.

Analysis indicates that the shape of survival vs. the TCP location is sensitive to the parameter *a,* but is less sensitive to *b* (Fig. A3.2). However, it is important to note that the survival over a range of TCP locations is relatively flat with any selected value of *b* such that the optimum TCP is relatively insensitive to *b* even though the optimum TCP location is sensitive to changes in *a*. Fortunately, *a* potentially can be estimated with some confidence while for *b*, an accurate estimate is not as critical for finding the optimal TCP location.

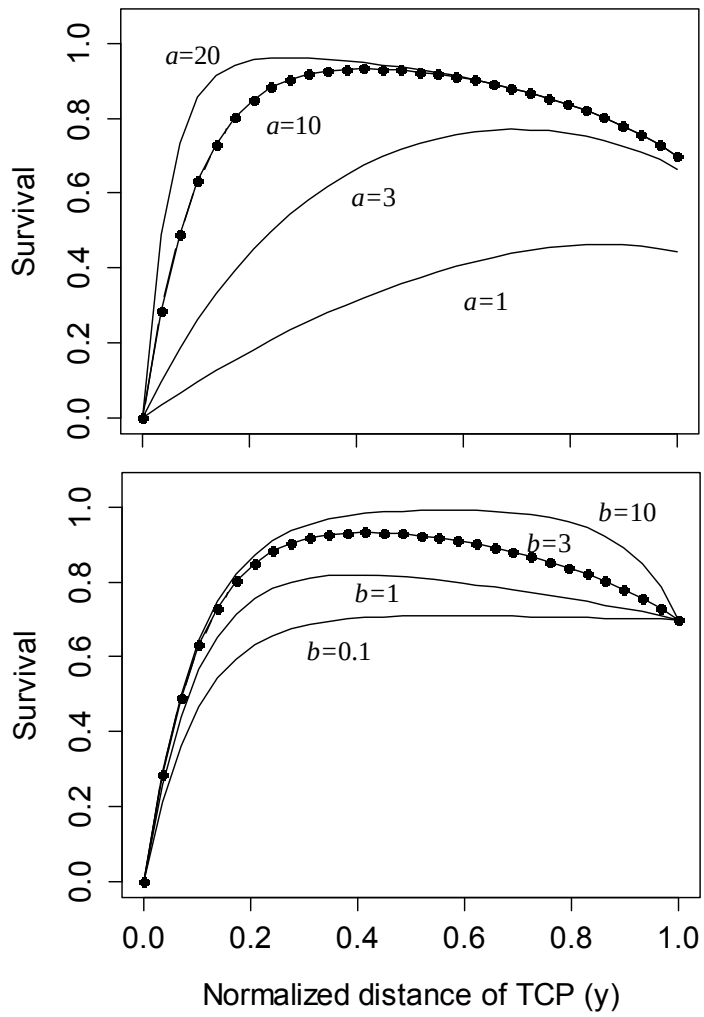

Fig. A3.2. Sensitivity of survival (S_{total}) with TCP distance *y* for differing values of *a* and *b* where base parameter values are sane as in Fig. A3.1.

For WY 2013 we assume b = 3 and μ = 0.3 then solving eq. (3.13) using the *uniroot* function in the R statistical package, the normalized optimum TCP location is y^* = 0.41. Thus, based on the Airport Road TCP (~ river mile 17) used in 2013 the model indicates the optimum TCP was at river mile 7. An exploration of the sensitivity of y* to variations of μ and b will give a measure of the uncertainty in the optimum. The salient points of this analysis are that it is feasible to estimate a TCP that optimizes survival across the two life stages and the optimum is likely to require less water than is used to meet the current TCP. Thus, it is possible the RPA can be adjusted to increase both fish survival and water operations flexibility.

Management - Optimal Temperature Compliance Point Model

A management model to forecast water release impacts could be developed in the basic framework of the heuristic model, but include spatial and temporal distributions of fish, river temperature and stage. The relationship between water releases, river stages and temperature would be input from a hydraulic model. The redd distribution could be characterized by redd survey information, not the distribution parameter λ in the heuristic model. The management could also use realistic temperature survival and growth models to characterize emergence timing and survival of eggs.

If detailed information were available on the distributions and environmental characteristics of redds and juvenile nursery grounds then management of a TCP location could be replaced by a management that optimizes survival across fish sites. The sites would include individual redds and juvenile habitats. Storage water releases would then seek to optimize the survival across the sum of sites and therefore the fish population itself.

Conclusions of Model Analysis

The heuristic model developed here illustrates that higher fish survival and greater flexibility in reservoir operations might be obtained by using a forecast model that accounts for the tradeoff of water allocations for different mortality processes and life stages. The model suggests that survival may be increased about 10%, which is moderate. However, the model also suggests that this improvement in survival might be attained with 50% less water than is currently used in maintaining TCPs defined by the RPA. Such a saving of storage water would be substantial for water years in which the location of the TCP extends significantly downstream of the majority of the redds. The IRP has in past reviews encouraged further integration of water operations with biology, and the model presented here illustrates the potential benefits of such an approach.

Appendix 4 - Delta smelt movements relevant to implementation of RPA Action 1

The underlying motivation for a preemptive Action as posed to the IRP in Question 2 involving RPA Action 1 is to reduce pumping flows prior to the fish entering the Old and Middle River environment, thus allowing the pre-spawning migrants to pass into the western and northern regions of the Delta without being drawn into the negative flow of the OMR. Developing an effective preemptive action requires understanding the behavior of delta smelt to their environmental cues during the migration. Below we address this issue, discussing alternative theories of delta smelt migration as based on the past and recent publications on delta smelt.

A working hypothesis of delta smelt movement

Delta smelt live in low salinity zones of the estuary and migrate upstream to spawn (Sommer et al. 2011). Previously it was believed that the fish migrated between the western and eastern portions of the delta. However, recent studies suggest that the life cycle is more complex. The adult population appears mostly as diffuse loci in and adjacent to the northern Delta's open waters from which individuals undertake landward movements to spawn (Murphy and Hamilton 2013). While the centroid of the adult population is located near the X2 low-salinity boundary (Feyrer et al. 2011) delta smelt are also found in Liberty Island, Yolo Bypass (Sommer and Mejia 2013) and as far north as Knights Landing (Vincik and Julienne 2012). The historical population distribution included the eastern and southern regions of the delta but currently these areas are largely without delta smelt (Murphy and Hamilton 2013).

Salinity and turbidity are key environmental variables that affect distribution of delta smelt, but the relative significance of these variables has been under debate in the literature (Sommer and Mejia 2013). Other variables have been identified as important including tidal velocity (Sommer et al. 2011), which correlates with other properties such as turbulence (Rippeth et al. 2001). How delta smelt respond to environmental variables is critical to developing a preemptive Action 1 to divert the movement of delta smelt in the OMR during their pre-spawning migration. Here we develop a straw-man or working hypothesis on the important variables to consider in designing an Action. We begin with a discussion of models or theories of delta smelt movement.

Two basic models have been proposed for how environmental variables affect delta smelt migration. One model identifies kinesis in which a fish moves with random and directed movements along a water property gradient, e.g., salinity. The rate of movement depends on the differential between an optimal salinity and the fish's local

salinity. Residence of delta smelt in the X2 region is achieved by setting the optimal salinity at the X2 salinity. Movement toward freshwater in the landward pre-spawning migration is produced by lowering the optimal salinity for pre-spawning adults (Rose et al. 2013a). In essence, to switch between X2 residence and pre-spawning migration the optimal salinity level is changed and the delta smelt swims toward lower salinity water upstream. The model describes the general life cycle distribution of delta smelt and was implemented in an individual based model to explore processes controlling population levels (Rose et al. 2013a). However, it was not strictly intended to be an accurate representation of the mechanisms of migration. The IRP suggests the concept of kinesis is not conceptually wrong, but it must be applied over the small scale at which delta smelt perceive their environment, not at the large scale on which it has been applied previously.

A second model describes movement in terms of tidal surfing, or tidally mediated migration, in which upstream movement is achieved by the smelt moving into higher velocity regions of the water column during the flood tide and lower velocity regions during the ebb tide. This model has more biological realism than the kinesis model and can reproduce the distributions and movement rates of delta smelt, but as currently applied (Sommer et al. 2011) it does not address the mechanisms controlling the tidal cycle movements between high and low velocities. More important, the tidal surfing model is mute on how a fish distinguishes between ebb and flood tides – an essential ability for tidal surfing. While knowing how fish distinguish and respond to hydrodynamic properties has scientific appeal, the knowledge is important for developing delta smelt protection since any action can only modify the hydrodynamics and thus the link to fish behavior is essential.

While both models can reproduce delta smelt distributions, the mechanisms are different and designing a preemptive Action 1 based on an incorrect model of delta smelt behavior may neither produce desired results nor be cost effective. However, the selection of which model is more realistic is not difficult because the kinesis model, as previously applied, has been largely rejected. A plan proposed in 2009 to divert delta smelt from the Central Delta with a gating system in the central delta (Two-Gates project www.usbr.gov/mp/2gates/docs/index.html) was based on delta smelt kinesis to salinity and turbidity fields. However, a review of the plan identified significant problems with the kinesis movement model (Anderson et al. 2009) and the project was eventually withdrawn (www.c-win.org/two-gates-project-expedient-delta-conveyance.html).

In contrast, recent studies provide clear support for the tidal surfing model. A SmeltCam, which visually identifies free moving fish, revealed that in the lower Sacramento River in November 2012 delta smelt were dispersed over the water column

during the flood tide and in the lower velocity regions near the bottom and side channels on the ebb time (Feyrer et al. 2013). The authors noted that the conditions were associated with the upstream migration of delta smelt to areas where spawning ultimately occurs during spring. The study essentially documented the fine-scale delta smelt distribution prior to the ‘‘first flush’’ and their upstream migration. Other studies have also documented delta smelt asymmetric behavior over tidal cycles. The pre-spawning migration velocity of delta smelt can be produced in a model with particles moving from the upper to the lower 10% of the water column between the flood and ebb tides (Sommer et al. 2011). In Suisun Bay, delta smelt feed predominantly on the flood tide in the day (Hobbs et al. 2006). To maintain residence in the dynamic low salinity zone of the western delta other species exhibit vertical migrations that are coordinated with the tides (Bennett et al. 2002). Thus, solid evidence (in the San Francisco Bay Delta system and many studies elsewhere not discussed) supports a model of tidally coordinated movement and indicates that tidal surfing is sufficient to produce the observed migration velocities and distributions of adult delta smelt and other species.

However, the tidal surfing model by itself does not describe how an animal coordinates movement with the tide. Perhaps the parsimonious perspective is to assume that delta smelt seek to maintain position in a favorable local environment, e.g., they seek a range of turbidity (small-scale kinesis), which because of estuary hydrodynamics occurs mostly on flood tides. Some support for this mechanism comes from (Hasenbein et al. 2013) who observed that delta smelt feeding performance was highest between 12 and 120 NTU and diminished otherwise. Also, higher levels of salinity stressed delta smelt. If delta smelt seek a favorable turbidity range when available, do not respond to turbidity when the level is low, and avoid higher levels of salinity, then a relatively simple correlation of small-scale distributions of turbidity and salinity with velocity profiles may be sufficient to explain movement behavior of delta smelt.

If delta smelt seek local regions of optimal turbidity then understanding movement in a tidal system reduces to correlating the optimal attraction regions with tidal velocities. Here studies indicate that turbidity levels are highest on the flood tides in the Carquinez Strait connecting San Pablo and Suisun Bay (Ganju and Schoellhamer 2008), in the Sacramento River above the confluence with the San Joaquin (Feyrer et al. 2013) and in channels of Cache slough in the northern Delta (Morgan-King and Schoellhamer 2013). These are all areas with significant delta smelt populations.

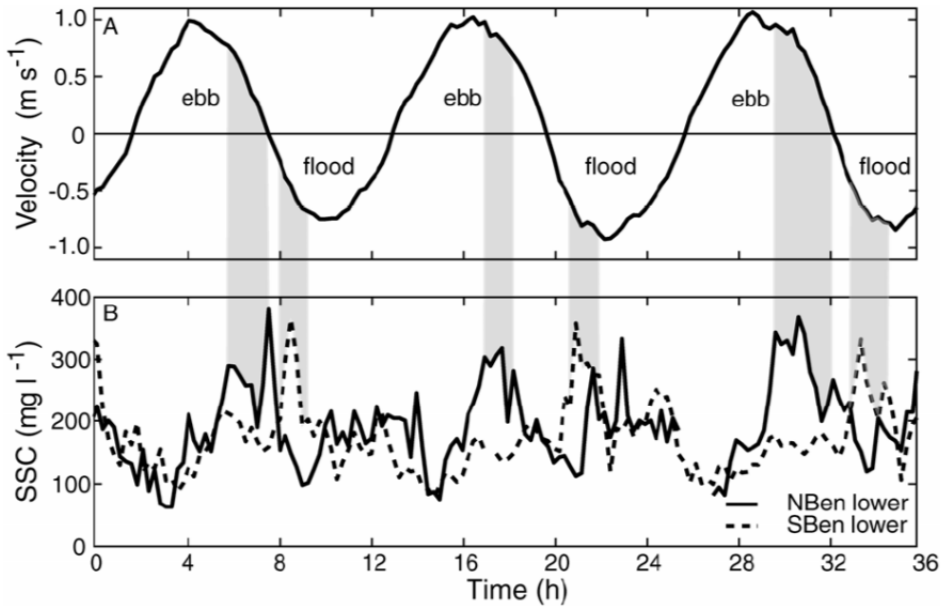

Figure A4.1. Water velocity and suspended sediment concentration (SSC) in Carquinez Strait and Suisun Bay. Carquinez Strait connects San Pablo Bay and Suisun Bay. Grizzly and Honker Bays are shallow areas of Suisun Bay. Sites NBen and SBen are located on piers of the I-680 Bridge. Depth is referenced to mean lower low water [from Ganju and Schoellhamer 2008].

Fig. A4.1 illustrates the asymmetrical patterns in turbidity across a tidal cycle in Carquinez Strait. In general, the pattern varies spatially, with flow and sediment availability such that the correlations of flood and high turbidity are expected to increase and decrease depending on conditions. Under the hypothesis that tidal surfing requires a high flood tide/turbidity correlation, then the propensity for movement against the mean flow will vary according to the estuarine physics. The flood/turbidity correlation is likely to be strongest in the western Delta and backwater sloughs because of tidal asymmetry in these environments (Morgan-King and Schoellhamer 2013). Strong tidal asymmetry and a high flood/turbidity correlation also would be expected during first flush events. In regions with low correlations, delta smelt movements should be more random. Furthermore, when turbidity throughout the water column is below the threshold for attraction, we expect that delta smelt would not seek higher velocity regions on either flood or ebb tides. Again, their movements would become random and we expect the net movement of the delta smelt would follow the mean flow.

While we frame the hypothesis in terms of tidal-scale changes in turbidity, we suggest the underlying mechanisms act at the scale of the fish's immediate environment. At the perceptive scale of the fish, optimal turbidity may occur in the low velocity regions near shore and bottom on the ebb tide, while on the flood tide the optimal turbidity is associated with higher velocities, which generally occur throughout the water column. Also note that the mechanism may involve asymmetric patterns of small-scale

turbulence over the tidal cycle. Fish can detect micro-turbulence in the water column (Chagnaud et al. 2008) and because turbulence induces resuspension of sediment, turbidity and turbulence may both appear to have an effect on delta smelt movement.

In summary, our working hypothesis is that tidal surfing behavior results because over the tidal cycle delta smelt seek water with intermediate turbidity, which depending on the asymmetry of the tidal cycle, tends to be in low velocity regions on the ebb tide and high velocity regions on the flood tide. Furthermore, the strength of tidal asymmetry varies spatially and seasonally so that delta smelt movements are expected to vary spatially and seasonally in a similar manner to the variability in tidal asymmetry.

As was indicated at the LOBO workshop, the USFWS seeks to fine-tune actions to protect delta smelt. The IRP realizes that considerable progress has been made in understanding delta smelt movement, but suggests that the best possible protection program requires explicit consideration of the small-scale physical properties to which fish respond. Below is a brief description of a straw-man program to test the hypothesis that delta smelt exhibit taxis to abiotic attraction zones that form and dissipate over the tidal cycle resulting in dispersion, retention or upstream tidal surfing depending on the bathymetry and flow of the local environment.

Program Hypothesis: By altering tidal asymmetry in critical channels and times, delta smelt movement towards pumps can be reduced.

Program Elements:

1. Characterize delta smelt responses (feeding, predator avoidance, taxis) to abiotic factors and identify an envelope of attraction, plausibly defined by ranges of turbidity, salinity and light levels. Example work: Hilton et al. (2013) and Hasenbein et al. (2013).
2. Characterize delta smelt distribution over tidal cycles. Example work: Feyrer et al. (2013), Bennett et al. (2002).
3. Characterize attraction envelope location and velocity properties over tidal cycles. Example work: Shchepetkin and McWilliams (2005), Ganju and Schoellhamer (2008; Morgan-King and Schoellhamer (2013), Jones et al. (2008).
4. Model delta smelt movement by linking behavior, attraction envelope and hydrodynamics. Example Goodwin et al. 2006, ROMs and DSM2 hydrodynamic models.
5. Using the model, identify hydraulic conditions that initiate upstream delta smelt movement and develop actions to disrupt delta smelt movement into inner delta.

Appendix 5 – Additional considerations- secondary channels of the Sacramento River

Most redds and stranding sites are associated with either secondary channels or smaller scale features (e.g., margins and geomorphically complex features of the main channel; Figs. A5.1 and A5.2). Secondary channels may be one of the most important options for river restoration because they appear to be a potentially important habitat resource for conservation and recovery of fall- and winter-run Chinook.

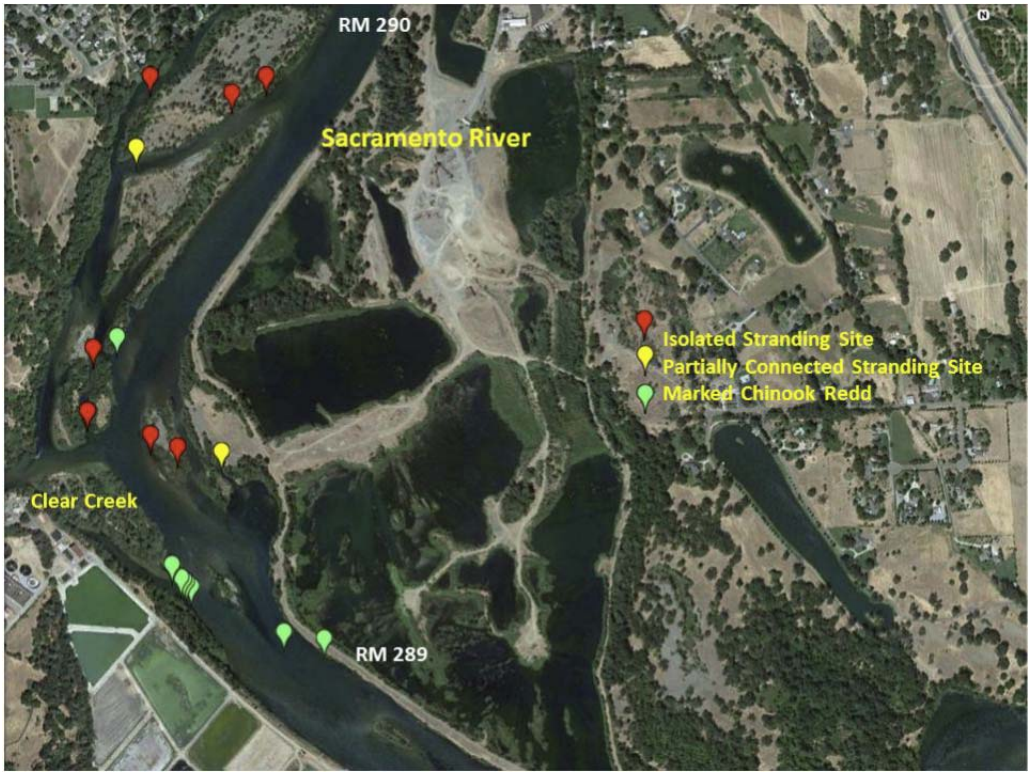

Figure A5.1. Strong association of stranding sites and redds with secondary channels in Sacramento River near Clear Creek. From Appendix D of Revnak and Killam (2013 RBFO Technical Report No. 01-2013).

Figure A5.2. Strong association of stranding sites and redds with secondary channels in Sacramento River near Highway 44 Bridge. From Appendix D of Revnak and Killam (2013 RBFO Technical Report No. 01-2013).

Existing and recently formed secondary channels should be identified and described by hydrogeomorphic variables such as average depth, width, length, and substrate type. Secondary channels so described can be sorted over a range of flows important to different salmon life stages. A description of their persistence should also be noted to address potentially important management issues. For example, have there been changes in the secondary channels through time, particularly since the closure of Shasta and Keswick Dams?

The IRP noted the presence of at least 8-9 secondary channels and more may be identified with a rigorous census that could even detect channels recently abandoned either from channel migration or avulsion processes. At least two important general categories of secondary channels can be identified – fully connected (both ends connect to the Sacramento River throughout the hydrograph) and partially connected (connected at the lower end only under low flows) – although other categories may also be discovered. Secondary channels that become disconnected at the upstream end and then become spring brooks because channel-bed elevation intercepts the top layer of the unconfined groundwater table may be particularly important juvenile rearing habitat (Stanford et al 2005,). Hyporheic water inputs are important in many rivers of the arid western U.S. because warm river water that flows from the open surface main channel into the underlying bed sediments is cooled before remerging as surface flow in the form of a spring brook (Hauer and Lorang 2004). Secondary channels that intercept

both hyporheic and regional groundwaters may be particularly valuable cool water refugia for salmon during times when cold water storage in Shasta Dam is limited. Partially connected secondary channels may be the cool water temperature refugia of last resort for salmonid early life stages under stressful temperature conditions.

Secondary channels are typically highly dynamic hydrogeomorphic features that can experience more dramatic hydrologic changes (fully wetted to dry conditions) than the main channel (Hauer and Lorang 2004, Lorang et al. 2013). The rates of change will likely not be constant. They will depend upon patterns of in-channel sediment dynamics, bank erosion, interaction with large woody debris, fluctuating water levels, succession of riparian vegetation and hydrologic events that cross geomorphic threshold levels (i.e., those discharges that mobilize and transport sediment) and do so for a sufficient duration to accomplish geomorphic work (i.e., cut-and-fill alluviation channel migration and avulsion) (Lorang et al. 2013, Nestler et al. 2012). The existing geomorphic complexity and inferred temporal dynamics suggest that future side-channel management plans must be carefully considered and developed.

As a precautionary note, channel modifications made by means other than natural processes may have major unintended consequences (Stanford et al. 1996). The diversity and productivity of salmonid rivers depends on maintaining a “shifting mosaic of habitat” (Stanford et al. 2005). For example bank erosion is often viewed negatively especially if mobilized sediments bury redds immediately downstream. However, those sediments are also key elements for the creation of new gravel bars that support the rejuvenation of riparian vegetation. Caution must be exercised when in-channel modifications are made to enhance production of single species because such actions may add a suite of stressors to other species which can result in a feedback loop to indirectly affect the species of concern (Tockner et al. 2010). The net effect of a single species focus is to reduce the diversity and persistence of the aquatic community as a whole (Tockner et al. 2010). In-channel modifications will only be successful through careful consideration of how they may affect natural first order hydrogeomorphic drivers for biogeochemical processes which are secondary response variables and hence tertiary drivers of food web dynamics within the river ecosystem. Simply having potential habitat visible from an aerial photo or mapped from the ground does not insure successful juvenile production unless that habitat structure provides the necessary habitat quality.

If secondary channels are recognized as important elements in future strategic efforts to protect and enhance salmonid populations in the Sacramento River, they should be incorporated as part of a holistic adaptive management approach that explicitly focuses on the geophysical processes that shape the dynamic abiotic and biotic structure of the

entire riverine ecosystem at multiple spatial and temporal scales. One of the most efficient ways to promote desirable ecosystem structure and functionality is to allow natural processes to self-maintain (Stanford et al. 1996).

Adaptive Management of Secondary Channels

Program-level restoration of secondary channels to serve as temperature refugia for salmonid early life stages may face difficult technical challenges and management issues. The SRTTG could take a formal collaborative adaptive management (AM) approach to restoration and conservation of secondary channels and similar small-scale habitat features in the Upper Sacramento River. An AM approach should include development of goals and objectives, guiding principles (e.g., self-maintenance), and conceptual models that describe how secondary channels contribute to salmon conservation and recovery. The conceptual models should be of sufficient detail and completeness that critical sources of uncertainty can be identified. These sources of uncertainty can then become the foci of studies that systematically improve the efficacy of management plans.

Report of the 2012 Delta Science Program Independent Review Panel (IRP) on the Long-term Operations Opinions (LOO) Annual Review

Prepared for: **Delta Science Program**

December 1, 2012

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Scope and Intent of Review: This report represents findings and opinions of the Independent Review Panel (IRP) assembled by the Delta Science Program to inform the National Marine Fisheries Service (NMFS) and the U.S. Fish & Wildlife Service (USFWS) as to the efficacy of the water operations and regulatory actions prescribed by their respective Long-term Operations Opinions' (LOO) Reasonable and Prudent Alternative Actions (RPAs) as applied from October 1, 2011 through September, 30 2012 (Water Year 2012). This year's annual review focused primarily on implementation of NMFS's RPAs for Clear Creek (RPA Actions I.1.1 – I.1.6) and the Spring 2012 Delta Operations joint stipulation agreement for water operations and fisheries that was required to be executed in water year 2012 in lieu of NMFS's RPA Action IV.2.1.

After reviewing a required set of written documents (Appendix 1), the IRP convened at a public workshop in Sacramento, CA on 31 October - 1 November 2012. The first day of the 2-day workshop provided a forum for the IRP to consider updated information and new research findings and to discuss issues related to the application of RPA actions. On the second day the IRP deliberated in a private session beginning at 8:30 a.m. in order to prepare and present their initial findings at the public workshop at 2:00 p.m., after which there was an opportunity for agency representatives, members of the public and the IRP to comment and otherwise exchange impressions and information.

[1] Dr. Nestler will provide advice to the Panel on subjects relative to his expertise on eco-hydraulics and coupled hydrodynamics and fish behavior modeling. He is not tasked with written assignments for the report development.

Subsequent IRP communication and deliberations were conducted via email and conference call in the course of drafting this final report.

EXECUTIVE SUMMARY

The review panel appreciates the unique challenges and constraints faced by all of the agencies attempting to balance existing commitments and mandated coequal goals of (1) providing a reliable water supply for California and (2) protecting, restoring and enhancing the Delta ecosystem from which water resources are derived for a multitude of human uses. We continue to commend all of the agencies charged with this daunting task for their efforts to date as they strive to cooperate and integrate activities directed at achieving this goal within the context of persistent change in environmental and socioeconomic conditions.

The dry 2012 water year presented a greater challenge to achieving specific RPA targets than was the case in the previous year and confirmed concerns expressed in Anderson et al. (2011) that some physical targets may not be routinely achievable. After three years of operating under the RPA actions, observations are available for a small sampling of both wet and dry years. Although it still remains too early to make definitive assessments of long-term effects on listed species populations, signs linking specific RPA actions to improved conditions remain elusive. Nonetheless, as noted by the two previous OCAP IRPs, the current LOO IRP emphasizes the continued need to explicitly link the success or failure of meeting physical targets prescribed in the RPAs to the biological/ecological responses of the listed species.

The IRP was encouraged by a perceived movement toward research aimed at measuring the survival and behavior of fishes within a spatially-explicit landscape relevant to water operations. Inclusion of more ecological and behavioral responses of the fish populations or life stages targeted by the RPA actions continues to be recommended as multiple years of observations become available.

The regular evaluation of goals and objectives is as much a part of an adaptive management strategy as are decisions to alter actions when justified by novel observations and response data that deviate from expectations. It is not too soon to step back and consider whether the intentions of habitat restoration efforts are tracking toward expected outcomes. If positive effects on listed species are not detectable following a series of “good” water years in the future, concerns about the detectability of effects under less favorable conditions will persist.

Findings from recent research reported at the 2012 LOO Workshop corroborated previous expectations of nonconformity in behavior of salmonid smolts and passive particles within the context of water flows and routing through the Delta. Consequently,

the application of passive particle models as a means of adjusting water operations to protect out-migrating salmonid smolts in real-time is not recommended. The IPR encourages a shift in the water management paradigm to include a more fish centric behaviorally and ecologically based perspective.

The IRP appreciated the opportunity to concentrate on a focal subset of RPA actions this year but wondered about progress, biological responses and consequences in applying the many other prescribed actions within the watersheds. The inclusion of maps for geographic orientation to the portion of the system under discussion was helpful to a degree and appreciated, but still fell short of expectations.

Finally, the time allotted at the workshop for panel deliberations (5.0-5.5 hrs) on the second day was again much appreciated and provided adequate time for the IRP members to organize thoughts and reach some consensus prior to presenting preliminary findings in the afternoon. We continue to encourage a similar time allotment for deliberation by future panels.

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INTRODUCTION

The Sacramento-San Joaquin watersheds and Delta comprise a complex system of distributaries, reservoirs, human-engineered channels, levees and a mix of agricultural and urban areas that have replaced former wetlands and floodplains. Significant structural alterations of the ecosystem date back to the mid-nineteenth century. Many of the anthropogenic changes in the Delta and its upstream tributaries were designed to store, redirect and convey water to meet human demands within the region, with little consideration for other biotic components of the ecosystem.

The chronic multi-decadal alteration of the natural ecosystem associated with meeting the demands of an increasing human population within and beyond the Central Valley watersheds have contributed to profound changes in the system's aquatic fauna, including a persistent decline in certain species of native fishes. Consequently, some of these jeopardized species have been afforded protection under the Endangered Species Act (ESA).

Within the historical context of engineered water resource management, formal legislative recognition that water and other habitats should be managed to restore and enhance the ecosystem as a coequal goal with providing a reliable water supply to California (Delta Reform Act) represents an ambitious and novel conceptual approach to water management within the region. Ultimately, the ability to meet this mandate appears to rest largely on adjusting existing water operations within the context and constraints of a system developed and engineered to primarily achieve one of these goals. If an appropriate combination of localized spatial and temporal deliveries of water cannot be found to maintain or restore the necessary ecological conditions to support the desirable species populations, the most feasible alternative may be to accept the ecosystem components that are sustainable within the constraints and limitations imposed by historical uses of the available limited resources.

***Background on the LOO RPA review process*:** NOAA's National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (USFWS) have each issued Biological Opinions on long-term operations of the Central Valley Project (CVP) and State Water Project (SWP, hereinafter CVP/SWP; Long-term Operations Opinions) that include Reasonable and Prudent Alternatives (RPA) designed to alleviate jeopardy to listed species and adverse modification of critical habitat. NMFS' Opinion requires the U.S. Bureau of Reclamation (USBR) and NMFS to host a workshop no later than November 30 of each year to review the prior water year's operations and to determine whether any measures prescribed in the RPA should be altered in light of new information (NMFS' OCAP Opinion, section 11.2.1.2, starting on page 583). Amendments to the RPA must be consistent with the underlying analysis and

conclusions of the Biological Opinions and must not limit the effectiveness of the RPA in avoiding jeopardy to the ESA listed species or result in adverse modification of critical habitat.

The purpose of both Long-term Operations Opinions (LOO) is to present the responsible agency's biological opinion on whether USBR's and DWR's long-term operations of the CVP/SWP are likely to jeopardize the continued existence or adversely modify the designated critical habitat for the ESA listed species under each agency's jurisdiction. Because both Long-term Operations Opinions concluded that the long term operations of the CVP/SWP are likely to jeopardize the continued existence or adversely modify designated critical habitats, the USFWS and NMFS prescribed RPAs to minimize CVP/SWP operations related effects to the level where these effects do not appreciably reduce the likelihood of jeopardizing the continued existence of ESA listed species or adversely modifying critical habitat. The RPA in NMFS' Long-term Operations Opinion (2009 RPA with 2011 amendments) includes both broad and geographic division specific RPA Actions. The RPA Actions in both Long-term Operations Opinions provide specific objectives, scientific rationales, and implementing procedures.

Since the Long-term Operations Opinions were issued, NMFS, USFWS, USBR, U.S. Geological Survey (USGS), California Department of Fish and Game (CDFG) and the DWR have been performing scientific research and monitoring in concordance with the implementation of the RPAs. Technical teams and/or working groups, including the geographic divisions specified in the NMFS' Long-term Operations Opinion, have summarized their data and results following implementation of the RPA Actions within technical reports. The data and summary of findings related to the implementation of the RPAs provide the context for scientific review regarding the effectiveness of the RPA Actions for minimizing the effects of water operations on ESA listed species and critical habitat related to the operations of the CVP/SWP. However, not all technical reports were included in the official review materials to be considered by the 2012 LOO IRP (see Appendix 1).

In January 2012, Public Water Agencies (PWA), State of California and Federal agencies filed a joint stipulation regarding project operations during April and May 2012 in the litigation relating to NMFS' Long-term Operations Opinion. The parties stipulated that if a rock barrier were installed at the head of Old River, the CVP/SWP would operate within an adaptive range of Old and Middle River flows in lieu of operating to the inflow:export ratio specified in RPA Action IV.2.1 of NMFS' Long-term Operations Opinion.

At the request of USFWS and NMFS, the Delta Science Program (DSP) employed the services of an independent science review panel to assist NMFS and USBR in reviewing the effectiveness of the implementation of NMFS Long-term Operations Opinion RPA and documents associated with the implementation of the joint stipulation. The role of the Independent Review Panel (IRP) is to provide a technical review to the agencies involved in implementing NMFS' Long-term Operations Opinion RPA.

The intent of the annual review is to inform National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS) as to the efficacy of the prior year's water operations and regulatory actions prescribed by their respective Reasonable and Prudent Alternatives (RPAs), with the goal of developing lessons learned, incorporating new science, and making appropriate scientifically justified adjustments **to the RPAs or their implementation** to support water year 2013 real-time decision making.

General scope and charge to the 2012 LOO IRP: The previous two annual reviews have considered all of the RPA Actions but this year's panel charge focused on a subset of the RPAs primarily related to water operations and populations of Chinook salmon (*Oncorhynchus tshawytscha*) and Central Valley steelhead (*Oncorhynchus mykiss*) within portions of the San Joaquin and Sacramento watersheds and Delta.

This year's annual review deals with the implementation of NMFS' Long-term Operations Opinion's Clear Creek RPA Actions (I.1.1 – I.1.6) and the Spring 2012 Delta Operations in lieu of NMFS' RPA Action IV.2.1 per joint stipulation (Spring 2012 Delta Operations) for operations and fisheries for water year 2012 (October 1, 2011 through September 30, 2012) and considers:

(1) Whether implementation of the Clear Creek RPA actions met the intended purposes of the actions;

(2) The agency's responses to and implementation of independent review panel recommendations from the prior year's Long-term Operations Opinion Annual Review on the Clear Creek RPA actions;

(3) Study designs, methods, and implementation procedures used; and

(4) Recommendations for adjustments to implementation of the RPA Actions or Suite of Actions for meeting their objectives.

Five questions (some multi-part) were posed to the 2012 IRP panel and defined the scope of the panel's charge. This report addresses each of the questions posed and provides additional observations and opinions where they seemed relevant and potentially useful from a scientific perspective.

***Acknowledgements*:** The members of the IRP appreciate and acknowledge the efforts of the agency and technical team representatives and contractors who prepared the written materials and delivered the workshop presentations that were the basis for this report. We recognize that much of the material had to be compiled, analyzed and organized in a relatively short time. Despite the many competing demands on the workshop participants, the materials were presented professionally, concisely, on schedule and often were responsive to the previous IRP's recommendations for format changes. The panel wishes to express a special thanks to the Delta Science Program, Peter Goodwin (Lead Scientist), Sam Harader (Program Manager) and the entire staff for providing the organization and logistical support to facilitate our task. In particular, Lindsay Correa (Environmental Scientist), as usual, expertly attended to a wide variety of technical and provisional details in support of the IRP's efforts before, during and following the workshop.

LOO IRP COMMENTS ON RPA ACTIONS IN WATER YEAR 2012

General comments and observations

Some of the NMFS RPA actions and Joint Stipulation commitments have yet to be implemented or completed and so the 2012 IRP is unable to develop an opinion as to whether or not they have or will meet their intended purpose. These include:

(1) Action I.1.2. Channel Maintenance Flows from re-operation of the Whiskeytown Glory Hole spills to include mean daily spills of 3250 cfs for one day to occur 7 times in a 10-yr period. This action was targeted for implementation in winter 2013 and will likely be delayed until 2014, so once again was not implemented and cannot be evaluated.

(2) Action I.1.3. Spawning Gravel Augmentation was once again performed but there was little information available to evaluate whether it is meeting the intended purpose. The written report from the Clear Creek Technical Team (CCTT) contained a note to "[insert section here]" that may have been intended to provide salmonid or macroinvertebrate responses to the RPA. During the LOO 2012 workshop in Sacramento the CCTT indicated that the data were not currently available.

(3) Action I.1.4. Replacement of Spring Creek Temperature Control Curtain in Whiskeytown Lake. This action was completed by the Bureau of Reclamation in June 2011, but there was no test of its effectiveness that would allow an evaluation of the intended purpose of the action. Furthermore, the intended effect of the curtain was to lower water temperatures delivered to the Sacramento River and not necessarily Clear Creek, which was the focus of this year's annual review.

(4) Action I.1.6. Adaptively Manage to Habitat Suitability/IFIM Study Results. Although the IFIM Study is completed, results were not provided for evaluation, so the IRP is unable to formulate an opinion this year.

(5) In the Joint Stipulation Order (Case 1:09-CV-01053-LJO-DLB, Document 660, filed 01/19/12, p 6 and 7 of 11), DWR committed to developing a study for a pilot predator removal and control program to be submitted to NMFS and CA-DFG for review and comment and "if a rock barrier is installed (at the head of Old River), a predator monitoring study will evaluate predation associated with the installation and operation of the rock barrier". At the workshop there was some verbal mention of these activities having been carried out, but no data were provided to the IRP for evaluation.

Hydrographic analysis

Annual planning and decisions on water operations are based, in part, on qualitative categories (e.g., wet, above normal, below normal, dry and critical) of water availability derived from indices of unimpaired runoff measured during two periods within the year, with an adjustment for the previous year's conditions. However, the approach provides little room for forecasting conditions in an upcoming water year, except perhaps for an implicit expectation of a relatively dry year (i.e., 60% of the WY categories are less than "normal"). The ability to plan for alternative decisions on water use based on predicted near-term climate conditions (e.g., global patterns in sea water temperatures driving El Niño-Southern Oscillation events) would contribute to the improvement of real-time responses required to meet the intentions of RPA Actions.

Given the wealth of annual flow records available to various technical groups, it is almost imperative that a more concise analysis of rainfall patterns and overarching landscape-level climatic patterns be accomplished in order to create the most effective adaptive management strategy. One of the goals of restoring the system will be to recreate or simulate previously existing hydrographic cues; that is, an effective benchmark period must be created. In most cases, the previous 20 to 40 years are not useful tools. . The effect of climatic change and other phenomena make this arbitrary period an inappropriate target which sets target flows. With increasing observations of linkage between long-term oscillations in oceanic temperature and/or changes in climatic trends *(*e.g., Werritty 2002, Hannaford and Marsh 2006, and Maurer et al. 2004), it is increasingly important to understand regional runoff patterns so that an effective benchmark target can be identified (Kelly and Gore 2008). Maurer (2007) and Cayan et al. (2008) have done extensive modeling of potential climate change scenarios and could offer insights into changes in runoff that might affect management decisions. The IRP suggests that a review of annual flow records to detect any predictable patterns influenced by the Pacific Oscillation as well as proposed scenarios for climate change in California will be useful exercises to "fine-tune" future management options.

IRP responses to questions defining the charge and scope of the 2012 LOO annual review

The 2012 Annual Review focused on NMFS' Long-term Operations Opinion's Clear Creek RPA Actions (I.1.1 – I.1.6) and the Spring 2012 Delta Operations:

Implementation of actions

1) **How well did implementation of the Clear Creek RPA Actions and Spring 2012 Delta Operations meet the intended purposes of the actions?**

<u>Clear Creek RPA Actions</u>

There were six Clear Creek RPA Actions to consider this year, but some were not conducted (e.g., Action I.1.2, Channel Maintenance Flows) or the information necessary to determine whether the intended purposes were met was sparse or lacking.

Spring attraction flows (Action I.1.1) provided pulses of 400 and 800 cfs from Whiskeytown Lake instead of the minimum of two 600 cfs pulses described in the RPA Action. The intention of this action is to attract adult spring-run Chinook holding in the Sacramento River into Clear Creek. Although the pulses moved gravel downstream (a stated secondary purpose), the CCTT report (Page 5, para. 4) opined that fish monitoring results were inconclusive - just as they were in 2010 - due to low adult counts. The IRP agrees that the 2012 counts were disappointingly low. However, one can still statistically evaluate the effects of pulses on the counts. In 2012, nine fish were seen before the first pulse, 13 after the first pulse, and 39 after the second. If the pulses had had no effect, then one would expect these 61 fish to have been equally distributed among the three surveys, with about 61/3 = 20 fish seen in each survey. However, a chi-squared goodness of fit test (Zar 2010) rejects this equal-distribution null hypothesis ($P<0.001$, chi-squared = 26.1, df=2). Thus, there is evidence for a nonrandom difference in counts between the surveys, presumably (but not necessarily) due to the pulse flows. This same test, using "exact" P-values, can also be applied to the even-lower counts of 2010 and 2011.

Channel maintenance flows (Action I.1.2) were not performed and were once again delayed until 2014. Discharges of about 3000 cfs were common events in the past and discharges above 5000 cfs are most likely required to establish geomorphic threshold crossing events. A one day spike of 3,250 cfs will not complete much in the form of geomorphic work other than water some rocks and result in negative ecological impacts to Clear Creek. Small pulses of 400 to 800 cfs have stage increases of 0.5 - 1 ft at the confined location of the Igo gauging station. These would barely be measurable

differences in terms of stage along the floodplain sites where most of the spawning and rearing habitat exists.

Spawning gravel augmentation (Action I.1.3) was intended to enhance and maintain previously degraded spawning habitat for spring-run Chinook and CV Steelhead. In 2011, 10,000 tons of gravel was placed at 5 sites in Clear Creek. Again there was no reliable metric to determine whether or not these augmentations are replacing or enhancing the quality of the spawning habitat for the targeted salmonid species or other fish and macroinvertebrate assemblages. Despite this lack of reliable metrics to gauge success, there is a clear intention to continue the spawning gravel augmentation project, with a concern expressed about the future source of gravel. The current plan is to use mine tailings that will be washed to remove the finer sediments containing mercury and potentially other contaminants and use a retention pond to permanently isolate those contaminants from the watershed. It is unclear how the quality of spawning habitat might be affected.

Replacement of the Spring Creek Temperature Control Curtain (SCTCC) (Action I.1.4) was intended to reduce adverse impacts of project operations on water temperatures for listed salmonids in the Sacramento River. The USBR replaced the SCTCC in Whiskeytown Lake on schedule in June 2011 at a cost of $3 million. However, unidentified “technical problems” with monitoring equipment apparently precluded pre-project monitoring to evaluate the effectiveness of this action. Effects, if any, of the SCTCC on temperatures in Clear Creek were not considered. However, in connection with the discussion on this temperature curtain, the IRP was informed that the Oak Bottom temperature control curtain (OBTCC) in Whiskeytown Lake was also damaged and in need of replacement or repair. While the agencies involved seemed to agree that the OBTCC should be replaced, no plan was advanced to test its effectiveness in meeting the intention of this action. It is unclear how the effectiveness of these temperature control curtains on water temperatures will be determined in either the Sacramento River or in Clear Creek.

Thermal Stress Reduction (Action I.1.5) was intended to improve conditions in Clear Creek for over-summering steelhead and spring-run Chinook during holding, spawning and embryo incubation. Seasonal temperature target maxima in Clear Creek at the USGS Igo gauge (about 6.5 miles downstream of Whiskeytown Dam) were set at 60° F during June 1 to September 15, and 56° F during September 15 to October 31. Thus far during 2009-2012, the temperature target was achieved consistently during the June to mid-September period, but frequently failed to be met during mid-September to October. In 2012, the temperature during this period exceeded the target maxima 69% of the time. During 2009-2011, temperatures exceeded the target 38% to 72% of the

time. In prior years (2001-2008) temperatures at the Igo gauge exceeded the temperature target during September and October only 7% of the time. Once again there was mixed success in meeting the physical targets set by this RPA Action and no biological response data on which to base an opinion as to the intended effects on salmonids.

The Clear Creek Technical Team (CCTT) put forth a complex hypothesis that involved potential impacts of an interaction involving the Oak Bottom and Spring Creek temperature control curtains and the effects of “power-peaking” at generating stations above Whiskeytown Lake as a possible explanation for the failure to meet the conditions of Action I.1.5 during mid-September to October in recent years. There seemed to be agreement among the agencies that the Oak Bottom Temperature Control Curtain (OBTCC) was in need of replacement but there was no consensus regarding the role of power-peaking in current conditions.

There was a paucity of hard evidence provided to the IRP on which to form an opinion as to the scientific soundness of alternative hypotheses to explain the temperature observations at the Igo gauge.

Adaptively Manage to Habitat Suitability/IFIM Study Results (Action I.1.6) was intended to improve habitat conditions for spring-run Chinook and steelhead by adaptive management of flow conditions that favor salmonid survival. This Action is associated with what is perhaps the least definable objective. Also the IFIM Study which began in 2004 has been completed but reports on the findings were not available to the 2012 IRP. Consequently, there is no basis on which to develop an opinion as to the effectiveness of this RPA Action at this time.

Spring 2012 Delta Operations

There were three objectives to the Spring 2012 Joint Stipulation agreement:

(a) to provide for minimum protection of out-migrating juvenile steelhead by managing flow conditions in the Delta in a manner expected to allow salmonids to successfully exit the Delta;

(b) to increase water exports consistent with the protection mentioned in (1) above;

(c) to generate real-time tracking information in order to better understand how pumping rates, flows in Old & Middle Rivers, and juvenile steelhead migrations relate to one another.

The agreement called for installing a rock barrier at the head of Old River and managing flows in Old & Middle Rivers within an adaptive range of -1250 to -3500 cfs during April and -1250 to -5000 cfs during May. A predation study associated with the rock barrier was also required as part of a predator control study. The rock barrier was not completely impermeable and had several open culverts through which water and fish could pass into Old River.

In terms of meeting the intended purpose of the joint stipulation, increased water exports (a portion of Objective b) was achieved. Exports were ca. 57,000 acre ft greater than would have occurred under the NMFS RPA Action IV.2.1 (inflow:export ratio). The water provision side of the stipulation was achieved. While this was described as a "modest" increase in water supply, its significance should be considered within the context of the 2012 water year (WY) being categorized as "critical" and only upgraded to "dry" near the middle of May and the end of the joint stipulation period. NMFS determined that no further adjustments were needed as a result of the change in WY classification.

As for meeting the intended purpose of the biological portion of the agreement (protection of juvenile steelhead and clarification of the relationships between fish migration and inflows/exports), the IRP was unable to determine the level of success or failure for several reasons including the following.

The decision to install a rock barrier at Head of Old River (HORB) was based upon an assumption that it would not enhance predation on salmonid smolts; a previously tested non-physical barrier (bubble curtain) was shown to enhance the risk of predation mortality on smolts, which was the primary reason given for not using that approach.

Estimates of mortality used in setting the triggers for the number of tagged smolts that could be entrained by water operations depended on the assumption that the HORB did not enhance predation risk. Although testing that assumption was one of the conditions of the Joint Stipulation agreement, the 2012 IRP was not informed as to the outcome of any study to test predation associated with the rock barrier.

Furthermore, findings of the 2011 VAMP acoustic tag study, which estimated route-specific survival rates of tagged Chinook smolts, found that the highest survival rate through the Delta was via Old River. Most (64%) of the tagged smolts surviving to Chipps Island did so via artificial transport from the CVP holding tank. The HORB was intended to inhibit migration of smolts via Old River (the shortest route to the CVP holding tank) and as a consequence enhanced negative OMR flows, which may have

encouraged higher smolt entrainment into the southern Delta via alternative routes. Data presented by the VAMP study showed that forcing smolts through the Delta by blocking the entrance to Old River decreased survival, presumably due to predation through the central Delta region.

The Spring 2012 plan for water operations focused on characterizing smolt movement with mean project operations, OMR flows, pump exports and I/E ratio. The plan appeared to be based upon the assumption that fish movements and survival would be correlated with measures of mean flow. However studies cited in the Tech Memo demonstrated weak correlations between smolt movement and particle tracking model studies and between project operations, OMR flows and smolt movement and survival. Studies available in the literature and many published in the region have demonstrated that fish movement across a wide range of taxa exhibit behavioral response to tidal oscillations. These behaviors facilitate either the retention of species in the Delta, or upstream/downstream movements necessary to complete their life cycles. The importance of tidal dynamics on smolt migration and interactions with predators and pumps received limited attention in the 2012 operations. When it was addressed it was in the context of tidal effects on passive particle movements.

It was emphasized by the 2010 OCAP IRP (Anderson et al. 2010, p 24) and confirmed by the Acoustic Tag Study conducted in April-May 2012 that steelhead smolts do not behave like passive particles and it was simply inappropriate to rely on the PTM to direct water operations intended to protect out-migrating juvenile steelhead. The effects on steelhead smolt survival could not be determined and this action cannot be described as providing any level of protection for steelhead.

The IRP believes that discerning behavioral responses of smolts and predators to tidal oscillations is crucial for understanding variation in salmonid survival within the Delta, and abundant information is available on the significance of tidal factors. Consequently, the IRP concludes that the best available information was not used in planning the 2012 Delta Operations.

<u>2011 IRP recommended adjustments for Clear Creek Actions</u>

2) **Where the 2011 Independent Review Panel made recommended adjustments to implementation of the Clear Creek RPA Actions,**
    a) **Were the adjustments made?**
    b) **How well did these adjustments improve the effectiveness of implementing the actions?**

The Clear Creek technical Team (CCTT) report and presentation frequently acknowledged the suggestions of the 2011 IRP. The recommended suggestion

regarding gravel size in the spawning gravel augmentation program were followed but there were no biological response data upon which to base an opinion regarding whether or not this suggestion improved effectiveness of the action.

Although the CCTT agreed with the 2011 IRP's suggestion for improved temperature and flow modeling in the system, especially for Whiskeytown Lake, this has yet to be undertaken.

Also, the IRP suggestion to give a more natural hydrograph shape to the pulse release flows was not done. The 2012 IRP reiterates these last two suggestions.

<u>Effectiveness of coordinating real-time operations with CCTT input</u>

3) **How effective was the process for coordinating real-time operations with the Clear Creek technical team analyses and input as presented in NMFS' Long-term Operations Opinion [NMFS' 2009 RPA with 2011 amendments (pages 8-9)]?**

The CCTT Report lists topics associated with coordinated long-term operations on eight dates between December 15, 2011 and September 20, 2012 but there appeared to be no real-time operation effects related to analysis and input. However, there appeared to have been at least two incidents relevant to the implementation of actions. These were (a) a week-long period (June 3-11, 2012) during which warmer than intended water was released from Whiskeytown Lake due to an upper release gate being "inadvertently" left open, and (b) operations at the Redding power station which apparently is not under the control of USBR. The presentations from the CCTT and USBR made at the workshop in Sacramento on October 31, 2012 along with subsequent discussions with the IRP suggested that there may be a need for improved coordination between real-time operations and some of the RPA Actions intended to benefit salmonid populations in Clear Creek.

<u>Indicators, study designs, methods and implementation procedures</u>

4) **(a) Were the scientific indicators, study designs, methods, and implementation procedures used appropriate for evaluating the effectiveness of the Clear Creek RPA Actions and the Spring 2012 Delta operations?**

The approach in the Tech Memo was clearly articulated. Whether it was supported by the best available science prior to the study is less clear. In general, there can be little certainty as to the effectiveness of the indicators, study designs, methods and

implementation procedures without reliable and accurate measures of biological responses.

Clear Creek RPA Actions

In general, the CCTT report tended to consider progress toward meeting RPA Action targets as a measure of success, which could be appropriate for actions intended to follow some expected trajectory over time (e.g., multi-year projects) but most actions are not defined in that manner.

A list of restoration goals have been created by the CCTT, but these goals must be continuously reviewed as studies are completed or different goals and endpoints are identified. These goals cannot remain static and the IRP urges the CCTT to review these goals annually to determine if the objectives and endpoints remain realistic. “River restoration” has been variously defined in the literature over the past three decades, ranging from “the complete structural and functional return to a pre-disturbance state” (Cairns 1991) to something less than ideal [“a return to an ecosystem which closely resembles unstressed surrounding areas”] (Gore 1985). Four overall targets can be identified (modified from Brookes and Shields [1996]):

Target	Definition	Management Approach
Full Restoration	Complete functional and structural return to an identified pre-disturbance conditions	Direct intervention, natural recovery, or enhanced recovery
Rehabilitation	Partial return to an identified pre-disturbance condition	Direct intervention or enhanced recovery
Enhancement	Any improvement in physical or biological quality	Mainly direct intervention
Creation	Development of a resource that did not previously exist, including “naturalization’ which creates a configuration of contemporary magnitudes and rates of riverine processes	Direct intervention

Gore and Shields (1995) argue that rehabilitation is probably the most likely obtainable target, yet the most expensive, while creation or abandonment of the project, is least expensive but most manageable. Targets continually shift in this broad spectrum of possibilities and the CCTT should consider modifying these targets as a component of their adaptive management strategy.

One of the goals of this project is the completion of the IFIM studies in order to create an adaptive management strategy. The successful completion of this study should allow the analysis of the appropriateness of other activities such as gravel augmentation and the achievement of restoration goals. It is imperative that the results of IFIM studies be reported. An adaptive management plan provides the flexibility that allows managers to respond to future change. These strategies must adapt to the actual results of the Clear Creek restoration plan as it progresses, yet one of the fundamental tools for the development of these strategies, after 16 years of restoration planning and work remains incomplete. The location, duration, and availability of habitat (as expressed as weighted usable area in PHABSIM or other habitat simulations]) over time under various operational scenarios can become a valuable planning tool.

Ultimately, completion of the IFIM study will require the correct choice of index period; that is, the previous historical records that best replicate natural hydrographs in the region, assuming that restoration of the hydrograph is, indeed, an acceptable restoration target. The choice of index period can be important as it must include a target condition prior to alteration *and* include the effects of regular climatic changes such as the Pacific Oscillation (see comparable work by Kelly and Gore, 2008, in the Southeastern US) and the effect of changing land use in PHABSIM predictions (Casper et al. 2011). For example, with changes in the Atlantic Multidecadal Oscillation, PHABSIM predicts a significant change in both fish and macroinvertebrate communities with each cycle (Warren and Nagid 2009) with shifts in dominant functional feeding groups and species composition, among macroinvertebrates, and top carnivores in the fish community. Such modeling results allow the focus of management strategies to shift as natural hydrographic conditions change.

During the CCTT presentation and later discussions at the workshop in Sacramento, it appeared that the team did not yet have an effective way to assess the effect of the temperature control curtains on temperatures of water releases from the reservoir into either the Sacramento River or Clear Creek. Also, there was a greater emphasis on relatively small (a few degrees) decreases in the temperature of the water released from Whiskeytown Lake rather than on stream water temperature when it reached targeted reach boundaries such as the Igo gauge, approximately 6.5 miles downstream or the lower reaches of Clear Creek approximately 12 miles from the dam.

Gravel augmentation has been a very active restoration activity in Clear Creek since 1996 (150,000 tons) and is planned to be continued into the future ($4.5 million). At this point there is insufficient data to support the ecological effectiveness of the gravel augmentation activities. It appears that two related responses follow this restoration

activity. Spawning increases a couple percentage points and then just as rapidly declines (Fig. 9 CCTT 2012 report).

The CCTT 2012 report alludes to physical monitoring since 1996 and Figure 10 and 11 in that report show that pulse flows since 2009 have moved gravel in the Dog Gulch site just below Whiskeytown Dam, but there was less movement of gravel in the Peltier site just downstream. The IRP was unable to determine the type of data that were collected to distinguish the spread of gravel from the existing stream bed or how the magnitude of movement was assessed.

Spawning seems to occur very near the channel banks which may be a species preference or it could be that these areas had less gravel. At the 2012 LOO workshop, it was indicated that the channel was deeper at the edges as a result of how the gravel was placed and perhaps how the river flow encountered the gravel deposits. However, this only underscores the need to step back and quantitatively evaluate a set of metrics aimed at testing the restoration goals.

An independent 2005 review specifically of gravel augmentation practices in the Central Valley listed 20 unanswered questions concerning gravel augmentation practices (Lave et al. 2005.). One of the largest data gaps for Clear Creek, and most likely for the other sites, is linking threshold entrainment to discharge and routing/deposition of gravel through Clear Creek system.

The long-term future source of material for the gravel augmentation activities will come from mining tailings and hence there may be a potential to introduce additional mercury contamination to the system. The direct transfer of mercury - and other metals from sediments - through the aquatic food chain is a concern wherever past mining is prominent, such as in the Clear Creek basin. Fine sediments contain the higher levels of mercury then gravel and the fine bed sediments of Clear Creek have been shown to contain mercury levels 2 to 10 times natural background levels (Moore 2002).

Gravel augmentation seems to encourage spawning and hence the excavation of redds. There is also an expectation that gravel augmentation will result in favorable alterations of channel morphology. Both small- and large-scale morphological changes to the bed can result in an increased flow of hyporheic water through the surface sediment. Merz et al. (2004) reported on the possible benefits of gravel augmentation on spawning bed enhancement showing that it increases survival and growth of Chinook salmon embryos in the Mokelumne River. Other authors have shown the exchange of hyporheic water enhances the formation of riffle complexes with measurable impacts in terms of moderating riverbed water temperature (Grant et al. 2006a, b, Hanna et al. 2009). Brown et al. (2007) showed that spatial variation in sediment source resulting from flood

transport of mine tailings along with temporal changes in hydrology, combine to dictate the role of the hyporheic zone in the transport and retention of arsenic.

In the lower reaches of Clear Creek bed sediments have mercury concentrations that are already above background levels and high flows that scour the bed reintroduce fine sediments into the flow. This coupled with gravel augmentation could be enhancing geomorphic change that in turn enhances hyporheic water flow through sites that encourage spawning soon after mobilization of the gravel. If so, gravel augmentation and flushing flows could be encouraging spawning in gravels where intra-gravel flow contaminated fines passed through incubating salmon embryos. The total net effect on salmon reproduction from the restoration activities of gravel augmentation coupled with flooding is unknown but it is not unlikely that gravel augmentation to encourage salmon spawning in an already highly contaminated creek bed could adding an additional layer of stress detrimental to the survival of the very species it is trying to help.

Indeed, Moore (2002) in discussing Clear Creek specifically states:

> *"Understanding the distribution of such widespread contamination is essential to river restoration, especially where dredging, filling, excavation, floodplain construction and changing sediment dynamics may lead to remobilization of contaminants from the riverbed/floodplain, making them more bioavailable. Specific river restoration efforts can also be stymied by bed-sediment contamination, especially those designed to increase/recreate fish spawning habitat. An example is the dependence of some salmonids on areas of upwelling through a gravel bed. If the bed is contaminated with mercury or other heavy metals, geochemical reactions within the bed can release contaminants to the water that irrigates fish eggs. This increased metal loading can decrease reproduction and productivity at spawning sites."*

The IRP recognizes that the plan is to wash the gravel used in the augmentation and remove the more heavily contaminated fine sediments, storing them in containment areas. However, this commits one or all of the agencies involved to the perpetual obligation of preventing the concentrated contaminants from entering the watershed.

The CCTT Report also included speculation about what may be learned through the use of both video and sonar. There are many "may"s here. The IRP suggests that CCTT members posit some specific, realistic outcomes from these two monitoring sources and think through exactly what conclusions could be drawn before investing substantial financial resources in video and sonar monitoring programs.

Spring 2012 Delta Operations

The study design for real-time operations using acoustic tagging material was inadequate to develop real-time operations. The operations were based on the arrival of fish at specific points in the inner Delta which were adjusted over the season because the fish arrived at the target points earlier than expected.

The general project operations have been managed in terms of the mean flows in OMR and in the San Joaquin River. This has been the fundamental approach for operations of the system for years but has resulted in inadequate protection for fishes. In part, this is because attempts to understand the movement and survival of fish through the Delta to date have not considered effects of tides, which are the dominant control on flow velocities and mean direction of flow.

Delta survival of steelhead, and especially Chinook, was extremely low based on tagging studies. Characterizations of survival in terms of river km or mean flow are inadequate because the rapid travel time and complex routing of fish through different reaches cannot be explained by these mean measures. The IRP suggests the travel, routing and survival of fish through the system needs to account for migrant behavior and the behaviors of the predators in response to the strong tidal influences in the Delta (see Appendix A2.2: Selective Tidal-Stream Transport).

The acoustic tagging experiment also had logistic and possibly methodological difficulties from the start, so reliability of the results is questionable for reasons that will be explained subsequently. Second, when difficulties were encountered, there was an attempt to use an “adaptive management” approach in real-time that only seemed to complicate the situation. Adaptive management requires that something be learned before adjustments are made, it was not intended to simply take another course when things are not going as intended in real time. There were two substantial examples of this:

(1) When the acoustic tagging study could not begin on April 1, the Particle Tracking Model (PTM) was substituted as a means of providing input into decisions regarding water operations for the purpose of protecting juvenile steelhead. As mentioned earlier, there was no means of determining whether or not this approach provided even minimal protection for out-migrating smolts.

(2) The original plan for the acoustic tag study was to run water operations in a manner that allowed OMR flows in the range of -1250 to -3500 cfs in April and -1250 to -5000 cfs in May. However, when the tagging study had logistical difficulties that delayed its start for 2 weeks a series of decisions was made that altered the experimental design.

After the first release of tagged smolts on April 16, when OMR flows of -3500 cfs were planned the number of tags entrained in the south Delta exceeded the trigger within 4 days and after a delay of 2 more days OMR flows were reduced to -1250 cfs through April 30. At this point, a decision was made to raise the trigger and switch the experimental treatment level to OMR flows of -5000 cfs instead of the -1250 cfs planned for May 1-15. Two days after release of the second group of tagged smolts the trigger was once again exceeded and, because of other constraints on water operations, flows were reduced to -1250 cfs for the remainder of the period (May 8-12) following a 5 day delay. The response was to raise the trigger once again and schedule operations to flows of -5000 cfs for the finally period as originally planned. Five days after the final release of tagged smolts, the highest trigger was exceeded and flows were reduced to -1250 cfs during May 23-28. Consequently, the apparent attempt at real-time "adaptive management" during this experiment resulted in a substantial alteration of the original experimental design that weakened the test for effects of flow on steelhead smolt survival and routing as follows:

Time Period	Original Plan	As Conducted – Spring 2012
April 1-15	-1250 cfs for 14 days	-1800 cfs Apr 1-7; -2500 cfs Apr 8-14; No Tags
April 16-30	-3500 cfs for 14 days	-2446 cfs for 7 days
May 1-15	-1250 cfs for 14 days	-2933 cfs for 7 days
May 16-31	-5000 cfs for 14 days	-5193 cfs for 7 days

Note that the changes implemented did not allow for any measurement of tagged smolt survival and routing under the lowest OMR flows (-1250 cfs) and the intermediate flow treatment level (-3500 cfs) was not achieved. Instead, two of the flow treatment levels were so similar (-2446 cfs and -2933 cfs) as to be functionally identical and there was no minimum flow regime included in the experiment as conducted. However, this did not seem to deter reaching the conclusion that there was no relationship between OMR flows and smolt entrainment to the interior Delta. This is too broad a conclusion to draw from the altered experimental design. It remains entirely possible that entrainment is related to OMR flows within any range between -2446 cfs and >0 cfs and becomes asymptotic at some threshold level of negative OMR flow.

Also, many of the study's initial conclusions are not adequately supported by the analyses because they fail to make use of statistical testing or confidence intervals. The analyses should be redone with greater statistical rigor, where possible. It is possible to test for evidence of a flow effect within the range of flow levels tested using the available data. We suggest recoding release groups 1 and 2 as "intermediate" OMR flow, and group 3 as "high" OMR flow. Then Groups 1 and 2 can be considered as independent replicates (n=2) of an "intermediate" flow treatment level, with Group 3 providing the only replicate (n=1) of a "high" flow treatment level.

Methodological issues with the acoustic tag study on steelhead smolts conducted under the 2012 Joint Stipulation Agreement.

The IRP recognizes that there were logistical, meterological and other difficulties beyond the control of the Department of Water Resources and their collaborators and contractors in conducting the Spring 2012 acoustic tag study. The LOO IRP also acknowledges that previous OCAP IRPs have consistently recommended studies to link biological responses and the physical targets in the RPA Actions. The attempt to move in this direction with the acoustic tag study was commendable and the following comments should not be interpreted as a criticism of those who attempted it.
As with most experiments, the credibility and reliability of the findings depends substantially on whether or not assumptions are reasonable or tested. The following were assumptions stated in the workshop presentation by Kevin Clark as applying to the Spring 2012 acoustic tag study:

(1) Tag detection probability at each location is high (>80%) and similar to the 2010 VAMP findings.

(2) Detection probability may vary among receiver arrays but not between release groups within arrays.

(3) No predator detection filter was required (i.e., all detections were assumed to be live steelhead, not tags carried by predators that had consumed tagged smolts).

(4) OMR flow differences between Group 3 and Groups 1 + 2 were sufficient to test the hypothesis that flows affect fish behavior.

(5) Sentinel hatchery steelhead and wild steelhead smolts behave similarly.

(6) Hatchery smolts released in the tidal portion of the San Joaquin River behave like river-run steelhead.

As to the first and second assumptions, the two studies used very different acoustic tags and receivers. The Joint Stipulation Study used VEMCO tags (V5) which transmit at 180KHz and VAMP uses Hydroacoustic Technology Model 795Lm tags which transmit at 307KHz. Both frequencies are suitable for use in freshwater but the detectable signal range of tags transmitting above 100KHz tends to be degraded with increasing salinity, turbidity, boat noise, etc. There was no mention of range tests conducted on the field arrays to verify this assumption. In tidal environments, one can also expect detection range to be affected by tidal movement and may differ at high and

low tides (for a good example see Pautzke 2008). These assumptions can and should be tested. If environmental variation within the Delta affected the detection range of the receivers that resulted in a systemic bias, it could result in reduced tag detections being incorrectly perceived as mortality. When detection probabilities are < 100% and are not properly accounted for, survival estimates are expected to be biased lower (Drenner et al. 2012).

The third assumption conflicts with observations from the VAMP acoustic tagging studies (Vogel 2010, 2011) which now attempts to apply a predator filter that accounts for a considerable number of tag detections.

The fourth assumption was considered earlier. The two points representing treatment level flows in this experiment are relatively high and so the findings only apply to OMR flows that are more negative than -2446 cfs. There is a large range of flows more positive than this value within which a relationship between flow and smolt behavior could still exist. This is a severe limitation on the findings of the Joint Stipulation Study.

The fifth and sixth assumptions are unlikely true, as several studies have demonstrated differences in the behavior and survival of out-migrating wild and hatchery salmonid smolts (e.g., Chittenden et al. 2008; also see reviews by Melnychuk et al. 2010 and Drenner et al. 2012).

Several other potentially important assumptions were not mentioned. Among these were that: (a) tagging does not affect survival, (b) there was little or no mortality from handling, (c) tag expulsion was minimal, (d) the tag burden (weight of tag:weight of smolt) was appropriate and similar across groups, and (e) that tags did not affect swimming performance or predator avoidance.

In a recent review of tagging studies to examine the behavior and survival of salmonids, it was noted that only 10.6% of studies reported in the 207 papers assessed tagging and handling effects and only about a third of the studies even acknowledged them (Drenner et al. 2012). Given that one of the logistical challenges mentioned in the joint stipulation study was a paucity of experienced personnel available to implant acoustic tags, this could have been a potentially important source of mortality and tag loss in this study. Given the constraints to conduct the study in Spring 2012 under difficult circumstances, it may be impractical to expect such an assumption to be rigorously tested, but lacking evidence to substantiate this and other assumptions provides reason to doubt the accuracy of the findings.

Information on the size of smolts used in each group was not provided, but VEMCO V5 acoustic tags weigh an average of 0.65 g. Ideally, tag burdens of no more than 2% are recommended for most species, and burdens in excess of ca. 5% are generally not recommend for salmonid smolts (e.g., Adams et al. 1998), suggesting that appropriate smolt sizes for V5 acoustic tags would be > 13 g. There have been very few studies assessing the effects of tag burdens on the behavior and survival of salmonids (Drenner et al. 2012). However, early short-term swimming performance and higher predation rates have been associated with juvenile Chinook salmon carrying surgically-implanted transmitters for radio telemetry (Adams et al. 1998).

Statistical issues with the acoustic tag study on steelhead smolts conducted under the 2012 Joint Stipulation Agreement.

Data analysis issues were not specifically addressed in the charge to the 2012 LOO IRP but the IRP believed it was necessary to comment on this aspect of the recent studies because statistical rigor is crucial for objectively interpreting apparent patterns in the results. For example, Figure 5 in the “Status Report for 2012 Acoustic Telemetry Stipulation Study” shows cumulative detections at different receiver arrays. Cumulative distributions can exaggerate differences between time series counts. In the upper panel, the green and blue curves appear quite different, and yet the time series differ only by a few fish on days 2 and 3. Because the counts are low, it is important to place confidence intervals on these curves, before claiming they differ. In addition, with low sample sizes, it is more realistic to plot cumulative counts as a stair-step rather than a smooth curve.

These same comments apply to the cumulative count figures in the PowerPoint presentation (e.g., slide 31, 37, 39) given on this topic at the workshop in Sacramento on October 31, 2012. Because of low counts, the confidence intervals on the curves in these figures will likely all overlap substantially.

It would also have been useful to place confidence intervals on the estimated proportions in Figure 6 in the same Status Report, and in all other figures that display similar estimates (Zar 2010). To test whether proportions differed across the three junctions, the IRP suggests fitting a logistic regression model with probability of entering the interior Delta as the response variable, and junction and flow level as the explanatory variables. Recoding groups 1 and 2 together as “Intermediate flows”, and group 3 as “Higher flow”, it would be possible to test for the hypothesized difference between the 2 flow levels and reach a supportable conclusion, at least within the range of flows observed.

The boxplots in Figure 11 of the Status Report on the 2012 Acoustic Telemetry Study are unclear with respect to the sources of variation represented. The IRP was unable to determine the sample sizes in each case, but if small (n < 10), then boxplots can be misleading, and perhaps the data should just be plotted as distinct points. Also, this figure includes data from earlier releases ("six year release groups"), then release group ID's 1, 2, 3 and their relation to flow have no clear meaning.

At the top of p. 18 of the Status Report, "a generalized linear model with binomial error structure" was applied to tag detections at receiver array 9 compared to either array 12 or 14. The IRP did not understand exactly what was being tested by this model.

The 2011 VAMP acoustic tagging study of Chinook salmon smolts.

The 2012 IRP recognizes that evaluating the Vernalis Adaptive Management Program (VAMP) studies was not specifically within this year's charge. However, during the workshop in Sacramento (October 31, 2012) the IRP was presented an update from Rebecca Buchanan on the findings of the 2011 VAMP Acoustic Tagging Study which estimated survival of hatchery-reared acoustically tagged Chinook salmon smolts along different potential emigration routes from Mossdale to Chipps Island. Within the context of the workshop, it was difficult to avoid making comparisons between the VAMP and Joint Stipulation Acoustic Tagging Studies given the similarities in the intentions and objectives of the research projects.

The VAMP findings were that overall survival along all routes combined was less than 2% in 2011 and that survival was greater through the southern Delta than through the mainstem of the San Joaquin River. Also, plots of findings from three years of the VAMP acoustic tag study (2008, 2010 and 2011) suggested that higher river flows at Vernalis resulted in lower survival of smolts along the San Joaquin River route. These results contrast with those from earlier coded wire tag (CWT) mark-recapture estimates (analysis by Newman) which have been the basis of the NMFS Biological Opinion on salmonids and to provide the rationale for RPA Actions involving water operations in the Delta (see Report on Spring 2012 Delta Operations in lieu of Action IV.2.1 per Joint Stipulation).

In the VAMP 2011 tagging study, detailed route-specific survival rates tended to decrease in down-river segments and were greatest along the Old River route leading to the CVP tank from which tagged smolts were transported by truck to Chipps Island. The findings, if reliable, suggest that transport from collection facilities associated with water operations provides the best survival chances for Chinook salmon smolts in the San Joaquin watershed. Moreover, it suggests that the use of rock and/or other barriers

at the head of Old River on the San Joaquin River that force smolts into the Delta interior where survival is less than 2% should be reconsidered. Indeed, it seems plausible from findings of recent acoustic tagging studies that higher smolt survival will be achieved through encouraging migration down Old River and towards the CVP tank.

The IRP is unaware of any current measure of smolt survival subsequent to transport and release at Chipps Island, but studies conducted in the Columbia River watershed have suggested that there was little evidence of “delayed” mortality associated with transport induced stress in spring Chinook smolts (Rechisky et al. 2012). The same study also suggested that survival to adulthood could still be impaired by early ocean entry as a result of transport. In the 2011 VAMP acoustic study, transported smolts reached Chipps Island in less than half the time (average of 2.6 days, n=24) as those taking an unassisted river route (average 6.3 days, n=8), so route-specific consequences for survival to adulthood remain uncertain.

The VAMP acoustic tagging program has been conducted annually since 2008 and so these studies have an experience advantage over the Spring 2012 Joint Stipulation Study (i.e., less likely to have experienced surgically-related sources of mortality and tag expulsion due to skill levels of personnel), but nonetheless are subject to many of the same criticisms regarding certain key assumptions, especially those related to array-specific detection probabilities under different environmental conditions. In fact, the use of HTI Model 795Lm acoustic tags, which transmit at a frequency of 307KHz would be expected to have an even smaller detection range in the tidal estuary than the VEMCO tags (180 KHz) used in the Joint Stipulation Study. Unless there have been array-specific range tests conducted across the entire environmental gradient that were not available to the IRP, there is reason to doubt the claim of high detection probabilities for every route and river segments between arrays, especially in tidal environments where salinity and perhaps turbidity are greater than in the freshwater reaches. A first step in addressing this issue would be to focus range detection tests on arrays associated with areas identified as mortality “hotspots” where survival was considered to be at or near zero.

There are a few other considerations that complicate comparisons between the VAMP acoustic tag studies and the CWT studies analyzed by Newman (2008). Perhaps the most important difference is that CWT studies depend on actual recaptures of tagged smolts so survival of individuals to the recapture point is a certainty. Acoustic tag studies – with the exception of smolts transported from the CVP tank – track tags and not smolts. The tags could be transported within predators that consumed smolts or could go undetected by a given receiver array due to imperfect detection probabilities.

Although there are filters that can be applied to adjust for these discrepancies, these are still estimates associated with a level of uncertainty.

Another difference between the CWT and acoustic tag studies is the route endpoint which was Jersey Point for the CWT studies and Chipps Island (over 10 miles farther down-estuary) for the VAMP acoustic tag studies. If smolt survival was low between Jersey Point and Chipps Island, it would help explain the difference in survival among the studies. However, the 2011 VAMP data are not consistent with this hypothesis given that smolt survival within that segment was estimated to be about 69% (see slide 22 in PowerPoint presentation by Buchanan et al., LOO Annual Review, October 31, 2012). Alternatively, differences may be due to inter-annual variation in smolt survival, which is known to be highly variable in other systems (e.g., Chittenden et al. 2010).

In any case, substantial uncertainties remain regarding the effects of water operations on the survival and behavior of out-migrating salmonid smolts. Conflicting findings of different studies and methodological issues associated with the approaches used to evaluate survival and routing behavior of out-migrating salmonid smolts have not yet provided a clear path to suggest that fine-tuning water operations will provide a successful means of maintaining or restoring salmonid populations that migrate through the southern Delta.

Clear Creek Technical Team Report specific questions

Were the approaches used to develop the recommended actions to reduce water temperatures scientifically appropriate?

The CCTT report provided a number of suggestions aimed at reducing water temperatures in discharges from the Whiskeytown Reservoir. The presumed effects of replacing the Oak Bottom Temperature Control Curtain (OBTCC) and power peaking on Clear Creek temperatures (Fig. 16 in the CCTT Report) were largely speculative and need to be verified through modeling, analysis of existing temperature data and controlled experiments, if possible.

Releases of colder water from lower in the reservoir as temperatures warm in the summer seems to be a common sense recommendation but still requires some verification with respect to the available volume of cooler bottom water in storage and how far downstream the intended effects on temperature are likely to extend under different climatic conditions, ranging from sunny and hot to cloudy and cooler.

What recommended adjustments to actions and implementation procedures for reducing water temperatures might be scientifically appropriate for the next year, while maintaining equal or greater protection for fish?

Any of the suggestions “might be” scientifically appropriate but require some objective testing to be certain. The IRP suggests that CCTT consider options for assessing the potential temperature-specific pools of water available, through modeling and real-time monitoring within Whiskeytown Reservoir and upstream.

Given that there seems to be consensus among the agencies in favor of repair/replacement of the OBTCC, the 2012 LOO IRP can see no reason to object but would strongly recommend that this action be conditioned on an evaluation of effectiveness that includes measurements before and after installation of a replacement curtain.

Spring 2012 Delta Operations specific questions

Was the approach to real-time operations, including the use of a rock barrier at the Head of Old River (HORB) and acoustic tagged fish for triggering real-time decisions, while providing equal or greater protection to out-migrating steelhead smolts under RPA Action IV.2.1, clearly articulated and supported by best available science in the NMFS February Tech Memo and supporting documentation?

The approach was clearly articulated in the February Tech Memo and supporting documentation but there was little basis for assessing the effects of the HORB on the intention of providing equal or greater protection for out-migrating smolts.

Survival models played a prominent role in decisions about the rock barrier and Old River flows, as evidenced in materials provided to the IRP. The models are also the kernel of the “HORB and survival exploration tool” spreadsheet. However, none of the material reviewed by the IRP discussed the uncertainties of these models, apart from the statement that survival estimates may be somewhat too high for present-day conditions (Report on Spring 2012 Delta Operations, Appendix D, pg. 3). Because of their management importance, the IRP believes it is critical to quantify and communicate the uncertainties of these models.

In addition, the IRP traced the constant survival estimates (flat lines in Figure 2 of the Report on Spring 2012 Delta Operations) back to the Newman (2008) report. However, the IRP could not locate the figure’s flow-dependent survival equations in that report,

nor could we find the idea of estimating a weighted average (mixed model) of the flow-dependent and flow-independent models.

In Appendix C (Summary of expected benefits of the Spring 2012 Delta Operations Report), the interpretation of relative survival in OMR vs. San Joaquin was unclear. Smolt survival was apparently lower (again, no uncertainty estimates) in the San Joaquin in 2009-2010, with an acoustic barrier in place. And San Joaquin survival in 2008 was higher when no barrier was in place. Nevertheless, a rock barrier (HORB) was installed at the Head of Old River in 2012,"… based on a preponderance of the data". What data constitutes "a preponderance" of evidence is unclear. Perhaps all comparable through-Delta survival estimates, from all years, should be tabulated and presented with key environmental conditions (barrier presence, flows, tagging method, etc.), to reveal the true variation in survival estimates and possible reasons for that variation.

There were several reasons one could reasonably speculate that the effects of the HORB were detrimental to survival of smolts. Given that the VAMP acoustic tag study results have indicated that Chinook smolt survival through the Delta is substantially greater when smolts are transported to Chipps Island from the CVP holding tank, routing smolts via the shortest river segments to the holding tank would seem the best option for protecting out-migrating salmonid smolts.

The HORB inhibits passage along one of the shortest routes to the holding tanks from the upper San Joaquin watershed. Also, the HORB increases negative Old and Middle River flows and potential opportunities for smolts to become entrained along routes in the southern Delta, where survival is considerably lower.

Also, it has simply been assumed that the HORB does not result in enhanced predation mortality on smolts as was shown to occur with the non-physical barrier tested in previous years. All of the calculations and recalculations of route-specific mortality on acoustic tagged smolts that resulted in increasing the number of entrained smolts required to trigger real-time decisions for adjusting water operations were all based on the assumption that the HORB was not associated with increased mortality from predators or other factors. Lacking evidence to the contrary, it is difficult to conclude that the HORB provided equal or greater protection for smolts.

Finally, even after the triggers for tagged smolts were exceeded, there were frequently substantial lags of several days before pumping operations were reduced. Taken together, it is difficult to conclude that the approach taken in the Spring 2012 operations provided even minimal protection for out-migrating smolts. Negative effects of such

artificial stresses may have even enhanced the higher natural mortality expected in a dry (or critical) water years such as 2012.

Were the weekly adjustments made consistent with the Tech Memo and supported by the available data and information, while providing necessary protections?

Weekly adjustments to operations appeared to be made within the season because the rapid movement of fish into the Delta was unexpected.

Is the overall approach of using acoustically tagged fish to adjust weekly operations scientifically supportable?

It was not clear to the IRP how water operations coordinated on the movement of acoustically tagged fish was protecting the passage of smolts. The study found that fish entrainment into the inner Delta was not related to pumping operations, suggesting that weekly adjustment of operations by fish movement is not scientifically supportable.

Were the scientific indicators (e.g., fish behavior or drivers of habitat conditions) used appropriate for evaluating the effectiveness of the Spring 2012 Delta Operations?

The lack of a relationship between fish movement and particle tracking model results and the lack of relationships between OMR inflows/exports and smolt movement/survival suggest that these were insensitive indicators for evaluating effectiveness of Delta operations on salmonids in Spring 2012.

Were the scientific indicators and methods used for classifying and detecting "smolt-type" vs. "predator-type" tags in real time appropriate for informing the Spring 2012 Delta Operations?

The Joint Stipulation study using acoustic tag did not determine if detected tags represented smolts or predators that had recently consumed tagged smolts. The approach to determining behavior relative to the tidal component may provide some classification regime. The 2012 IRP also noted that estimated survival - even without adjusting for predators (i.e., assuming no predation of observed tags) - was so low that the run may not be sustainable. Thus, although the classification of tag status is important, especially for identifying smolt movement patterns, the results may be of limited value in evaluating the impact of Delta operations on salmon and steelhead.

How well did the particle tracking model predict fish behavior relative to acoustically tagged data?

The acoustic tracking data as analyzed provide little information of fish behavior. However information in the tidal component of the particles may provide an approach to interpreting fish behavior. See Appendix 2 at the end of this report.

What are the most important analyses to complete for the 2012 data set? What scientific methods for analyzing voluminous response data (e.g., tag detections throughout the acoustic receiver array) and treatment conditions data (e.g., magnitude and direction of flow near specific receivers) might be more appropriate for evaluating the effectiveness of the Spring 2012 Delta Operations?

The question assumes that the 2012 data set is sufficiently reliable and contains important information extractable by analysis.

An important analysis is to evaluate survival and routing relative to Delta hydraulics including the mean and tidal flow components on a reach specific basis. See Appendices 2.1 and 2.2.

What scientific indicators and methods used for classifying and detecting "smolt-type" vs. "predator-type" tags in real time might be more appropriate for informing the Spring 2012 Delta Operations?

How to detect smolt-type vs. predator-type behavior is a subset to the larger issue of how tides affect predatory-prey interactions in the river and Delta. See Appendix 2.3 for further discussion.

What adjustments to the particle tracking models, as informed by the acoustically tagged fish studies, might be more effective for predicting fish behavior and informing future acoustic study design?

Information on mean and oscillatory (tidal) components of the flow over reaches and at reach junctions are likely to provide important information predator-prey and migration behavior as influenced by tides. See Appendices 2.3 and 2.4. However, the 2012 IRP reiterates the suggestion of the 2010 OCAP IRP that rather than making adjustments to the PTMs, a behavioral model for how species in the Delta respond to their local environment should be developed from first principles.

How should the experimental design be adjusted in future years to test key habitat drivers of smolt behavior and survival, and support weekly operational decision making?

Behavior-based fish movement modeling is gaining increasing acceptance as a potentially important tool in water and living resource management in the Bay-Delta and Sacramento River. Despite its potential, behavioral modeling is still a relatively new and

developing technology whose optimum future use will depend on decisions made in the near-term. The IRP believes that actions need to be taken soon to help ensure that this technology contributes to future difficult management decisions.

Fish movement modeling and its many possible derivatives such as time-dependent or distant-dependent mortality forecasting should be considered in its broadest context. A useful way to understand fish movement modeling is to relate it to Computational Fluid Dynamics (CFD) modeling. CFD modeling is used to develop a virtual representation of a flow field which is then input to mathematical algorithms that attempt to capture sensory acquisition, sensory processing, and cognition.

Time varying, multi-dimensional CFD codes may be many thousands of lines long so that their connection to a behavioral model may be difficult and time-consuming. It is important for the region to formulate and address the strategic questions inherent in using fish movement models to address the many pressing questions faced by the region. Poor decisions made without fully understanding either the full range of possible modeling approaches, or before the full range of tentative uses are identified, can result in future performance or application challenges.

An effective way of addressing this would be through a series of technology workshops in which uncertainties in the optimum development and application of fish movement models can be identified and discussed. These workshops should include experts in fish movement modeling at different scales, fish tagging experts to answer questions about collection, calibration and validation of data, CFD modelers to answer questions concerning optimum hydraulic modeling, regional living resource experts to identify and refine potential applications, and living resource managers to describe important management questions that must be addressed. Each workshop should produce a guidance document that can be used to strategically develop behavioral modeling with specific application to the Bay-Delta watersheds.

The results of tagging studies to date (through the 2012 study), show little correlation between operations and fish movement, and so do not currently support using salmon to manage operations on a weekly basis. In Appendices 2.1 to 2.4 the IRP presents hypotheses on how migration and survival may be influenced by tidal oscillations in the river and Delta. If ongoing or future research identifies significant mechanisms affecting fish on tidal cycles, then managers might consider adjusting Delta operations on this scale. However, considerable work will be required to evaluate this hypothesis, and if supported, to design a tidally-based management program.

The 2012 IRP also raises the question of whether salmon populations are sustainable in the San Joaquin River (Appendix 2.5). While the IRP realizes that the Biological Opinion for the operations of the SWP and CVP is not charged with addressing the viability of the run, the IRP believes the question eventually needs to be addressed in this or another process.

5) **How should multi-year data sets on NMFS' Long-term Operations Opinion RPA Action implementation be used to improve future implementation of the Clear Creek RPA Actions?**

The hydrologic system that is used to control the flow of water in Clear Creek below Whiskeytown reservior is extremely complex, involving 3 reservoirs two tunnels, flow and temperature demands in the Trinity, Sacramento Rivers and power production for the City of Redding. In addition, water management in this river system must contribute to meething the co-equal goals of providing a reliable supply of water for human needs and provide for healthy ecosystem functioning. Componding the physical complexity is the high level of interagency involvement, communication and data sharing required to operate the system at peak potential. Moreover, decisions need to be made based on forecasting water supply months ahead of time.

Because of this complexity in system structure, opertational demands and interannual climate variation, it would be useful to develop an expert decision system to assist in making operational decisions on how water is routed through the system

Existing physical water routing models based on Computational Fluid Dynamics (CFD) could be developed in such a way as to link the hydrologic system of reservoirs, tunnels and river outflows to climate modeling and prediction output. This would allow for better strategic planning and action rather than relying primarily on reactive operation. One suggestion is to seek the input of an expert in this type of modeling to help guide an initial phase of investigation into models and feasibility.

A major problem addressed by the 2011 OCAP IRP (Anderson et al. 2011) was the need to enhance communication and data sharing through a common web-based clearing house along with easily accessible monitoring data to assess and ensure regulatory compliance. This same message has been voiced by all agencies, consultants, participipating scienctists, academic institutions and other review panels (Lave et al. 2005.). However, no progress in this direction seems to have been made. What is needed is a web-based collaboration tool that can buid multidisciplinary collaboration, centralize data and information, including development of robust yet easy to use search and display tools, that communicate complex information from large-scale modeling results and network sensors in a way that allows various stakeholders to view

decisions and their effects. These tools exist and can be applied to resolve not only issues related to Clear Creek but the whole Central Valley system.

The IRP suggests that the Delta Science Program could facilitate a workshop where industry and academic leaders in this field can present their approaches and potential solutions to the agency partners. Perhaps the Clear Creek working group could provide a test bed model to start building such a web-based collaboration tool.

Another significant need for the Clear Creek group and restoration effort is that of an independent synthesis of all the restoration work and systems management to date. There has been 16 years of restoration effort in Clear Creek below Whiskeytown reservoir without an apparent synoptic review of that work. Instead, the CCTT continues to emphasize perpetual spawning gravel augmentation and changes to the timing and magnitude of reservoir releases without an objective assessment of what has been accomplished to date.

Temperature control in Clear Creek is directly related to the manner in which water flow is managed within the Trinity-Whiskeytown reservoir complex. A temperature control curtain has been replaced in Whiskeytown reservoir near the Spring Creek Tunnel intake and is expected to force more cold water toward that outflow. However, there has not been any data to corroborate that assumption. It is not known how this repair action has or could impact temperature control actions in Clear Creek through operation of the upper and lower intake gates at the Glory Hole intake tower. However, water temperature measured at the Whiskeytown outflow while water intake was shifted between the upper and lower intakes indicates that changes in water temperature outflow can be achieved (Figs. 6 and 16 of the CCTT 2012 report). Indeed, even a mix of water (refered to as middle gate) from both intakes shows an immediate change in water temperature that brackets the entire temperature regime from May to November measured over the past 12 years (Fig. 16, CCTT 2012 report). This suggests that water temperatures in Clear Creek can be controlled to benefit spring-run Chinook and steelhead, but it remains to be seen how far downriver temperature reductions can be maintained.

What is not clear from the CCTT 2012 report is how to assess the potential to achieve this in different water years and whether cooler temperatures in Clear Creek can be extended below the Igo gauging station throughout the summer.

Two planned pulsed flows of 400 cfs and 800 cfs from Whiskeytown reservoir were released in May and June of 2012 with the intent of attracting spring-run Chinook salmon into the upper reaches above Igo. Snorkel data conducted before and after the

pulsed flows showed that Chinook salmon moved upstream but it was unclear that they did so in response to the pulsed flows. Reaching such a conclusion would require comparable snorkel surveys without pulsed flows, which could not be done simultaneously.

The 2012 LOO IRP reiterates the suggestion of the 2011 OCAP IRP that if pulsed flows are going to be released they should follow a more gradual rising limb with a longer smooth falling limb.

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APPENDIX 1 – Materials for IRP Review

Review Materials Available to the 2012 LOO Independent Review Panel

I. The following documents were provided in electronic format as required reading by the IRP prior to the 2-day workshop in Sacramento, CA on 31 October -1 November 2012:

1) Draft 2012 Clear Creek Technical Team Report for the Coordinated Long-Term Operation BiOp Integrated Annual Review

2) Spring 2012 Delta Operations in lieu of NMFS' RPA Action IV.2.1 per joint stipulation
    - Appendix A: Joint stipulation
    - Appendix B: RPA Action IV.2.1
    - Appendix C: Summary of expected benefits from alternative operations
    - Appendix D: NMFS Technical Memorandum issued March 16, 2012
    - Appendix E: Tabular summary of Spring 2012 operations and cumulative tag detection data
    - Appendix F: NMFS Determination for Operations per Joint Stipulation During April 1-7, 2012
    - Appendix G: NMFS Determination for Operations per Joint Stipulation During April 8-14, 2012
    - Appendix H: NMFS Determination on April 12, 2012
    - Appendix I: NMFS Determination on April 27, 2012
    - Appendix J: NMFS Determination on May 4, 2012
    - Appendix K: NMFS determination on May 11, 2012
    - Appendix L: Water supply impacts of operations under Joint Stipulation relative to RPA Action
    - Head of Old River Barrier and survival exploration tool

3) Preliminary Report (Phase 1 Analyses) for the 2012 Acoustic Telemetry Stipulation Study

II. The following additional reports were made available in electronic format for supplemental use in providing historical context for the IRP:

- Smelt Working Group (SWG) Annual Report on the Implementation of the Delta Smelt Biological Opinion on the Coordinated Operations of the Central Valley Project and State Water Project ("OCAP" Biological Opinion) Water Year 2012
- Sacramento River Temperature Task Group (SRTTG) Annual Report of Activities
- American River Group (ARG) Annual Report of Activities

- Stanislaus Operations Group (SOG) Annual Report of Activities
- Delta Operations for Salmonids and Sturgeon Group (DOSS) Annual Report of Activities
- Report of the 2011 Independent Review Panel (IRP) on the Implementation of Reasonable and Prudent Alternative (RPA) Action Affecting the Operations Criteria And Plan (OCAP) for State/Federal Water Operations (December 9, 2011)
- Federal Agencies' Detailed Response to the 2011 Independent Review Panel's Report (June 20, 2012)
- Report of the 2010 Independent Review Panel (IRP) on the Reasonable and Prudent Alternative (RPA) Actions Affecting the Operations Criteria and Plan (OCAP) for the State/Federal Water Operations
- Joint Department of Commerce and Department of the Interior Response to the Independent Review Panel's (IRP) 2010 Report of the Reasonable and Prudent Alternative (RPA) Actions Affecting the Operations Criteria and Plan (OCAP) for the State/Federal Water Operations
- NMFS' 2009 RPA with 2011 amendments
- USFWS Biological Opinion on the Long-Term Operational Criteria and Plan (OCAP) for coordination of the Central Valley Project and State Water Project (pages 279-282 and 329-356)
- RPA Summary Matrix of the NMFS and USFWS Long-term Operations Opinions RPAs
- National Academy of Science's March 19, 2010, report
- VAMP peer review report
- State Water Board's Delta Flows Recommendations Report
- NMFS RPA, Appendix 2-B, Task 4: Green Sturgeon Research
- 2011 OCAP Review Materials, Background Information and Presentations (http://deltacouncil.ca.gov/science-program/2011-ocap-review-materials-background-information-and-presentations)
- 2010 OCAP Annual Review Materials and Presentations (http://deltacouncil.ca.gov/events/science-program-workshop/workshop-ocap-integrated-annual-review)

APPENDIX 2 – Framework for Addressing Salmonid Issues

Framework for addressing effect of Old and Middle River flows on reach-scale survival rate

A2.1: XT Survival Model

The current paradigm for characterizing movement of smolts through the Delta reaches relies on mean flow to characterize the movement and routing of fish. The tagging studies in 2012 and earlier years clearly indicate that this characterization is inadequate. Below is a mechanistic approach to consider smolt movement, routing and survival through the Delta in terms of the dynamics of encounters of predators and smolts as based on the XT survival model (Anderson et al. 2005).

The underlying equation characterizes survival in terms of both the distance traveled *x* and the time *t* to travel through a reach. The concept is that if smolt (prey) mortality over a distance is the result of predators then survival depends on both the mean travel time and the relative random velocity between the predator and smolt. Survival is

$$S = \exp\left(-\frac{x}{\lambda}\sqrt{1+\left(\frac{\omega}{U}\right)^2} \right) \tag{1}$$

where ω is the root mean-squared (rms) random component of velocity of the predator relative to the smolt, *U* is the mean velocity of the smolt through a river reach and *x* is the reach distance. The final term λ is the mean free-path length a smolt travels before a predation event and is defined

$$\lambda = \frac{1}{\pi r^2 \rho} \tag{2}$$

where ρ is the predator density per unit volume, and *r* is the predator-smolt interaction distance that on the average results in a predation event. The interaction distance *r* depends on the visual field of the predator and therefore depends on light levels and turbidity.

Because in Equation (1) survival depends on the ratio of two velocities to understand what controls survival, an understanding of the velocities is important. To illustrate their nature assume that the predators are territorial while smolts move with the water and exhibit selective tidal-stream transport (discussed in A2.2). Then the random predator-

prey velocity ω is essentially the mean tidal velocity and the smolt velocity *U* is the reach length divided by the smolt's mean travel time through the reach. When $U/\omega > 1$, the mean smolt velocity is large compared to the tidal velocity so a predator gets only one chance at a passing smolt. However, when $U/\omega < 1$ the tidal velocity is larger than the mean smolt velocity and the tidal flow can bring the smolt into the predator's territory multiple times.

Figure A2.1 illustrates how smolt velocity and tides interact. Based on Equation (1), *x* and λ are constant for a reach so the shape of the survival curve depends only on U/ω. When U/ω is large, survival approaches its maximum value $S_{\max} = \exp(-x/\lambda)$ which depends only on reach distance, predator density and the capture distance, but not on either the smolt velocity or the tidal velocity. When U/ω drops below 1, (i.e., the tides become important) survival precipitously declines. Note that in total smolt survival depends on five variables, not simply smolt mean velocity. Furthermore, survival does not directly relate to particle velocity *V.* In other words, smolt velocity is only one of five variables affecting survival and the impact of particle movement on smolt survival is ambiguous.

The current operation schemes focus on controlling particle travel time which is controlled through project exports, the E/I ratio, and OMR flow. The 2012 stipulation study examined the survival and movement of acoustically-tagged steelhead in relation to project exports and OMR flows. The study demonstrated that under the conditions examined, fish travel time was not related to particle movement nor was route selection of the fish related to Delta operations. While the study to manage Delta operations considered smolt survival, with its focus on fish travel time, it did not consider other factors that control survival through reaches. In particular, smolt survival depends on the relative predator-smolt encounter velocities, as outlined above, and routing. Below we consider factors that determine fish migration velocity (Appendix 2.2), predator-smolt encounter velocities (Appendix 2.3) and fish routing (Appendix 2.4).

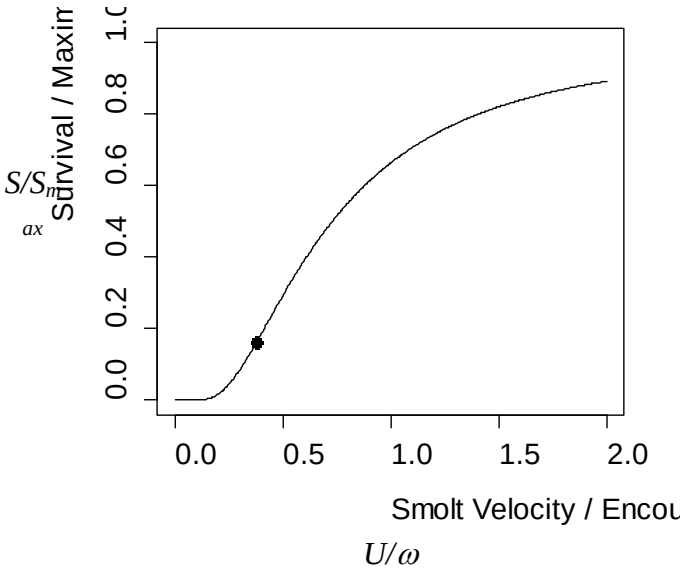

Figure A2.1. Relative reach survival depends on the ratio of the mean smolt migration velocity U to the relative predator encounter velocity ω. Maximum survival S_{max} depends on reach length x and mean free-path length before a predator encounter λ . Estimate of relative survival of fall Chinook from San Joaquin River to Chipps Island denoted by (●).

A2.2: Selective Tidal-Stream Transport (STST)

The stipulation study using acoustically tagged steelhead smolts clearly demonstrated particle and fish movements were poorly correlated. For example, calculated with hydraulic models, particles take 20 to 40 days to move through the Delta while observations on fish passage time are typically 10 days and can be less (Figure A2.2). It is well known that fish and zooplankton perform vertical migrations over the tidal cycle to remain in the Delta (e.g., Bennett et al. 2002, Kimmerer et al. 2002). Additionally many fish species (Gibson 2003), including salmon smolts (Moore et al. 1995) exhibit selective tidal-stream transport (STST) during migration. Here we illustrate the feasibility that salmon and steelhead smolts use STST to move quickly through the Delta.

> In selective tidal-stream transport (STST) an animal moves in and out of low velocity regions of the water column on selective parts of the tidal cycle to facilitate upstream or downstream movement. To speed downstream migration salmon smolts move into the higher velocity surface layer on ebb tides and lower velocity near shore regions on flood tides (Clements et al. 2012).

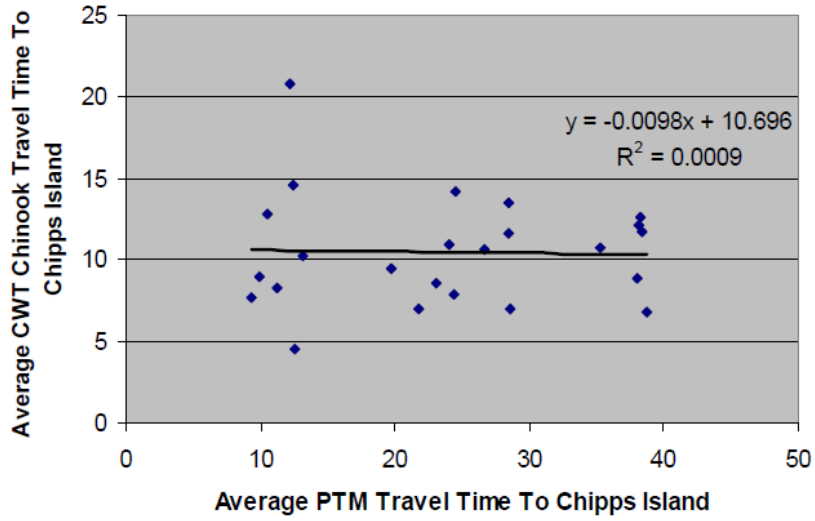

Figure A2.2. Release CWT Chinook salmon in the lower San Joaquin River and the associated Particle Model arrival time to Chipps Island in (LOO Annual Review 2012) Appendix H page H-24).

To demonstrate the feasibility that smolts use STST migrating through the Delta, assume the fish move with the ebb tide and hold in low velocity areas during the flood tide. The resulting across-ground velocity of a smolt can be expressed

$$U = V + \varphi v \qquad (3)$$

where V is the mean particle velocity experienced by the smolt, v is the rms tidal velocity and φ measures the contribution of STST behavior to migration. In the simplest view, φ is a measure of the fraction of the tidal cycle that smolts hide in low velocity regions. If $\varphi = 0.5$ then the smolts effectively hide in low velocity areas during the entire flood tide and drift downstream during the ebb tide. Values less than 0.5 indicate tidal selective movement occurs during only part of flood tide or that the smolts move into low velocity, but not zero-velocity areas on the flood tide. Figure A2.3 illustrates an idealized behavior where a smolt moves into a zero-velocity region during 3 hrs about the peak flood tide. Additionally, if STST is estimated over multiple reaches, φ represents an average of reach properties and behavioral responses.

Thus, Equation (3) hypothesizes that the difference between the observed smolt velocity and the mean particle velocity can be explained by the smolt STST behavior. To evaluate this hypothesis consider the difference in the estimated travel time of particles and CWT smolts traveling from the Lower San Joaquin River to Chipps Island (Figure A2.2) which gives T_{smolt} = 10 d, T_{ptm}= 25 d. Assuming the distance traveled by the smolts is approximately 2 x10^5 ft, then the average fish and particle velocities over the reach are $U = T_{smolt}/x$ = 0.23 ft/s and $V = T_{ptm}/x$ = 0.11 ft/s. Measurements of water

velocity including tidal and mean flow indicate a typical maximum tidal velocity of 1 ft/s (Figure A2.4) which gives a rms tidal velocity of v = 0.7 ft/s. Then arranging Equation (3) to give $\varphi = (U - V)/v$ the STST index is φ = 0.17.

In other words the travel time of fish through the San Joaquin River can be explained by the fish exhibiting a moderate amount of selective tidal-stream transport.

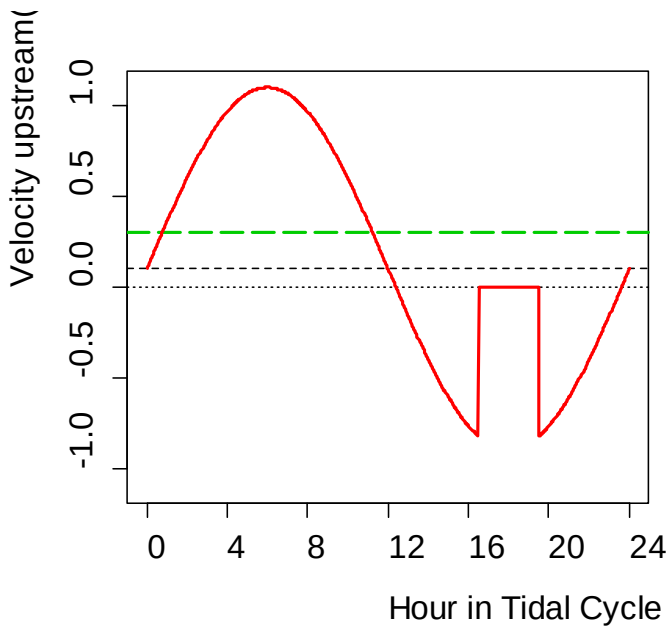

Figure A2.3. Illustration of selective tidal-stream transport. The reach water velocity is composed of a tidal component and residual (- - -) from the mean river flow. Smolt velocity (——) follows the water velocity until upstream velocity exceeds a threshold triggering fish to move into a low velocity area. The average smolt velocity over the tidal cycle (— — —) exceeds the average water velocity (- - - -).

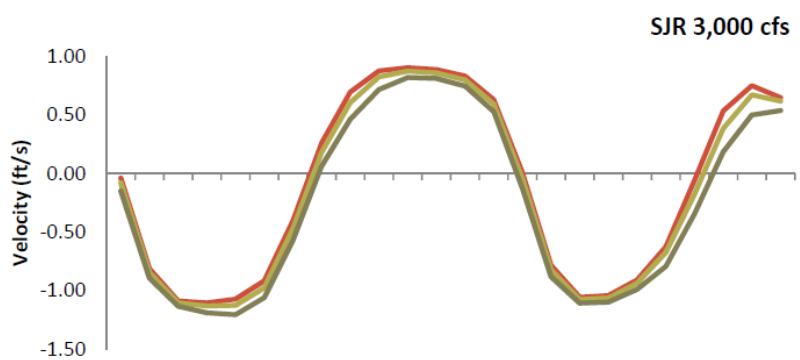

Figure A.2.4. Instantaneous average velocity values across 24 channel segments from the mouth of Middle River to Export facilities. Velocity data for each channel were taken from a single day (May 7, 2007) (LOO Annual Review 92012) Appendix A, page D-50).

Discussion of STST behavior.

The parameter φ quantifies STST behavior over the Delta and the correlation of φ with environmental conditions should provide insight to the mechanisms controlling fish migration behavior. For example, we might hypothesize that fish are able to detect the direction downstream by asymmetric changes in the environmental properties over a tidal cycle. The signal may include asymmetric patterns in the vertical or temporal distributions of turbidity and micro turbulence. For example, turbulence should be highest on the flood tide, possibly triggering movement into a low velocity region. Furthermore, in tidal rivers and estuaries the flood tide may move through progressively smaller cross-sectional areas causing the tidal currents to become progressively more asymmetric in both speed and direction (Wells 1995), which could facilitate detection of the tidal signal. Furthermore, if asymmetry in the channel configuration alters the signal triggering behavior then the complexity of the Delta may result in complex STST behavior. For example, fish moving from the San Joaquin River into Franks Tract may first experience a strong signal of tidal direction but once inside the track where the channel widens the signal may virtually disappear. With heterogeneity in STST signal strength we expect φ to vary over reaches and flow conditions.

Action.

The IRP suggests researchers evaluate the relationships of φ with differing environmental and hydraulic properties of the reaches. As a null hypothesis to the STST behavior, assume fish swim downstream independent of tidal conditions. In this case there would be no correlation of φ with Delta geometry. Note that the null hypothesis is also biologically possible if salmon navigate using the geomagnetic signals that indication location. However, even if fish use geomagnetic navigation they may do so in the context of STST behavior.

A2.3: Predator-Smolt Encounters

Equation (1) proposes that the importance of the downstream velocity of the smolts in determining their migration survival depends on the encounter velocity of the smolts to predators. Furthermore, the probability of encounters and predation events is expected to change over tidal and diel cycles and depend on the avoidance strategy of the smolts and the search strategy of the predators. While numerous studies have documented STST behavior, the panel is unaware of specific studies exploring predator-prey interactions in STST conditions. In a general sense, the smolt STST strategy is to move out of the Delta and avoid predators while the predator STST strategy is to remain in the Delta and encounter prey. Competing predator and prey strategies have been viewed

as a predator-prey shell game that depends on the ability of the predator to adjust its strategy to the temporal flux of prey (Lima 2002). A recent study suggests a type of shell game may occur in Atlantic cod foraging on Atlantic salmon during their post-smolt estuary migration (Hedger et al. 2011). The cod exhibited a more focused foraging distribution during the smolt outmigration, but their distribution was not influenced by the tides, i.e. they held station against the tides. Delta predators may use a similar mechanism. We illustrate the implications of such strategies in the example below that combines the XT survival model and the STST hypothesis.

We begin by defining the random encounter velocity between predator and prey (Anderson et al. 2005) as

$$\omega = \sqrt{u_{smolt}^2 + u_{pred}^2} \tag{4}$$

where u_{smolt} and u_{pred} are the rms random velocities of smolts and predators respectively. With STST behavior, relating smolt rms random velocity to acoustic tag observations may be problematic since in the model part of the tidally-correlated movement of the smolts is attributed to the mean movement. However, approximations of the rms random velocities can be developed based on assumptions of the behavior of predators and smolts. Assume that predators hold station during the ebb tide such that smolts pass through a gauntlet of predators, while on the flood tide the smolts are stationary and the predators move with the flow searching for prey. Assume the combined effect of these two strategies depends on STST behavior and the rms tidal velocity, which we take as a surrogate for the random search velocity of the predators. Then, the random predator-smolt encounter velocity might be expressed $\omega = (1-\varphi)v$ and the ratio of mean smolt migration velocity to the predator-smolt random encounter velocity is

$$\frac{U}{\omega} = \left(\frac{V}{v} + \varphi\right) \Big/ \left(1-\varphi\right) \tag{5}$$

Using the example for travel time of CWT Chinook from the lower San Joaquin River to Chipps Island gives $U/\omega = 0.38$.. Including Equation (5) in Equation (1), survival over the reach is on the order of 16% of the maximum survival, S_{max} (Figure A2.1). If the maximum observed survival through the Delta is on the order of S_{max} = 20% then survival should be 3%, which is about what was observed in 2012.

The salient point is the XT predation model and selective tidal transport hypothesis together provide a mechanistic explanation for both the observed rapid movement and low survival of smolts in the Delta.

If smolts and predators exhibit distinct behavioral patterns relative to the direction and velocity of the water currents over tidal cycles then classification of smolt and predatory-type tags may require correlations of tag movement with the proximal water velocities. Distinct behavior patterns may be most evident on peak flow or slack water periods.

Action.

Much information is known about the behavior of organisms on tidal oscillations, but little is known about the effects of tidal oscillations on predator-prey interactions. The panel suggests that prior to additional field work in this area a workshop be held bringing experts together on tidal physics, foraging ecology and predator-prey theory. The panel suggests a mix of local, national and international experts comprise the workshop membership.

A2.4: Fish Routing

The 2012 joint stipulation study found that movement into the inner Delta appeared independent of the OMR flow which suggests that route selection is influenced by proximal conditions at the junctions of the channels. We hypothesize that routing is determined mainly by the response of the fish to the flow field as structured by the channel shape and the flow, which is comprised of the pure tidal flow and the residual flow generated by river flow and pump operations. Thus, it is reasonable to hypothesize that the behavioral factors that produce STST are also important in route selection at reach junctions.

The IRP proposes studying route selection at two spatial-temporal scales: a *reach scale* involving the asymmetric patterns of hydrodynamics of the tidal cycle and a *junction scale* that considers the flow structure over the scales directly perceived by fish during the passage through junctions. Frameworks for studying entrainment at reach and junction scales need to be based on working hypotheses of how hydraulic and behavioral factors interact to determine routing. Examples of reach and junction scale hypotheses are briefly outlined below. These are not intended to be complete or necessarily correct; their purpose is to illustrate general approaches and levels of detail that may be needed in designing analyses and frameworks at each scale. The panel encourages this two-pronged approach as a way to derive a working understanding of fish routing mechanisms while developing analysis that can draw on the existing, coarser scale data available through CWT and the finer scale acoustic tagging studies. As an aside, the panel suggests that mechanisms of STST and route selection in salmon will also have value for understanding the movement of resident Delta fish such as delta smelt and longfin smelt.

Reach scale analysis framework.

As an example of a reach scale routing hypothesis begin with the assumption that if smolt STST occurs in reaches it also occurs in junctions. Based on the STST hypothesis detailed in Appendix 2.2 smolts exhibit asymmetric behavior to selectively move downstream by moving into low velocity regions when triggered by signals indicating a flood tide. Note also, that reversal of OMR flows may disrupt and confuse this signal. The strength of the STST should be reach specific and might be quantified by φ (Equation 2) characterizing the fraction of a tidal cycle over which fish seek lower velocity regions. For a working hypothesis, assume that routing at a reach junction depends on the reach-specific φ, the junction hydrodynamic *v*, and the junction geometry, expressed here as cross-sectional area *A* (Figure A2.5). Then an equation expressing the fraction *f* of fish routed through reach 1 might be written

$$f_1 = \frac{\varphi_1 v_1 A_1}{\varphi_1 v_1 A_1 + \varphi_2 v_2 A_2} \qquad (6)$$

and fraction passing through reach 2 becomes $f_2 = 1 - f_1$. The important feature of this framework is that routing involves three factors, behavioral, hydraulic and geometric properties. The challenge is to formulate measures that are mechanistically meaningful and measurable. Three trial hypotheses/analyses (developed in conversation with R. Buchanan) are outlined below:

Hypothesis 1: assume φ_i from reaches Equation (3) applies to Equation (6) and the $\varphi_i A_i$ is the junction volume transport averaged over a tidal cycle.

Hypothesis 2: assume reach-specific φ_i and v_i represent rms velocities.

Hypothesis 3: assume φ_i is junction-specific and must be characterized by correlating fish and water movements with the junction.

Again, these approaches are presented to illustrate an approach for conducting analyses based on underlying transport mechanisms.

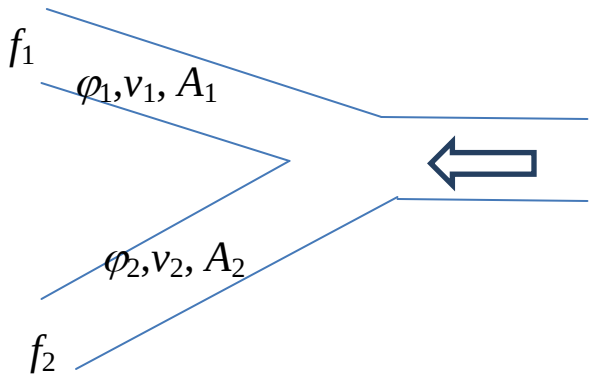

Figure A2.5. Reach routing model based on STST behavior and tidal dynamics.

Junction scale analysis framework.

An alternative, higher resolution, approach is available through the melding of computational fluid dynamics models with models of the rheotactic response of fish. Such studies are being carried out in the Sacramento River by David Smith of the Army Corps of Engineers Cognitive Ecology and Ecohydraulics Research group el.erdc.usace.army.mil/emrrp/nfs/index.html. A description of ecohydraulics to study fish routing derived from the research groups follows:

> The Eulerian–Lagrangian–agent Method (ELAM) provides a framework to analyze fish habitat occupancy as a function of environmental change. We create a 'virtual reality' of the environment and then analyze/forecast habitat occupancy as a function of discharge, channel morphology, habitat complexity, and water quality using a fish habitat selection algorithm coupled to a particle–tracking model (PTM). We model the cognition, adaptation, and learning of fishes along with their physiological sensory capabilities instead of using habitat suitability criteria or reach–scale habitat classification (e.g., pool, riffle, run, shear zone, etc). Reach–scale habitat occupancy patterns are resolved from responses to physical and chemical stimulus at the microhabitat scale. Thus, we can forecast fish response to changes in river channel morphology derived from hydrographic manipulation or construction of engineered structures. Traditional habitat suitability criteria and reach–scale habitat classifications limit flexibility and the level of fidelity that can be used in analysis of a restoration project. The ELAM approach is a "plug–and–play" tool that supports management decisions in a theoretically– and mathematically–rigorous manner (el.erdc.usace.army.mil/emrrp/nfs/fishhabitat.html).

For further discussion, see the response to question “How should the experimental design be adjusted in future years to test key habitat drivers of smolt behavior and survival, and support weekly operational decision making?”

A2.5: Is the San Joaquin River a salmon sink?

The low Delta passage survival of fall-run Chinook and steelhead on the order of 1-3%, begs the question as to whether the San Joaquin River can support salmon populations in the future or whether it is a sink habitat receiving adult Chinook from other Central Valley rivers. The high stray rate of the hatchery raised fall Chinook (e.g., Mesick 2001) may suggest natural production in the system is not being maintained or will not be in the future with increased Central Valley warming by climate change. The IRP recommends that this possibility be consider through an analysis of source-sink population dynamics of the Sacramento/San Joaquin populations.

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Abstract:
The delta smelt (*Hypomesus transpacificus*) is a small and relatively obscure fish that has recently risen to become a major focus of environmental concern in California. It was formally abundant in the low-salinity and freshwater habitats of the northeastern San Francisco Estuary, but is now listed as threatened under the Federal and California State Endangered Species Acts. In the decade following the listings scientific understanding has increased substantially, yet several key aspects of its biology and ecological relationships within the highly urbanized estuary remain uncertain. A key area of controversy centers on impacts to delta smelt associated with exporting large volumes of freshwater from the estuary to supply California's significant agricultural and urban water demands. The lack of appropriate data, however, impedes efforts to resolve these issues and develop sound management and restoration alternatives.

Delta smelt has an unusual life history strategy relative to many fishes. Some aspects of its biology are similar to other coastal fishes, particularly salmonids. Smelts in the genus, *Hypomesus*, occur throughout the Pacific Rim, have variable life history strategies, and are able to adapt rapidly to local environments. By comparison, delta smelt has a tiny geographic range being confined to a thin margin of low salinity habitat in the estuary. It primarily lives only a year, has relatively

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low fecundity, and pelagic larvae; life history attributes that are unusual when compared with many fishes worldwide. A small proportion of delta smelt lives two years. These individuals are relatively highly fecund but are so few in number that their reproductive contribution only may be of benefit to the population after years of extremely poor spawning success and survival. Provisioning of reproductive effort by these older fish may reflect a bet-hedging tactic to insure population persistence.

Overall, the population persists by maximizing growth, survival, and reproductive success on an annual basis despite an array of limiting factors that can occur at specific times and locations. Variability in spawning success and larval survival is induced by climate and other environmental and anthropogenic factors that operate between winter and mid-summer. However, spawning microhabitats with egg deposition have not been discovered. Spawning success appears to be timed to lunar periods within a water temperature range of about 15 to 20°C. Longer spawning seasons in cooler years can produce more cohorts and on average higher numbers of adult delta smelt. Cohorts spaced in time have different probabilities of encountering various sources of mortality, including entrainment in freshwater export operations, pulses of toxic pesticides, food shortages and predation by exotic species. Density dependence may provide an upper limit on the numbers of juvenile delta smelt surviving to the adult stage. This may occur during late summer in years when juvenile abundance is high relative to habitat carrying capacity. Factors defining the carrying capacity for juvenile delta smelt are unknown, but may include a shrinking volume of physically suitable habitat combined with a high density of competing planktivorous fishes during late summer and fall.

Understanding the relative importance of anthropogenic effects on the population can be improved through better estimates of abundance and measurements of potentially limiting processes. There is little information on losses of larval delta smelt (less than 20 mm fork length, FL) to the export facilities. Use of a population model suggests that water export operations can impact the abundance of post-larval (about 20 mm FL) delta smelt, but these effects may not reflect on adult abundance due to other processes operating in the intervening period. Effects from changes to the estuarine food web by exotic species and toxic chemicals occur but measuring their influence on population abundance is difficult.

Although delta smelt recently performed well enough to meet the current restoration criteria, analyses presented here suggest that there is still a high probability that the population will decline in the near future; the most recent abundance index (2004) is the lowest on record. Overall, the limited distribution, short life span and low reproductive capacity, as well as relatively strict physical and feeding requirements, are indications that delta smelt is at risk to catastrophe in a fluctuating environment. Unfortunately, options for avoiding potential declines through management and restoration are currently limited by large gaps in knowledge. Monitoring of spring water temperatures, however, may provide a useful tool for determining when to reduce entrainment in water export facilities. Actions that target carrying capacity may ultimately provide the most benefit, but it is not clear how that can be achieved given the current state of knowledge, and the limited tools available for restoration. Overall, a better understanding of the life history, habitat requirements, and limiting factors will be essential for developing tools for management and restoration. Therefore, given the implications for managing California water supply and the current state of population abundance, a good investment would be to fill the critical data gaps outlined here through a comprehensive program of research.

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Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California

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ABSTRACT

The delta smelt (*Hypomesus transpacificus*) is a small and relatively obscure fish that has recently risen to become a major focus of environmental concern in California. It was formally abundant in the low-salinity and freshwater habitats of the northeastern San Francisco Estuary, but is now listed as threatened under the Federal and California State Endangered Species Acts. In the decade following the listings scientific understanding has increased substantially, yet several key aspects of its biology and ecological relationships within the highly urbanized estuary remain uncertain. A key area of controversy centers on impacts to delta smelt associated with exporting large volumes of freshwater from the estuary to supply California's significant agricultural and urban water demands. The lack of appropriate data, however, impedes efforts to resolve these issues and develop sound management and restoration alternatives.

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Overall, the population persists by maximizing growth, survival, and reproductive success on an annual basis despite an array of limiting factors that can occur at specific times and locations. Variability in spawning success and larval survival is induced by climate and other environmental and anthropogenic factors that operate between winter and mid-summer. However, spawning microhabitats with egg deposition have not been discovered. Spawning success appears to be timed to lunar periods within a water temperature range of about 15 to 20°C. Longer spawning seasons in cooler years can produce more cohorts and on average higher numbers of adult delta smelt. Cohorts spaced in time have different probabilities of encountering various sources of mortality, including entrainment in freshwater export operations, pulses of toxic pesticides, food shortages and predation by exotic species. Density dependence may provide an upper limit on the numbers of juvenile delta smelt surviving to the adult stage. This may occur during late summer in years when juvenile abundance is high relative to habitat carrying capacity. Factors defining the carrying capacity for juvenile delta smelt are unknown, but may include a shrinking volume of physically suitable habitat combined with a high density of competing planktivorous fishes during late summer and fall.

Understanding the relative importance of anthropogenic effects on the population can be improved through better estimates of abundance and measurements of potentially limiting processes. There is little information on losses of larval delta smelt (<20 mm fork length, FL) to the export facilities. Use of a population model suggests that water export operations can impact the abundance of post-larval (about 20 mm FL) delta smelt, but these effects may not reflect on adult abundance due to other processes operating in the intervening period. Effects from changes to the estuarine food web by exotic species and toxic chemicals occur but measuring their influence on population abundance is difficult.

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KEYWORDS

San Francisco Estuary, California, endangered fishes, *Hypomesus*, fish ecology, life history strategies, ecotoxicology, water management, non-native invasive species, stage-structured population models, population viability analysis

INTRODUCTION

The delta smelt (*Hypomesus transpacificus*) is currently at the forefront of environmental concern in California. It is a small (typically <80 mm fork length) translucent fish with a steel-blue lateral stripe and a pleasant cucumber-like aroma. Delta smelt have a small geographic range, being endemic to the low-salinity and freshwater habitats of the northeastern San Francisco Estuary (SFE, Figure 1). Formerly abundant (see Tables 17-19 in Erkkila 1950; Radtke 1966), delta smelt were harvested commercially with other smelt (Osmeridae) and silverside (Atherinidae) species during the 19th and early 20th centuries in a prosperous “smelt” fishery (Skinner 1962; Sweetnam and others 2001). In the early 1980s, however, abundance declined dramatically resulting in its listing as threatened under the Federal and California State Endangered Species Acts (ESA) in 1993 (Federal Register 1993, Appendix A-1 Sweetnam and Stevens 1993). The decline in delta smelt abundance is generally attributed to the highly urbanized state of the SFE, although the underlying causes currently remain a mystery. Of the many human alterations to the ecosystem, a conspicuous feature is an elaborate system of dams, pumping facilities, and aqueducts that transfer large quantities of fresh water from the Central Valley watershed and estuary to supply California’s valuable agriculture and growing human population (Nichols and others 1986; Arthur and others 1996; Moyle and others 1992). Since the ESA listings protective measures to reduce losses of delta smelt in diverted freshwater have raised substantial controversy because they can have a major influence on how water is managed and allocated throughout California.

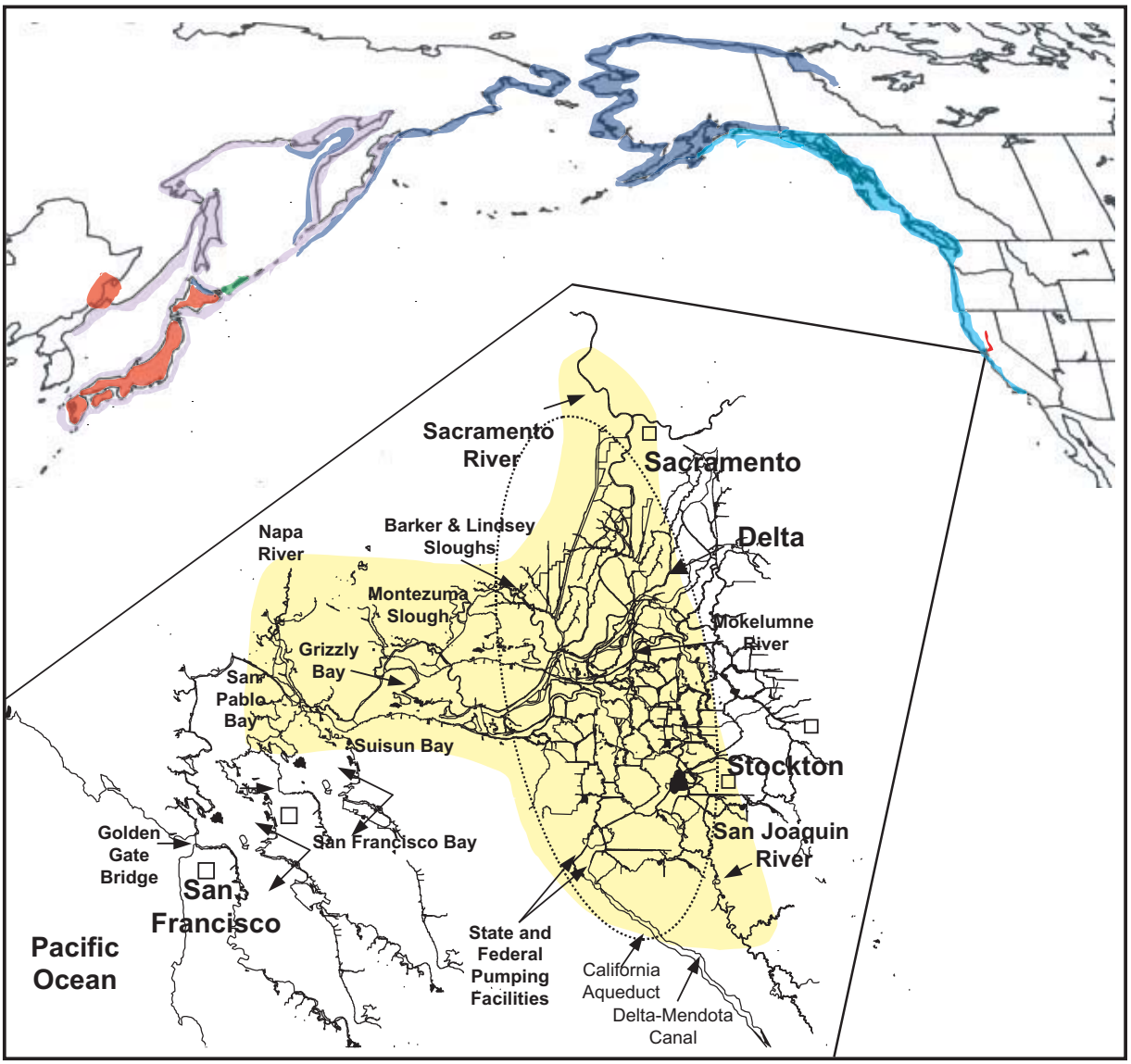

Figure 1. Known distribution of *Hypomesus* throughout the Pacific Rim. Six species are currently recognized including wakasagi (*H. nipponensus*, red shading), chishima wakasagi or Kunashir smelt (*H. chishimaensis*, green shading), ishikariwakasagi or pond smelt (*H. olidus*, blue shading), chika or silver smelt (*H. japonicus*, purple shading), and surf smelt (*H. pretiosus*, cyan shading). Inset displays the distribution of delta smelt (*H. transpacificus*, yellow shading) and the Delta (dotted oval) in the San Francisco Estuary.

New information on delta smelt has increased substantially since the ESA listing. Aspects of their biology and ecology were first compiled by Moyle (1976; Moyle and others 1992) and then by the resource management agencies (Stevens and others 1990; Sweetnam and Stevens 1993; DWR–USBR 1993; Sweetnam 1999). Since then much has been learned about delta smelt biology and ecology, prompting the need for

comprehensive synthesis. Even with this new information, three fundamental questions remain:

1. Should the species continue to be listed under the ESA, or, what is the probability of extinction?

2. What is the impact of human activities, particularly water export operations, on population abundance?

3. Are there potential avenues for restoration and recovery?

My primary objective is to review and synthesize what is known about delta smelt, and to provide an ecological foundation for addressing the above questions. However, little is known and published about delta smelt relative to other fishes in the SFE. As a result, I rely heavily on grey literature, pre-published results and personal communications, as well as extensive analysis of unpublished data. Synthesis of this information raises a variety of questions and key uncertainties rather than conclusive statements regarding delta smelt ecology. Thus, the current state of knowledge will hopefully evolve rapidly as a result of this work. The paper is organized into sections describing delta smelt biology and natural history, factors influencing annual abundance, and implications for restoration. Finally, major uncertainties impeding progress in answering the above questions are summarized as key issues for future research. Overall, this synthesis indicates that significant advances have been made in understanding delta smelt, however, the current level of this knowledge and research effort is fragmented. Delta smelt is a fish species unique to the SFE. Therefore, to develop a solid understanding of human activities and natural perturbations on the population will require a significant and coordinated research effort to develop fundamental aspects of its population ecology. This knowledge will be essential for future management actions and the development and evaluation of sound restoration alternatives.

Population Abundance

Limited understanding of delta smelt abundance over time remains the most critical obstacle to effective management and restoration. Most of what we know is derived from long-term sampling programs conducted by the Interagency Ecological Program for the San Francisco Estuary (IEP). At least eight such surveys regularly collect delta smelt during routine sampling, providing extremely valuable sources of long-term information. Detailed descriptions and methodology are well described elsewhere (Stevens and others 1990; Herbold and others 1992; Moyle and others 1992; DWR–USBR 1993) and key aspects are shown in Table 1. The surveys vary considerably in sampling methodology, the life stage they collect, spatiotemporal coverage, as well as calculations used to construct indices of abundance (Table 1), but all show a dramatic decline in delta smelt in the early 1980s that eventually prompted the ESA listings (Figure 2). The majority of sampling surveys employ some type of net, however, estimates of fish entrained in water export flows also provide an extensive time series for individuals over about 20 mm in length. Although such “sampling” is fixed at the south Delta export facilities, annual trends in fish entrained also indicate a decline in the population during the early 1980s (Figure 2F). Therefore, trends in the population are well represented by all sampling gears and life stages of delta smelt.

The trustworthiness of the abundance indices is essential for understanding the population ecology and appropriate ESA status of delta smelt. In this review I focus primarily on data from four surveys; the catch data from two are compiled into abundance indices. The Summer Tow-Net Survey (TNS, Figure 2C) samples primarily the juvenile life stage during July and August, whereas the Fall Midwater Trawl Survey (MWT, Figure 2A) collects primarily pre-adults from September through December (Table 1). Although these monitoring programs were initially devised for

Table 1. Key aspects of monitoring surveys that sample delta smelt in the San Francisco Estuary

Survey / Gear Type (Institution[a])	*Year*	*Months (Frequency)*	*Locations (Stations)*	*Life Stages*
Fall Midwater Trawl (MWT, DFG)	1967-present	September–March (monthly)	San Pablo Bay–Delta (53–113)	Juvenile–adult
Summer Tow-Net (TNS, DFG)	1959-present	June–August (bi-weekly)	Suisun Bay–Delta (~30)	Juvenile–adult
20-mm Tow-Net (DFG)	1995-present	March–June (bi-weekly)	Napa River–Delta (~30)	Larvae–juvenile
Spring Kodiak Trawl (DFG)	2002-present	March–May (~bi-weekly)	Suisun Bay–Delta (30–40)	Maturing–spawning
Bay Study Midwater Trawl (DFG)	1980-present	January–December (monthly)	So. San Francisco Bay–Suisun Bay (42)	Juvenile–adult
Otter Trawl (UCD)	1979-present	January–December (monthly)	Suisun Marsh (~18)	Juvenile–adult
SWP / CVP Water Projects (DWR, USBR)	1979-present	January–December (daily)	South Delta near Tracy (2)	20-mm post larvae–adult
Midwater Trawl (USFWS)	1976-present	April–June (~dailly)	Chipps Island (1)	Juvenile–adult
Beach Seine (USFWS)	1977-present	~January–June (~bi-weekly)	Delta–Sacramento River (23)	Juvenile–adult

a. All monitoring surveys are coordinated under the cooperative Interagency Ecological Program (IEP) for the San Francisco Estuary. California Department of Fish and Game (DFG); University of California, Davis (UCD); California Department of Water Resources (DWR); U.S. Bureau of Reclamation (USBR); U.S. Fish and Wildlife Service (USFWS).

sampling young striped bass (*Morone saxatilis*), they provide the most extensive spatiotemporal records for delta smelt. From these surveys, abundance indices are calculated for juveniles (TNS) and pre-adults (MWT) by extrapolating the numbers of fish caught at 30 to 80 fixed stations using a weighting factor that accounts for differences in water volume in various sub-regions from San Pablo Bay through the Delta. Temporally, stations are sampled at roughly bi-weekly intervals throughout the summer and fall months (Table 1). A subset of stations and months sampled in the MWT survey are also used to calculate the Recovery Index: the measure of delta smelt performance used in the original ESA recovery criteria (Figure 2B, Moyle and others 1996). I also examine data from the 20-mm Survey that has been sampling larvae and post-larvae (defined on page 16) during spring (April–June) since 1995, and the Spring Kodiak Trawl survey that has sampled adults during the spawning season (March–June) since 2002. These are the only two surveys designed specifically for sampling delta smelt.

Moderate increases in the Recovery Index from 1998–2002 (Figure 2A, B) were sufficient to satisfy the original recovery criteria (Moyle and others 1996). However, these criteria were developed at a time when little was known about the biology or ecology of delta smelt. Thus, following the apparent recovery, the ESA listing of delta smelt was challenged by stakeholder groups, leading to a formal revision of the Biological Opinion (http://sacramento.fws.gov/ea/news_releases/2004%20News%20Releases/Delta_Smelt_OCAP_NR.htm) undertaken in a collaborative effort by the U.S. Fish and Wildlife Service (USFWS), U.S. Bureau of Reclamation (USBR), NOAA Fisheries Service, California Department of Water

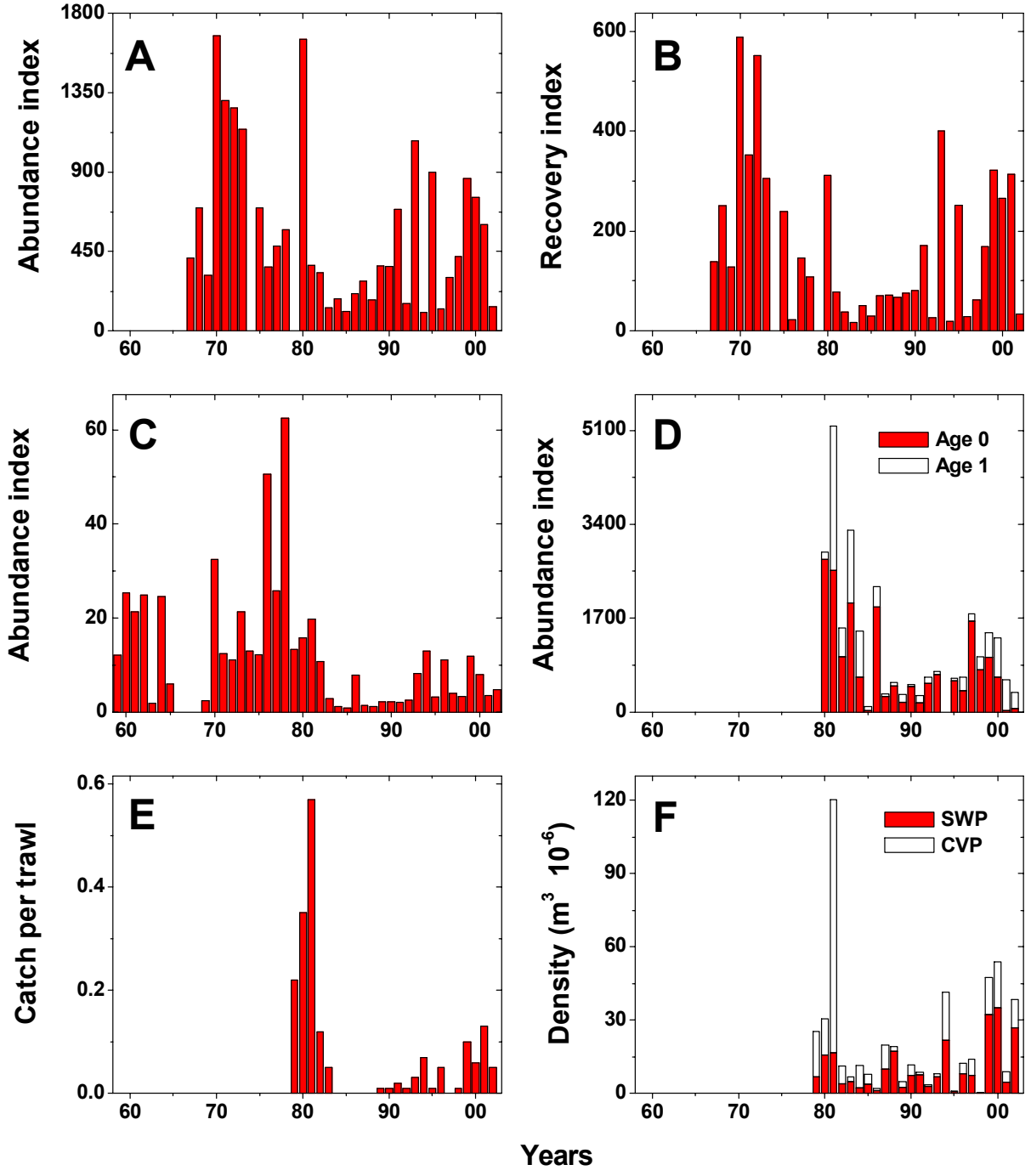

Figure 2. Indices of abundance from five monitoring programs that regularly collect delta smelt including the Fall Midwater Trawl Survey (MWT) (A), the delta smelt Recovery Criteria Index based on a subset of MWT samples (B), the Summer Tow-Net Survey (TNS) (C), the Bay Study Midwater Trawl Survey that collects age-0 and age-1 fish (D), the UC Davis Suisun Marsh Survey (E), and fish entrainment monitoring at the Federal Central Valley Project (CVP) and California State Water Project (SWP) facilities. These and other surveys that intermittently collect delta smelt are summarized in Table 1.

Resources (DWR), and the California Department of Fish and Game (DFG). The opinion concluded that the status of population abundance and poor understanding of limiting factors still justified the listing of delta smelt as a threatened species. During this process the population experienced three consecutive years of low abundance, including the lowest ever recorded in the indices (MWT = 74, in 2004).

Recently, the sampling design, methodology, and calculations used to develop the TNS and MWT abundance indices have been called into serious question by scientists and stakeholders. The fundamental limitation with these abundance indices is that they are dimensionless numbers, thus it is unclear what any particular index means in terms of population abundance. In addition, there is no way to compare among life stages (i.e. TNS and MWT indices) to examine population vital rates (e.g. mortality), or to measure the variation in abundance estimated by each index. Therefore, it is unclear how well one year compares with a previous year. Although these problems have been recognized before, using the indices to reflect abundance has persisted in part because of several logistical problems with applying conventional abundance estimation methodologies to the extremely fragile delta smelt (Herbold 1996).

There is also little confidence in the effectiveness of the sampling gears used in the various surveys. For instance, Kodiak trawls tow a net between two vessels sampling the top half of the water column. They consistently appear to out-fish (in terms of catch per unit volume sampled) the traditional midwater trawls that tow a net directly behind a single craft. However, this knowledge is based on only personal observations, two sampling days, and 12 concurrent samples in September 1994 (Sweetnam 1994). All sampling gear used also have a size-selection bias. In another pilot study, the effectiveness of the standard MWT net (12.7-mm mesh) was examined by covering it with a 3.2-mm mesh net, that retained fish passing through the larger mesh (Sweetnam and Stevens 1993). In August 1991, the standard MWT net was only about 30% effective for delta smelt and 80% for striped bass, whereas in January 1992, effectiveness improved to about 55% for delta smelt and 100% for striped bass presumably because the fishes had grown larger (Sweetnam and Stevens 1993). Although preliminary, the study suggests that estimates of abundance based on catch alone in the MWT would be highly biased, and overall points to considerable uncertainty underlying the effectiveness of sampling gears used for delta smelt. Resolving these biases, however, will require a considerable effort (Miller 2000; Brown and Kimmerer 2002). Nonetheless, developing an abundance estimate and addressing sampling effectiveness will be crucial for improving our understanding of the population status, as well as the limitations on delta smelt abundance.

To address the need for more quantitative abundance estimates and facilitate synthesis of the available information, I estimated delta smelt abundance using the methodology developed by Kimmerer and others (2000, 2001) for young striped bass. Essentially, abundance estimates for delta smelt in the TNS, MWT, and 20-mm (post-larvae) surveys were calculated by dividing the raw catch of delta smelt at each station by the estimated volumes of water sampled, using an overall mean of 865 m^3 for the 20-mm Survey, 700 m^3 for the Summer Tow-Net Survey, and 7,000 m^3 for the Fall Midwater Trawl Survey. These estimates were then weighted by the total volume of the delta smelt habitat including Suisun Bay and the Delta. Volume estimates were compiled using bathymetric information developed by the U.S. Geological Survey (http://sfbay.wr.usgs.gov/access/Bathy/index.html). The “first-order” abundance estimates and 95% confidence limits derived by this method (Figure 3) are based on the unrealistic assumption that delta smelt occupy a constant volume of habitat at different life stages and among years, and do not account for size-selectivity by the sampling gears. However, because they are based on the raw

catch data, annual trends in estimated abundance are highly correlated with the original indices (Figure 4A, B), and with catch per unit effort from the 20-mm Survey over a fewer number of years (Figure 4C, D). Moreover, they offer a promising alternative to the indices by allowing some understanding of sampling variance (Figure 3C, D) and mortality among life stages (see "Water Exports"). Throughout this review, analyses using these first-order abundance estimates are presented alongside those using the original indices.

Current Scientific Understanding

Biology and Natural History

Taxonomy

The life history and ecology of delta smelt can best be appreciated in the broader context of the genus *Hypomesus*. Six species are currently recognized in *Hypomesus* (Saruwatari and others 1997). They are true smelts of the family Osmeridae, an ancient group in the order Salmoniformes. All species have similar morphology and when freshly caught most give off a characteristic fragrance of fresh cucumber (McDowall and others 1993). Saruwatari and others (1997) recently revised the genus based on morphometric characteristics, distinguishing three species groups, as well one new species in the Pacific Rim region (Figure 1).

- ***H. nipponensis* group**: estuarine to freshwater habitat

  1. *H. nipponensis* (wakasagi or icefish). Wakasagi is an estuarine species, yet has been extensively transplanted to freshwater throughout Japan where it supports a prosperous fishery.

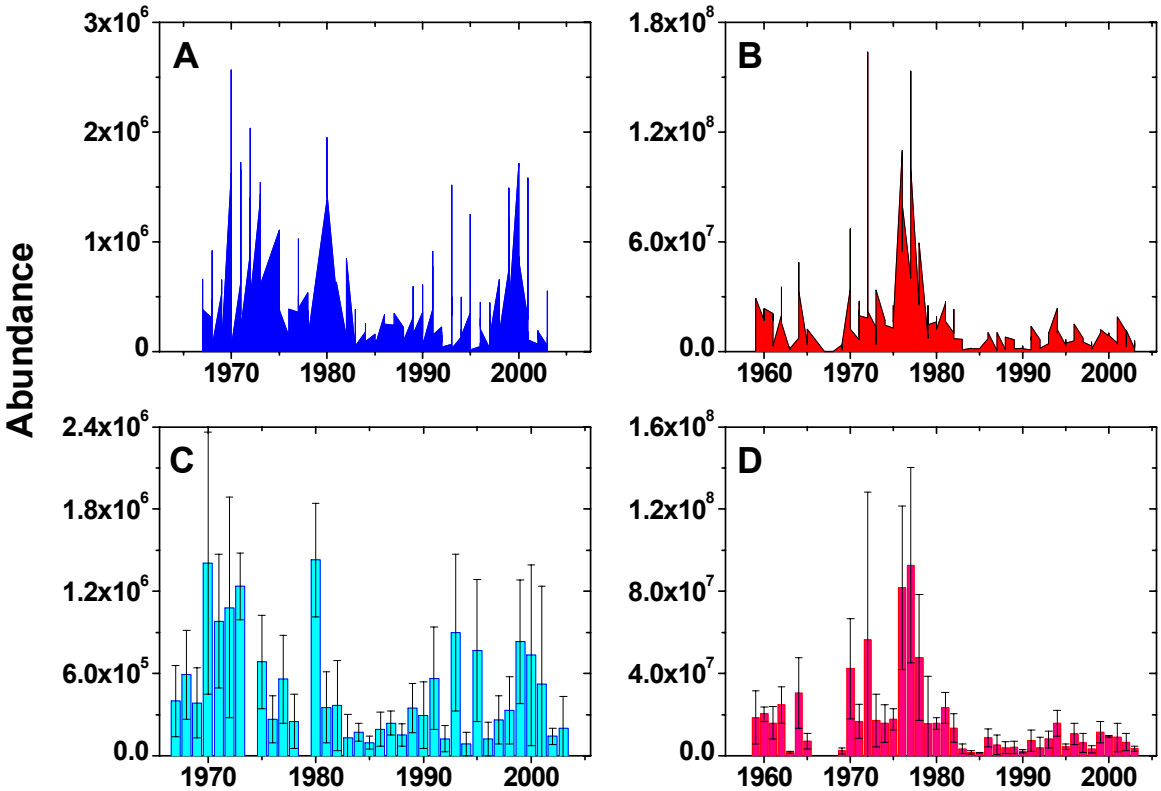

Figure 3. Estimates of abundance derived from catch-per-unit-effort (CPUE) expanded over the volume of the delta smelt habitat for each sampling period in the Fall Midwater Trawl Survey (MWT, A) and Summer Tow-Net Survey (TNS, B). Annual estimates for the MWT (C) and TNS (D) are shown with 95% confidence limits.

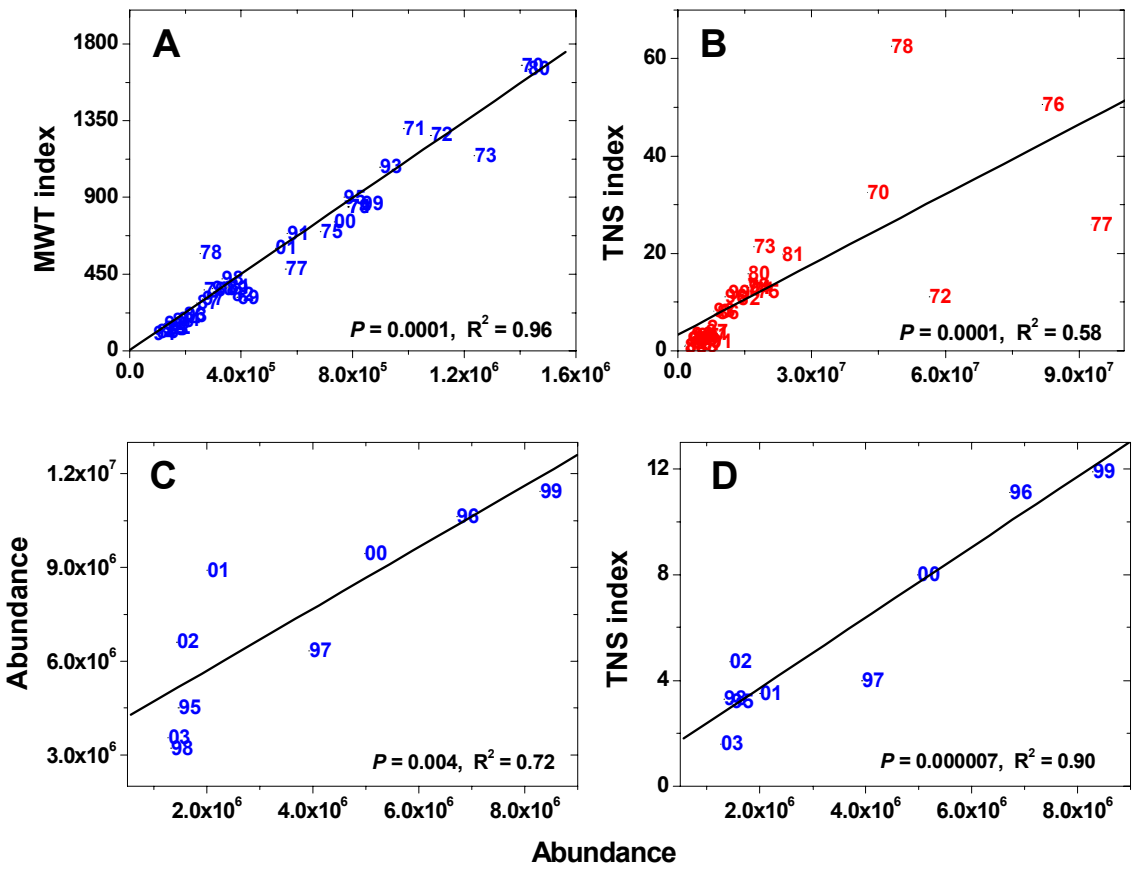

Figure 4. Relationships between the abundance indices and abundance estimates for the Fall Midwater Trawl Survey (MWT, A) and Summer Tow-Net Survey (TNS, B). Relationships are also shown between juvenile abundance estimates (C) and TNS (D) with CPUE in 20-mm (post-larval) Survey. Fitted lines are from linear regressions.

Scattered reports indicate wakasagi was also introduced to China and southeastern Russia (Tang and others 2002; Chereshnev and others 2001). The California population resulted from eggs introduced in 1959 into Central Valley reservoirs above the Delta to serve as a forage fish, before wakasagi and delta smelt were considered separate species (Wales 1962).

2. *H. transpacificus* (delta smelt). Delta smelt is confined to the low salinity and freshwater reaches of the San Francisco Estuary.

3. *H. chishimaensis* (chishima wakasagi or Kunashir smelt). Saruwateri and others (1997) recently distinguished *H. chishimaensis* as a species restricted to lakes in the southern Kuril Islands (Figure 4). However, little is known of its life history.

- ***H. olidus* group**: freshwater to marine habitat

4. *H. olidus* (ishikariwakasagi or pond smelt). Pond smelt is widely distributed, with a landlocked population on Hokkaido, Japan, and anadromous populations occurring throughout the

Pacific Rim to Alaska and the Yukon River (Platts and Millard 1995).

- ***H. japonicus* group**: marine to estuarine habitat

  5. *H. japonicus* (chika or silver smelt). *H. japonicus* occurs in the coastal ocean and bays off Japan, as well as estuaries and rivers entering the Sea of Okhotsk and Bering Sea in south-eastern Russia (Chereshnev and others 2001).

  6. *H. pretiosus* (surf smelt). Surf smelt is common along the western coast of North America, supporting important fisheries from the Alaskan Peninsula south to about Long Beach, California. Surf smelt is caught infrequently in the fish monitoring surveys in the SFE.

The similar morphology and variable life-history strategies imply that *Hypomesus* species can adapt rapidly to local environments. Wakasagi, by far the most thoroughly studied species, occurs with genetically distinct sub-populations and several life-history strategies throughout Japan (Katayama and others 2001). Most wakasagi are annuals with a few individuals living two years (Katayama and Kawasaki 1994). Coastal lakes often harbor a small resident form coexisting with a large, genetically indistinguishable, anadromous form that migrates to the ocean and then returns to spawn (Katayama and others 1998, 2000, 2001; Kudo and Mizuguchi 2000). Similar population substructure and life history variability is widespread among other smelts, salmonids and sticklebacks (Hutchings and Morris 1985; Snyder 1991; Mingelbier and others 2001).

The prevalence of life-history variability in *Hypomesus* and recent genetic information suggest delta smelt may have evolved from a group of surf smelt that became isolated as the SFE was forming over the past 8,000 years. Delta smelt, however, was not officially recognized as a distinct species in the U.S. until 1970 (Moyle 1976; Stanley and others 1995). It was originally considered a disjunct population of pond smelt, and then later as a subspecies of *H. transpacificus*, with wakasagi (McAllister 1963; Moyle 1976). Russian scientists, however, regarded delta smelt as a separate species before 1970, although their work was not appreciated until the end of the Cold War (Moyle 1976). Soon after the ESA listing their complicated taxonomic status and the recent expansion of wakasagi to the Delta prompted genetic investigations comparing delta smelt with wakasagi, surf smelt, and sympatric longfin smelt (*Spirinchus thaleichthys*). The genetic studies confirmed that delta smelt is a distinct species and more closely related to surf smelt than wakasagi (Stanley and others 1995; Trenham and others 1998).

Population Distribution and Fundamental Ecological Niche

Delta smelt occur from western San Pablo Bay east to the freshwater rivers and sloughs of the Delta (Figure 1). Previous accounts indicate they are found at 0 to about 18 practical salinity units (psu) surface salinity (Baxter and others 1999), although most are caught from about 0.2 to 2.0 psu, with older juveniles and adults being found at the higher end of that gradient (DWR–USBR 1993). Laboratory studies indicate delta smelt cannot tolerate salinities above 19 psu (Swanson and others 2000).

Cumulative distributions of salinities and water temperatures from the TNS and MWT indicate that over 70% of juvenile and 60% of pre-adult delta smelt are caught at salinities less than 2 psu, with over 90% occurring at less than 7 psu (Figure 5A). Thus, delta smelt abundance tends to be centered near or slightly upstream of 2 psu, in the entrapment, or low-salinity, zone (Bennett and others 2002). Water temperatures over about 25°C are also lethal, and can constrain delta smelt habitat especially during summer and early fall (Swanson and others 2000). Overall, the

majority of juveniles and adults in the TNS and MWT have been caught at water temperatures less than 22°C (Figure 5). Temperatures above 20°C during spring can also lead to higher mortality of newly spawned larvae (see "Spawning and Egg Stages"). Nevertheless, salinity appears to be the key environmental feature most often defining the physical scope of delta smelt habitat, or fundamental ecological niche (Hutchinson 1957).

The close association with salinity implies that distribution is determined by complex interactions among fish behavior, tidal currents, freshwater outflow, and diffusive movements rather than by geographical features per se. Thus actual distribution can fluctuate by many kilometers in a day due to tidal forcing. Similarly, while life-stages have specific seasonal and behavioral characteristics that are tied to location, overall geographical distribution can also vary dramatically in years of low versus high river discharge. In years of low discharge, delta smelt occur primarily in the lower Sacramento River and northern Delta. In contrast, high river discharge expands their distribution throughout Suisun Bay, Suisun Marsh channels, and into San Pablo Bay and the Napa River (Sweetnam 1999). They are also widely dispersed throughout Suisun Bay in moderate outflow years. Overall, however, the historical sampling record indicates they have remained several fold more abundant in northern Suisun Bay and Suisun Marsh channels than southern Suisun Bay and Delta, with the highest catches consistently occurring near Sherman Island and Decker Island in the lower Sacramento River (Figure 1, Errikla 1950; Radkte 1966; Bennett and others 2002). Thus, the highly persistent but variable size and location of the delta smelt habitat may also explain why the population appears largely panmictic, as indicated by genetic studies (Trenham and others 1998). In the past, some have attempted to distinguish between annual trends in a south Delta "population" and a north

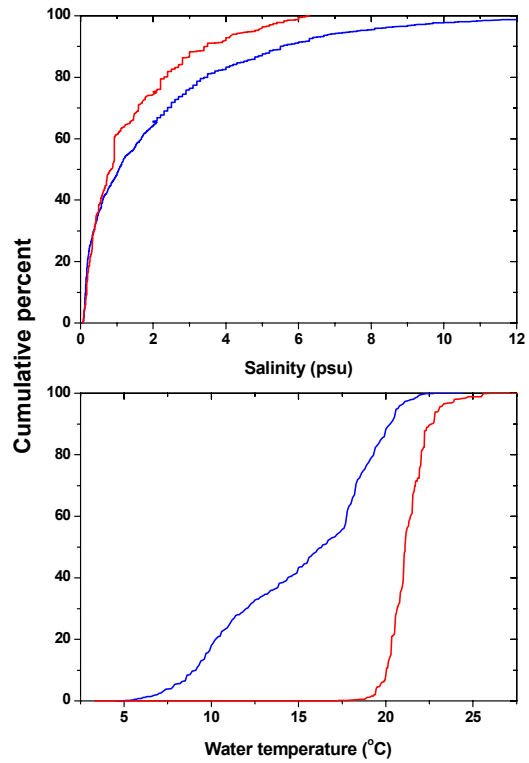

Figure 5. Cumulative percent of delta smelt catch in relation to salinity and temperature in the Fall (pre-adult) Midwater Trawl Survey (blue line) and Summer (juvenile) Tow-Net Survey (red line). Over 90% of delta smelt are caught at salinities <6 psu, and at water temperatures <20°C.

Delta or Suisun Bay "population" (DWR–USBR 1993, Sweetnam and Stevens 1993). The high spatial lability and genetic contiguity of delta smelt indicate the futility of haphazardly subdividing the population based on geography.

Conceptual Life History Model

Information on delta smelt biology and life history is accumulating rapidly. In the following discussion a conceptual life-history model organizes this information to identify key areas of uncertainty. Delta smelt has a primarily annual life cycle with rapid growth and high mortality occurring during recruitment, defined here as survival of eggs and newly hatched fish to the next reproductive season each year. A

hypothetical pattern of recruitment is depicted by plotting egg mortality per female throughout the annual sequence of delta smelt life stages (Figure 6A). Recently estimated individual growth and mortality among life stages are also shown (Figures 6B and 6C, Bennett and Hobbs, unpublished data).

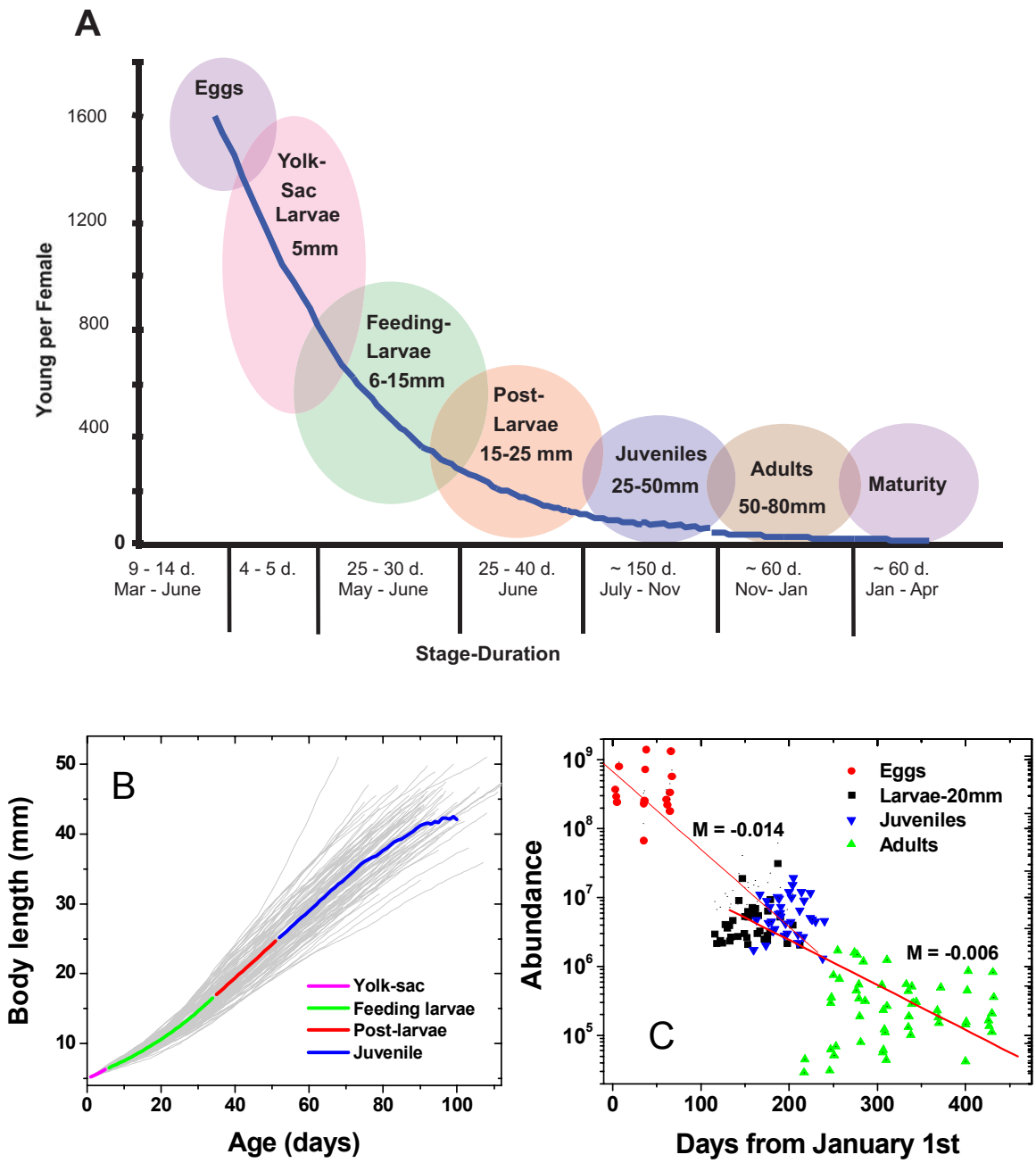

Figure 6. Conceptual model of delta smelt life history. A hypothetical pattern of mortality (dark blue line) for young produced by a female is shown with the approximate life stage durations (A). Also shown is a pattern of individual growth calculated from 144 otoliths during 1999 (B), and mortality as represented by the slope of regression lines (M) among different life stages (C) (Bennett and Hobbs, in prep.).

Overall, delta smelt appear to have a life history strategy that is relatively unusual. Several life history attributes such as small size and short life span classify delta smelt as "opportunistic" under the classification scheme derived by Winemiller and Rose (1992) for North American fishes, as well as in a similar version recently developed by Vila-Gispert and others (2002) that also includes fishes from Europe and South America. Other aspects of delta smelt life history, however, such as low fecundity, spawning frequency, and a protracted spawning season classify it as an "equilibrium" species (Winemiller and Rose 1992; Vila-Gispert and others 2002). Delta smelt also fit well with a distinct salmonid life history strategy (Winemiller and Rose 1992; McCann and Shuter 1997). But by comparison, delta smelt invest far less into each offspring, having pelagic larvae rather than benthic and relatively well-developed elvers produced by salmonids. Therefore, the information outlined below indicates delta smelt are a small, primarily annual species, but with a reproductive strategy more like a perennial, as well as several other very specific environmental requirements that may render the species susceptible to catastrophe in a fluctuating environment.

Spawning and Egg Stages. Delta smelt are semi-anadromous, spawning in the freshwater reaches of the SFE and primarily in the Delta (Figure 1). However, actual spawning locations are unknown and inferred from catches of very young larvae and fish as they transition from ripe or spent condition. In years of low freshwater discharge, most ripe females and yolk-sac larvae are found in the Sacramento River and particularly around Prospect Island and the Barker-Lindsey slough complex (Figure 1, 7). For example, about 75% of all yolk-sac larvae were caught in this region in 1991 (a drought year; Wang and Brown 1991). In years of high freshwater discharge spawning distribution is broader, encompassing most of the Delta, Suisun Marsh channels, and the Napa River (Sweetnam 1999). Investigations during the wet spring of 2002 placed the majority of spent females in the Sacramento River, even though the majority of maturing fish were in Suisun Marsh (Sousa 2002). In early 2003, the majority of females appear to have been spawning around Prospect Island and the Barker-Lindsey slough complex: a pattern consistent with a dryer year scenario (Figures 1 and 7, K. Sousa, DFG, pers. comm.).

Spawning can occur from late February to June, although larvae are typically most abundant from mid-April through May. In March 2002, 89% of females examined were still maturing and were not ready to spawn (Sousa 2002). Wang (1986) first observed larvae from February to mid-July, and suggested that delta smelt may spawn at water temperatures between 7 to 15°C, whereas in aquaculture spawning is observed at temperatures between 12 to 22°C (B. Baskerville-Bridges, UCD, pers. comm., Lindberg and others 1997).

Lunar phase can also be an important cue for spawning, particularly for fish depositing eggs in tidal or intertidal habitat (Moyle and Cech 1996). For example, spawning is closely tied to lunar phases in coastal silversides (Atherinidae), most notably for grunion (*Leuresthes tenuis*) that spawn en-masse at night on California coastal beaches. Peak spawning in *H. japonicus* also occurs at night during full moons (Hirose and Kawaguchi 1998a), whereas surf smelt are reported by local fishermen to spawn on beaches at night during new moons (Bennett, pers.obs.). Spawning of delta smelt in aquaculture also occurs at night with several males attending females as they broadcast eggs on the bottom of laboratory tanks (Mager 1996; Lindberg and others 1997; Mager and others 2004).

To examine a potential lunar influence on spawning, I compared the frequency of spawning for delta smelt in aquaculture with the lunar influence on tidal velocity occurring nearby (Figure 8A). In 2000–2002, more than 75% of successful spawns (Chi-square = 33.2, df = 7, $P < 0.0001$) occurred on spring tides as indexed by a root-mean-square (RMS) of tidal

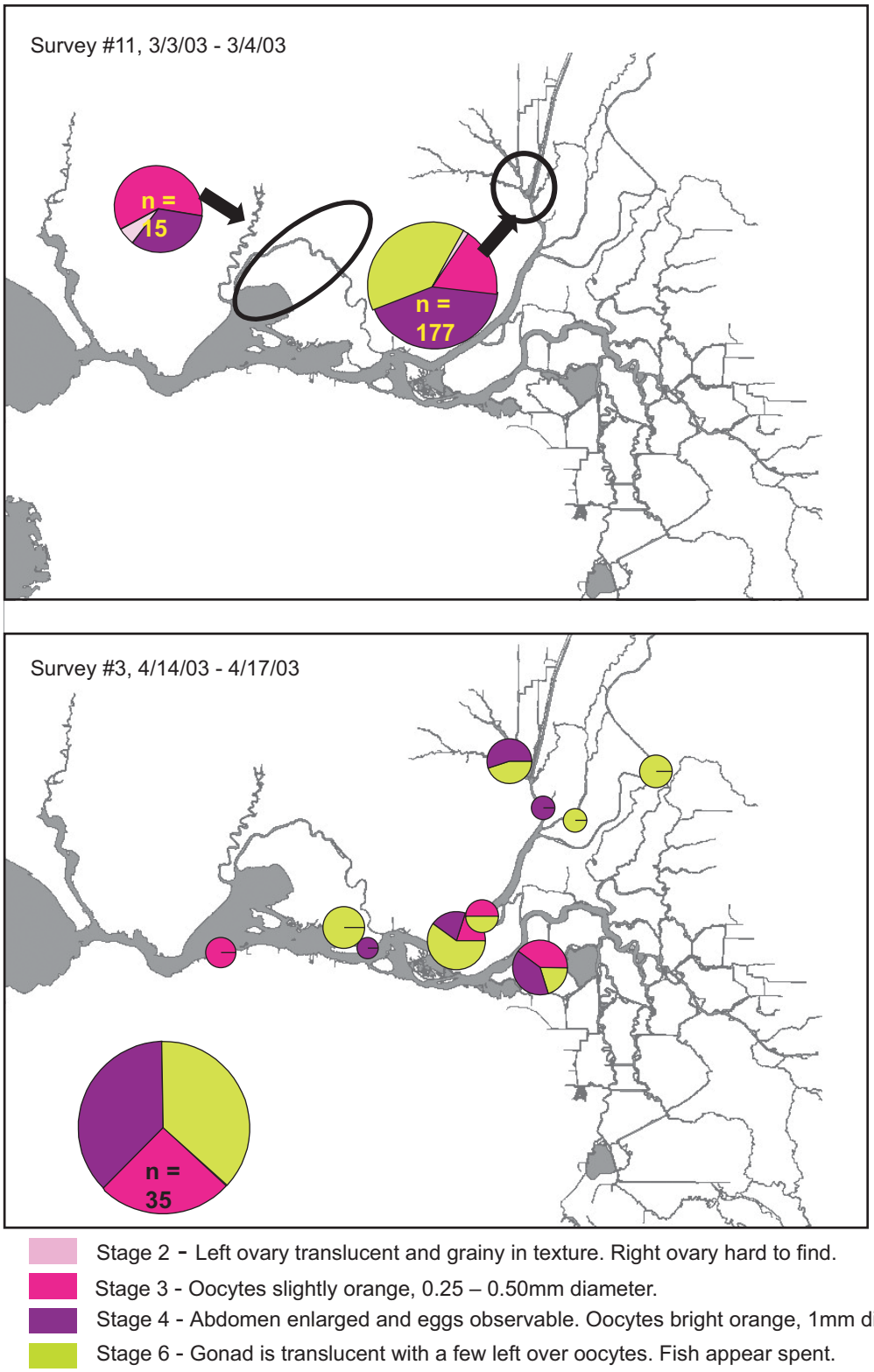

Figure 7. Maturity status of female delta smelt from the spring Kodiak trawl survey in 2003. Graphs courtesy of K. Sousa, DFG. (See also Sousa 2002).

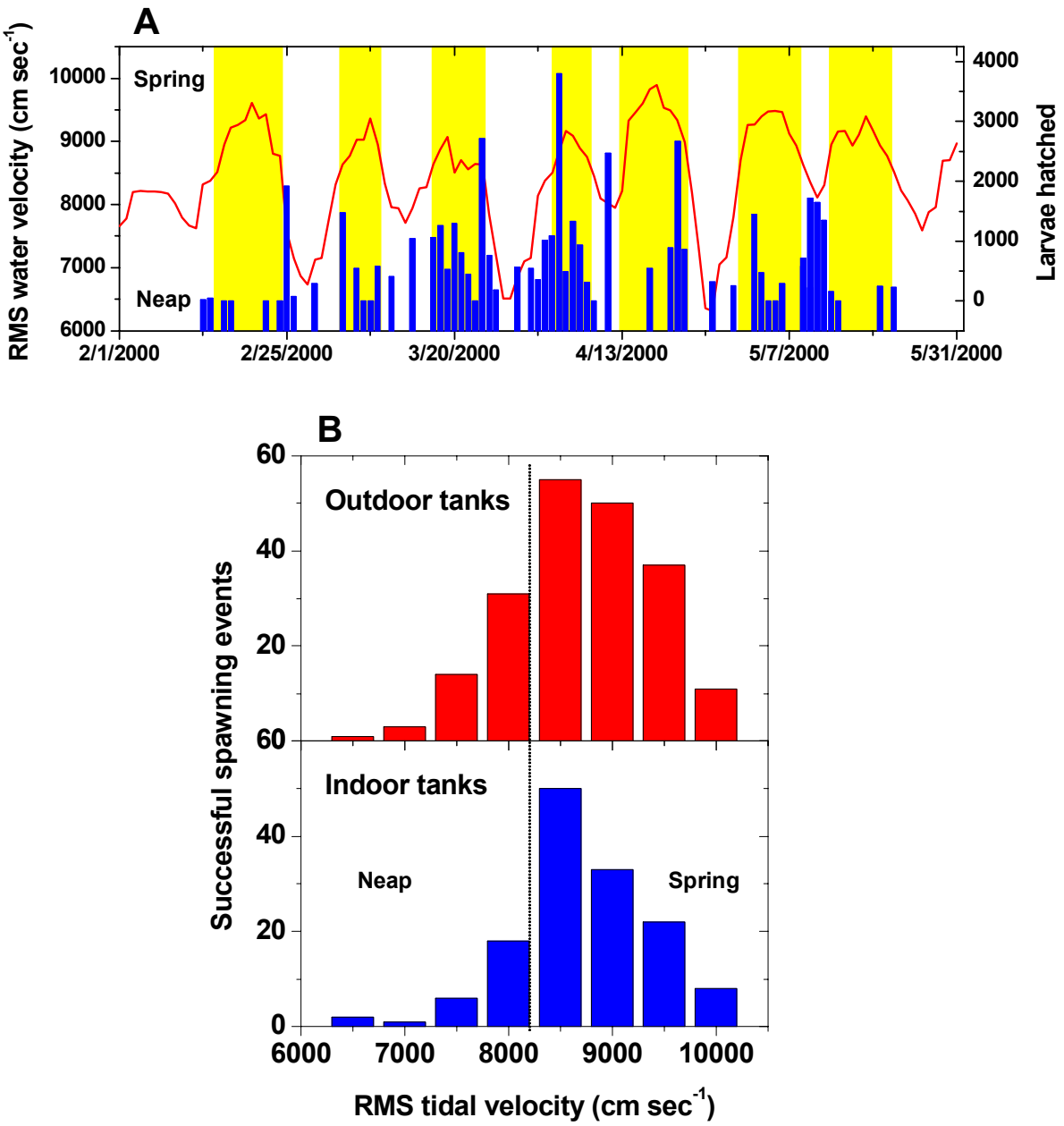

Figure 8. Numbers of hatching eggs spawned (blue bars) for delta smelt in aquaculture with root mean square of tidal velocity (RMS, red line) in Old River near the Federal Central Valley Project intake (Figure 1) during spring 2000 (A). Yellow shading indicates spring tidal periods (RMS >8,000 cm sec^{-1}). Data pooled from 2000–2002 with RMS used to characterize spring *vs*. neap tidal phases (B). Delta smelt spawning data provided by J. Lindberg and B. Baskerville-Bridges, UCD. RMS data provided by J. Burau and C. Ruhl, USGS.

velocity over 8000 cm sec^{-1} (Figure 8B). This implies that hatching may often occur during neap tidal periods because egg incubation lasts about 11 to 13 days at 14 to 16°C (Mager 1996, Mager and others 2004), and 8 to 10 days at 15 to 17°C (Baskerville-Bridges and others 2004). If this is the case, delta smelt may often spawn below the low water margin

during spring tidal phases (potentially new moon phases) to minimize stranding eggs in intertidal habitats, or because peak tidal flows provide optimal egg aeration during incubation. Hatching during periods of low tidal velocity may then reduce dispersion and help larvae to remain near spawning locations. Considering that a spring-neap tidal cue would be partially obscured in spawning tanks, lunar periodicity in spawning may be more pronounced in the wild. However, there is currently no field information to support whether lunar phase influences spawning.

Early studies suggested that females may spawn over a brief period as one-year-olds before dying (Moyle and others 1992), however, observations from aquaculture suggest a capacity to spawn twice during a season (Mager 1996; B. Baskerville-Bridges, UCD, pers. comm.). Female gonads ripen during winter and early spring. The paired gonads are asymmetric such that the left gonad is typically larger, containing about 1,000 eggs (Mager 1996). Asynchronous development of ovaries and within-season iteropary also occurs in wakasagi, as well as in a variety of other fishes (Katayama and others 1999).

Delta smelt fecundity increases with female size. Previous accounts indicate that ripe females contain 1,247 to 2,590 eggs that when unfertilized are about 1 mm in diameter (Wang 1986; Moyle and others 1992). Although Moyle and others (1992) initially did not detect such a size-specific fecundity pattern, Mager (1996) observed a fecundity-length relationship ranging from 1,196 eggs for a 56 mm (FL) female to 1,856 eggs for a 66 mm (FL) female. Recent studies show that over a broader size range, larger females in aquaculture typically have more eggs, but individual variability also increases substantially (Figure 9; B. Baskerville-Bridges, UCD, pers. comm.). Although such relationships are common in fishes, overall fecundity in delta smelt is low relative to wakasagi and other smelts (Gritsenko and others 1984a,1984b; Degraaf and others 1996; Katayama 2001). Low fecundity in a primarily annual species is an unusual life history strategy (Winemiller and Rose 1992; Vila-Gispert and others 2002).

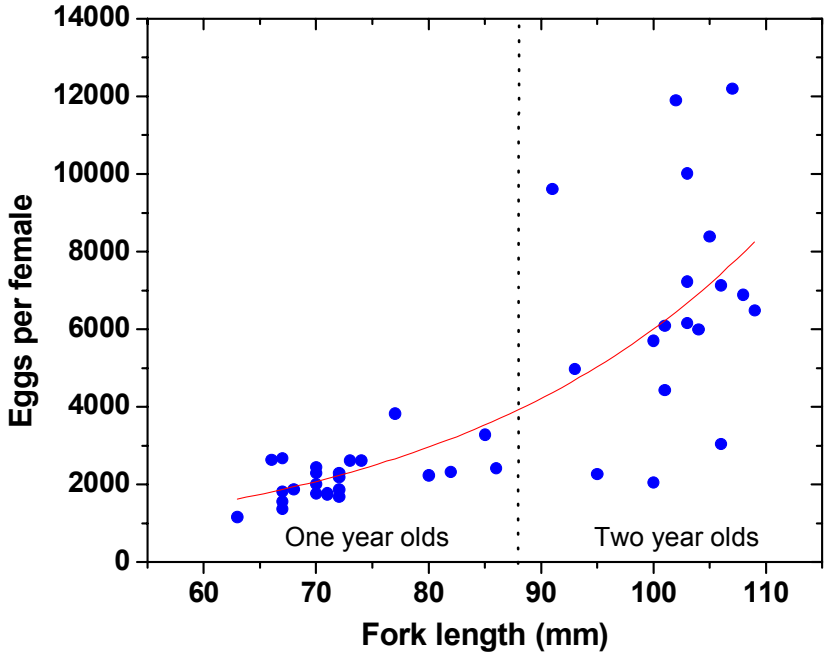

Figure 9. Numbers of eggs produced by delta smelt in aquaculture. Fitted line is an exponential regression. Data courtesy of B. Baskerville-Bridges, UCD.

The spawning microhabitat for delta smelt is unknown; eggs have not been found in the field. Laboratory observations indicate delta smelt spawn primarily at night as they swim against a slight current, broadcasting their eggs a few centimeters above the substratum (Mager 1996; Lindberg and others 1997). Spawned eggs are demersal and adhesive, attaching to substratum with an adhesive stalk formed by the outer layer (chorion) of the egg. Moyle (1976) suggested that suitable substrata are most likely submerged vegetation, rocks, or tree roots. However, Lindberg and others (1997) found few eggs attached to vertical substrata (plants, tank sides) in her studies. Recent experiments offered delta smelt six potential spawning substrata in high (8.8 cm sec^{-1}) and low (1.4 cm sec^{-1}) velocity flows (J. Lindberg, UCD, pers. comm.; Brown and Kimmerer 2002). In each of two trials, females deposited 84% and 54% of their eggs on gravel in high flow. Although the closely related surf smelt, wakasagi, and *H. japonicus* are known to select similar, primarily sandy, spawning substrata (Hirose and Kawaguchi 1998b; Katayama and others 1999), gravel beds are rare in the areas that delta smelt presumably spawn in the SFE. It will be interesting to determine whether sandy beaches such as used by most *Hypomesus* spp., or larger rock rubble, rip-rap, that has been used to strengthen the sides of many Delta levees also serve as viable spawning substrate. Studies such as these will be crucial for eventually defining delta smelt spawning habitat and whether it is limited in the estuary.

Fertilization and hatching success for delta smelt are highly variable and sharply defined by water temperature. From 1994–1996, fertilization success in aquaculture ranged from 21% to 40%, whereas hatching success varied from 29% to 81% (Mager 1996). Similar variability was observed by Lindberg and colleagues (1997). Recent studies show that optimal hatching success and larval survival in aquaculture occurs at 15 to 17°C (Figure 10; B. Baskerville-Bridges, UCD, pers. comm.). While incubation temperatures below 15°C have generally lower hatching success, temperatures exceeding 20°C decrease the egg incubation period, mean hatch length, time to first-feeding, as well as larval feeding success, leading to overall higher mortality (Figure 10; B. Baskerville-Bridges, UCD, Davis, pers. comm.).

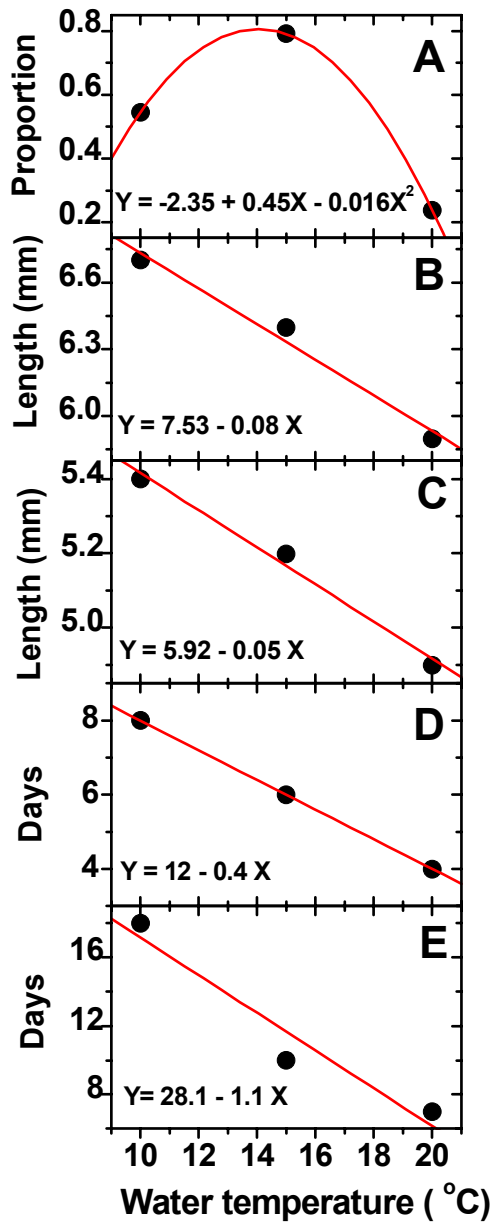

Figure 10. Influence of water temperature on proportion of larvae hatching (A), larval length at hatch (B), larval length at first-feeding (C), days to first-feeding (D), and incubation time (E) for delta smelt in aquaculture. Data courtesy of B. Baskerville-Bridges, UCD.

Therefore, delta smelt spawning success may be variable when temperatures fall below 15°C, but appears more sharply limited by those above 20°C. Although extrapolating from laboratory studies to field conditions can be problematic, temperatures within 15 to 20°C appear to limit the number of cohorts comprising size-frequency distributions of post-larvae (Defined in "Swim Bladder Development and Post-Larval Stage") from the 20-mm Survey (Figure 11A). Furthermore, larval surveys during 1993–1994 suggest a similar temperature window of spawning success with a possible refinement to about 14 to 18°C (Figure 11B).

Yolk-Sac and First-Feeding Larval Development. Larvae hatch at 4.5 to 6 mm total length and are transparent with an oval-shaped yolk-sac containing an oil globule (Figure 6, Wang 1986; Wang and Brown 1991; Mager 1996; Mager and others 2004). During the next 4 to 6 days the young larvae swim continuously and are positively phototactic, remaining near the water surface in aquaria. They grow very little as they absorb the yolk sac and oil globule but develop jaw and mouth parts (Figure 6; Mager 1996; Mager and others 2004). When the yolk sac is almost fully absorbed, the larvae begin exogenous feeding. In aquaculture, first-feeding larvae only ate unicellular algae and rotifers presented to them in turbid conditions (Baskerville-Bridges and others 2004; Mager and others 2004). In the field, however, an evaluation of gut contents in nearly 1,500 young delta smelt showed that feeding was size-based with first-feeding larvae (5 to 8 mm SL) consuming sub-adult cyclopoid and calanoid copepods (Nobriga 2002). Larvae swim continuously, and feeding success requires practically bumping into prey items rather than a coordinated attack behavior (Bennett, pers. obs.). Thus, the stochastic nature of co-occurring with, and capturing, food implies that feeding success is related to prey densities (Nobriga 2002). In 1999, larvae in the wild grew at about 0.35 mm per day, although with typically high variability among individuals (Bennett and Hobbs, unpublished data; Figure 6B). Actual growth rates for larvae among cohorts and years are extremely difficult to determine, because field samples typically only represent those individuals that have survived the first-feeding period.

All remaining life stages of delta smelt consume adult copepods. Older larvae (10 to 15 mm) begin to consume adult copepods and may select the cosmopolitan calanoid copepod, *Eurytemora affinis* (Nobriga 1998). However, since the dramatic decline of *E. affinis* in 1989 (Kimmerer and others 1994), it becomes locally and intermittently abundant only during early spring. When available, larvae and juveniles appear to utilize *E. affinis*, but gradually they include the exotic calanoid copepod, *Pseudodiaptomus forbesi*, as this prey item increases in abundance during late spring. As a result, *P. forbesi* has been the dominant prey item for delta smelt since the decline in *E. affinis* at all but the earliest feeding life stages (Moyle and others 1992; Lott and Nobriga 1998). However, *P. forbesi* abundance has been declining in recent years concurrent with a rise in the abundance of another exotic copepod, *Limnoithona tetraspina*, that is apparently too small to be consumed by delta smelt (Bouley 2004; Hobbs 2004; L. Mecum, DFG, pers. comm.).

Swim Bladder Development and Post-Larval Stage. Delta smelt swim bladders finish developing and fin-folds begin to appear in the 14 to 20 mm size range, or at about 25 to 40 days post-hatch (Figure 6; Wang and Brown 1991; Bennett, pers. obs.). However, Mager and others (2004) didn't observe this until 40 to 60 days post-hatch. Here I refer to this life-stage as post-larvae, because these milestones of development influence their behavior and distribution. For example, in the 20-mm Survey the post-larvae are generally caught in the western Delta and Suisun Bay where they accumulate at the landward margin of the low salinity zone (Grimaldo and others 1998). Juveniles (20 to 40 mm) are generally more widely distributed, but also maintain an association with the low salinity zone.

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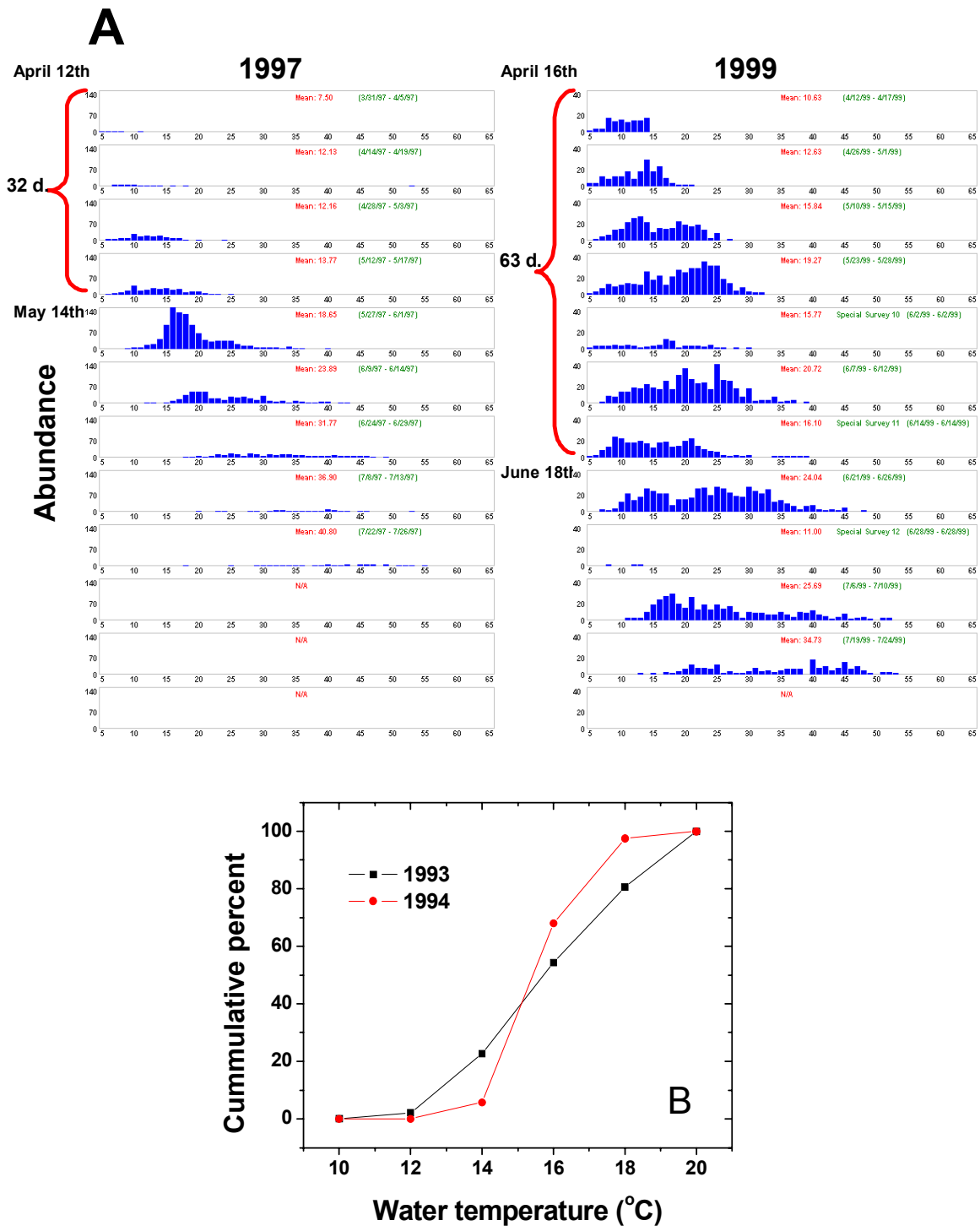


Figure 11. Delta smelt size-frequency distributions from bi-weekly sampling in the 20-mm Survey during 1997 and 1999 (A). Brackets show the water temperature range 15 to 20°C. Note that when temperature exceeds 20°C in late spring, larvae no longer enter the survey. (B) Cumulative percent of delta smelt larvae caught as a function of water temperature in larval surveys from 1993 and 1994; larvae occur in the samples at water temperatures of about 14 to 18°C. Data courtesy of M. Nobriga, DWR.

Several young fishes appear to employ behavioral strategies to prevent advection seaward and remain in the low-salinity zone after they develop swim bladders (Kimmerer and others 1998; Bennett and others 2002). During June 1996, Bennett and others (2002) sampled young fishes at three discrete depths in northern (Suisun Cut, adjacent to the southeastern corner of Grizzly Bay) and southern (ship) channels of Suisun Bay (Figure 1). Sampling encompassed the low-salinity zone as it passed fixed stations over three complete tidal cycles (about 30 hr) during spring and neap tidal phases. Abundance at the Suisun Cut location, however, was about eight-fold higher than at the Ship Channel and consisted of relatively larger individuals (Figure 12A; Aasen 1999). In the Ship channel, most fishes and zooplankton appeared to undergo tidal vertical migrations, occurring near the surface during flood tides and at depth on ebbs (Figure 12B; Bennett and others 2002; Kimmerer and others 1998, 2002). Tidal migrations may reduce advection seaward as well as facilitate feeding success (Bennett and others 2002). However, in Suisun Cut some fishes, including delta smelt, appeared to undergo reverse diel migrations, remaining near the surface during the day and at depth during the night (Figure 12B; Bennett and others 2002). This behavior also may have facilitated retention by promoting horizontal exchange with shallow-water habitats in Grizzly Bay and Honker Bay (Figure 1). Also, gut fullness and individual condition measures were considerably higher for delta smelt in Suisun Cut than in the Ship channel (Hobbs 2004). At both locations successful feeding appeared to be restricted to daylight hours during flood tides (Hobbs 2004), a pattern also observed for rainbow smelt (*Osmerus mordax*) in the St. Lawrence Estuary (Sirois and Dodson 2000). Overall, the close association with the low salinity zone and dense patches of zooplankton may help to explain rapid growth (about 0.5 mm per day) observed during the post-larval period in 1999 (Figure 6B). These findings support the hypothesis that the low-salinity and shallow-water areas of Suisun Bay constitute vital nursery habitat for delta smelt and other young fishes during years of moderate to high outflow (Herbold and others 1992; Moyle and others 1992).

Less is understood concerning the vertical distribution of delta smelt in other locations in the SFE. Rockriver (2004) examined vertical distribution for post-larval smelt in the lower Sacramento River and San-Joaquin River in 2000–2001. Although the results indicate that in the freshwater portions of these rivers post-larvae were significantly more abundant at depth during the day relative to night, the results are difficult to interpret without accompanying hydrodynamic information. The pattern may also have been influenced by the very low abundance of delta smelt in the catch.In general, young delta smelt appear to be more dispersed in the water column during hours of darkness. Indeed, higher dispersion during night also may have contributed to the pattern of reverse diel migration identified by Bennett and others (2002), as well as to higher entrainment of delta smelt in an agricultural diversion siphon observed by Nobriga and others (2004). Overall, however, more work is needed to fully understand vertical and horizontal distribution patterns, as well as their underlying mechanisms. Such work is especially needed in the vicinity of the water export facilities in the south Delta.

Juvenile and Adult Stage. Juvenile delta smelt finish developing fins and the majority of adult morphological characteristics by about 25 to 30 mm (Figure 6A). As a result they have the swimming ability to select habitats and are generally more widely distributed. Growth continues during the summer months (at about 0.35 mm d^{-1}) and then slows as average fork lengths reach 40 to 50 mm in September (Figure 6B; see Tables 17-19 in Erkkila and others 1950; Ganssle 1966; Radtke 1966; Moyle and others 1992). Mortality is typically inversely associated with fish size, thus it tends to be considerably lower during the transition from juvenile to adult stage than in egg and larval stages (Figure 6C).

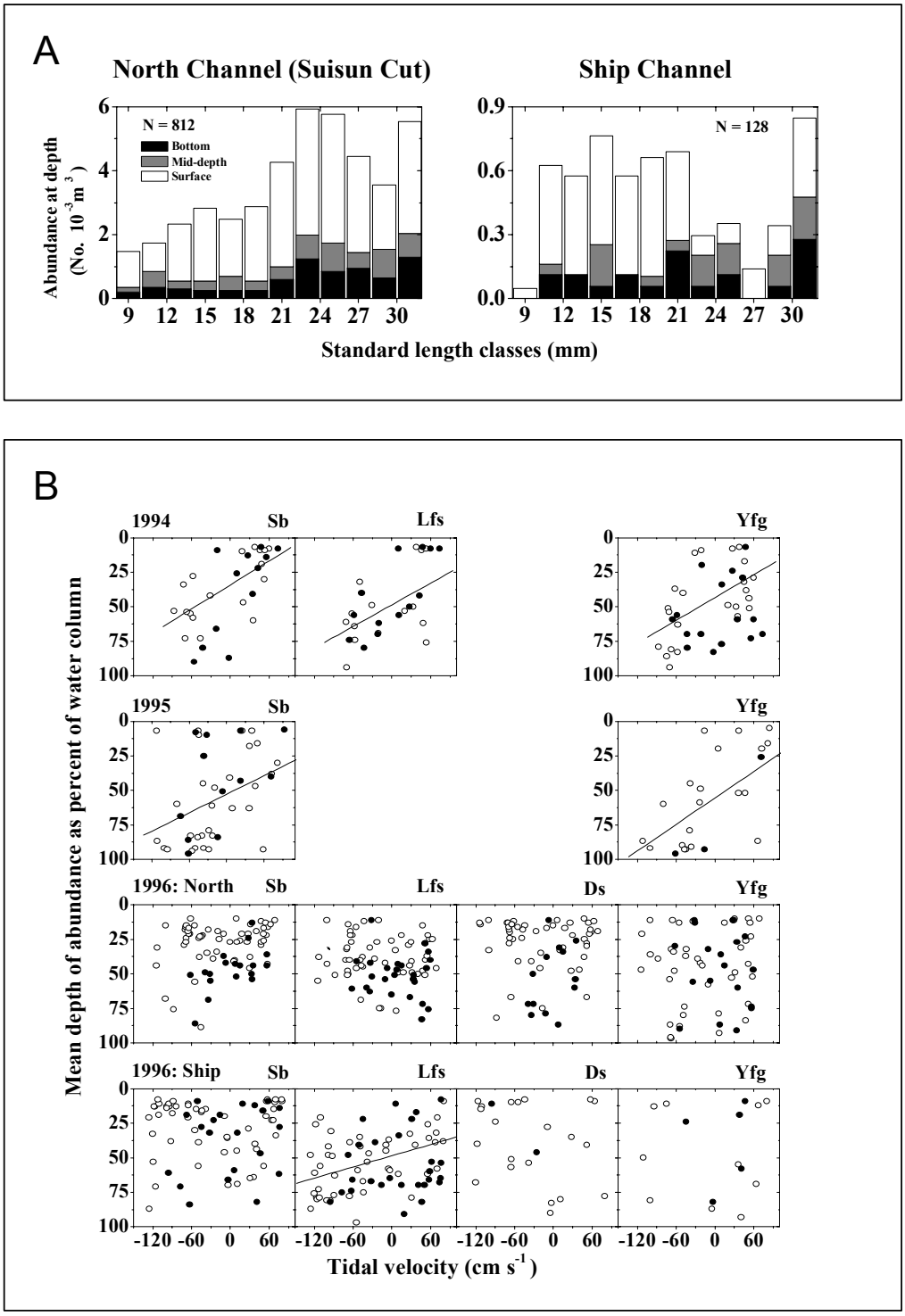


Figure 12. Vertical distribution of delta smelt at depth according to length classes sampled in 1996 (A), and mean depth of fish abundance as a percent of the water column with tidal velocity in samples from 1994–1996 (B). Hourly samples were collected during the day and night over complete tidal cycles for striped bass (Sb), longfin smelt (Lfs), delta smelt (Ds), and yellowfin goby (Yfg). Lines are significant regressions. Graphs are from Bennett and others 2002.

Juveniles and adults may occur in loose aggregations rather than tight schools, judging from the patchiness of fish catch in the monitoring surveys (Bennett, pers. obs.). This may result from their unique swimming behavior. Laboratory flume studies of swimming performance (Swanson and others 1998) indicate that while 58% (N = 109) of juvenile-adult fish were capable of maintaining moderately high swimming velocities (27 cm s^{-1}, for 10 min), the remaining 42% were unable or unwilling to swim at velocities of 10 to 20 cm s^{-1}. At velocities below 10 cm s^{-1}, delta smelt employed an irregular stroke-and-glide swimming behavior. The extent to which this swimming behavior occurs in the wild is unknown. If so, such a swimming strategy appears to be adaptive for an estuarine planktivore, helping to conserve energy and maintain position in favored habitat. Irregular swimming and a translucent body may also help them to be cryptic.

During the fall, delta smelt gradually begin a diffuse migration landward to the freshwater portion of the Delta, and during wetter years to channels and sloughs in Suisun Marsh and the lower Napa River. Growth during this period is very slow and difficult to measure in otoliths (J. Hobbs, UCD, pers. comm.), implying that energy may be allocated to gonad development before the spawning season.

Longevity. The majority of adult delta smelt (50 to 80 mm) live one year. A few adults live two years, and may spawn in one or both years. Length-frequency data suggest that adults become rare during spring, with juveniles dominating summer catches in the TNS (Erkkila and others 1950; Radtke 1966; Moyle 1976; Stevens and others 1990; Moyle and others 1992). Otoliths from some individuals over 70 mm (FL) in the summer have distinct annual rings, confirming that a few fish do live beyond a year (Figure 13A). In addition, fish over 80 mm in length comprised 2.3% and 9.3% of the individuals in mature spawning condition collected in 2002 and 2003 respectively (Figure 13B). However, some of these larger individuals do not appear in reproductive condition on the spawning grounds (K. Sousa, DFG, pers. comm.). In Japan, a similar proportion of wakasagi typically live two years and are iteroparous, spawning in both years (Katayama and Kawasaki 1994; Katayama and others 1999).

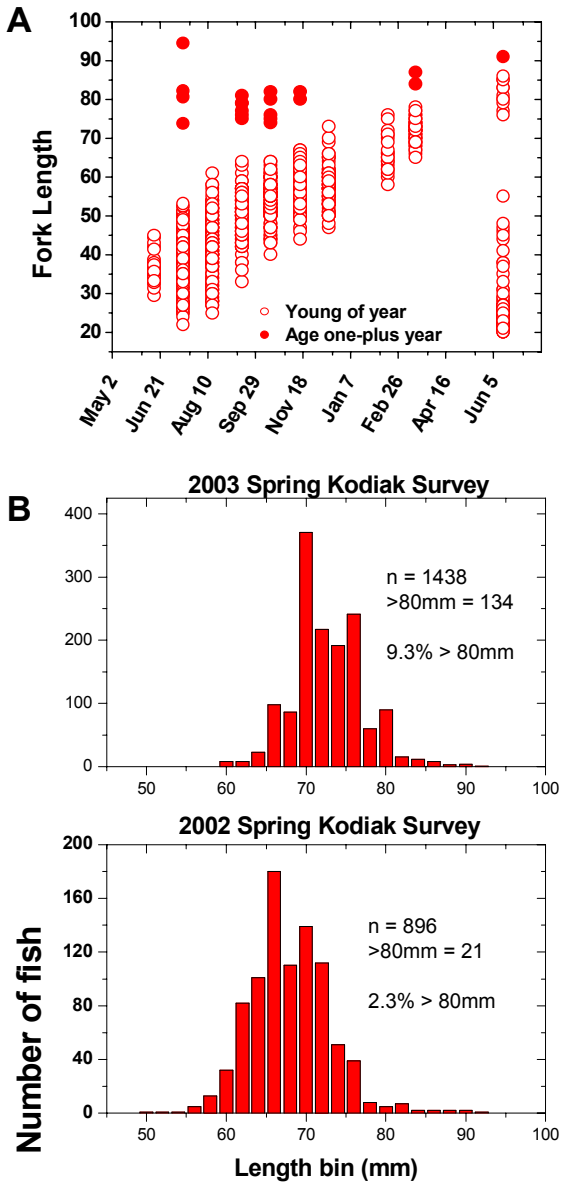


Figure 13. (A) Length of young of the year and 1+ year adults as determined from otolith evaluations (N = 876) in 1999–2000 (Bennett and Hobbs, in prep.). (B) Size-frequency distributions of delta caught during the spawning season by the spring Kodiak Trawl Survey in 2002–2003.

Two-year-old females could have an important influence on population dynamics by augmenting spawning success after years of poor recruitment. In most fishes, older females are also known to have more eggs of higher quality, and improved reproductive success by provisioning eggs well in select microhabitats or at optimal times during the spawning season (Chambers and Lambert 1996; Brooks and others 1997). One-year-old delta smelt females in aquaculture produce about 2,000 eggs, whereas two-year-old females in aquaculture can produce more than twice this number (Figure 9). In addition, wakasagi fecundity is known to increase with fish size, with two-year-old females also producing larger and more eggs than one-year-old females (Katayama and others 1999). If employed by delta smelt, such a tactic would enable their unusual life history strategy to persist, and thus reduce the probability of extinction. Reproductive tactics that spread reproduction over time are typically termed bet-hedging (Stearns 1992), and are a common response employed by fishes to compensate for poor recruitment or high adult mortality (Wootten 1984; Rochet 2000). Therefore, research is needed to identify the proportion of two-year-old fish, their reproductive capacity, and spawning strategies to determine the potential significance of bet-hedging for delta smelt population dynamics.

Implications and Uncertainties

The current information on delta smelt biology and life history suggests it is an unusual species. Several aspects of their life history are similar to those of other coastal fishes. However, delta smelt are not well classified into any of three basic life history strategies employed by many fishes worldwide (Winemiller and Rose 1992; McCann and Shuter 1997; Vila-Gispert and others 2002). It is a small and primarily annual species but with low fecundity and a protracted spawning season: key traits that are typically associated with a perennial life history strategy. Delta smelt also do not appear to compensate for their limited reproductive capacity by having precocious offspring like most salmonids. This contradiction renders the species at risk to extinction because it occurs in a fluctuating environment, has relatively low reproductive output, but must have successful recruitment each year.

Delta smelt is also highly susceptible to local environmental catastrophes because it has a tiny geographic range compared with most *Hypomesus*, occurring only within a thin margin of low salinity habitat in the northeastern SFE (Figure 1). In addition, spawning success may be successful only within particular lunar phases, a specific temperature range, as well as for eggs deposited on suitable substrate. Moreover, feeding is almost exclusively restricted to copepods that must become abundant at the appropriate life stages spatiotemporally with those of delta smelt. Therefore, because of these unique and very specific requirements, delta smelt may employ a bet-hedging tactic in which a small proportion of individuals survive, become highly fecund, and spawn in a second year. Such a tactic would help to compensate for years of poor recruitment success and maintain population persistence.

Several aspects of the above conceptual model for delta smelt are uncertain. Key issues in need of resolution include the following, listed by life sequence rather than relative importance.

Fecundity and Reproductive Success. Currently there are no field-based data on the size-specific patterns of fecundity, spawning cues and microhabitats, or spawning success in under different environmental conditions. Such information is essential for understanding the life history strategy and developing population models for delta smelt.

Feeding Success. Information on the mechanisms underlying first-feeding success for delta smelt on recently introduced copepods is necessary for evaluating the suitability of the ever-changing feeding environment.

Swimming Behavior. The patterns and processes that determine delta smelt spatial distribution at meso-scales (meters, hours) have been explored in detail only within the low salinity zone. Similar information is lacking for other regions of the delta smelt habitat, specifically in the south Delta and in vicinity of the major water export facilities.

Longevity. The numbers, fecundities, and reproductive success of two-year-old fish during spawning seasons with different environmental conditions needs to be resolved. This information is crucial for assessing the potential importance and processes underlying a possible bet-hedging tactic that may enhance persistence of the delta smelt population.

Influences on Annual Abundance

Understanding what factors limit delta smelt abundance remains a challenging and urgent concern. Despite intensive monitoring of distribution and abundance, relatively little work has been directed at specific processes that may determine annual abundance. A short life span and low fecundity implies that maximizing recruitment success, or survival of eggs and newly hatched fish to the next reproductive season each year, is vital because the majority of adults does not spawn in multiple years; there is little population carryover among years (Warner and Chesson 1985). However, teasing apart the factors regulating recruitment has proven to be a frustrating if not intractable pursuit for fishes (Houde 1989; Lawrence 1990; Leggett and Deblois 1994; Cowan and others 1996). This is because recruitment is regulated by complex interactive mechanisms that can change in importance episodically, or as subtle processes (Bender and others 1984; Houde 1989; Bennett and Moyle 1996). Nonetheless, measuring and predicting recruitment success is crucial for devising effective management strategies for delta smelt.

As a first-step toward understanding the importance of potential processes limiting delta smelt, long term trends in abundance can be explored with various environmental factors. Although statistical relationships can be identified with this approach, the results cannot reliably demonstrate causation. In addition, key mechanisms may be difficult to measure (e.g. toxic chemical concentrations; Bennett 1996; Moon and others 2000), may not be recognized (e.g. climate change; Bennett and Moyle 1996), or have synergistic effects that require including several factors in analyses that can outstrip the statistical power of the data (Jassby 2000). Exploratory data analyses can provide a valuable service, however, by sharpening the scope of questions that should then be addressed as part of a comprehensive program of research. With these caveats in mind, various analyses are presented below and compared with direct measurements where possible. The objective is to develop a conceptual model that conveys what is currently known, as well as to highlight some of the likely factors limiting delta smelt abundance.

Generation Time

Previously the question was posed whether two-year-old fish may spawn successfully and influence the dynamics of the population. However, if two-year-old females have higher fecundity but are so few in number, can they influence population dynamics? I examined the potential influence of these fish using the auto-correlation structure of the abundance indices and abundance estimates. Auto-correlation functions (Chatfield 1984) correlate a time series with itself at different time lags. For delta smelt, significant auto-correlation occurs in the TNS and juvenile abundance estimates at lags of one and two years and in the MWT and pre-adult abundance at a lag of two years (Figure 14). Although these patterns could arise from autocorrelation in other mechanisms that are closely tied to abundance, a more likely explanation is that the relationships arise from interactions within a biological population (Hare and Francis 1995; Downton and Miller 1998). As shown

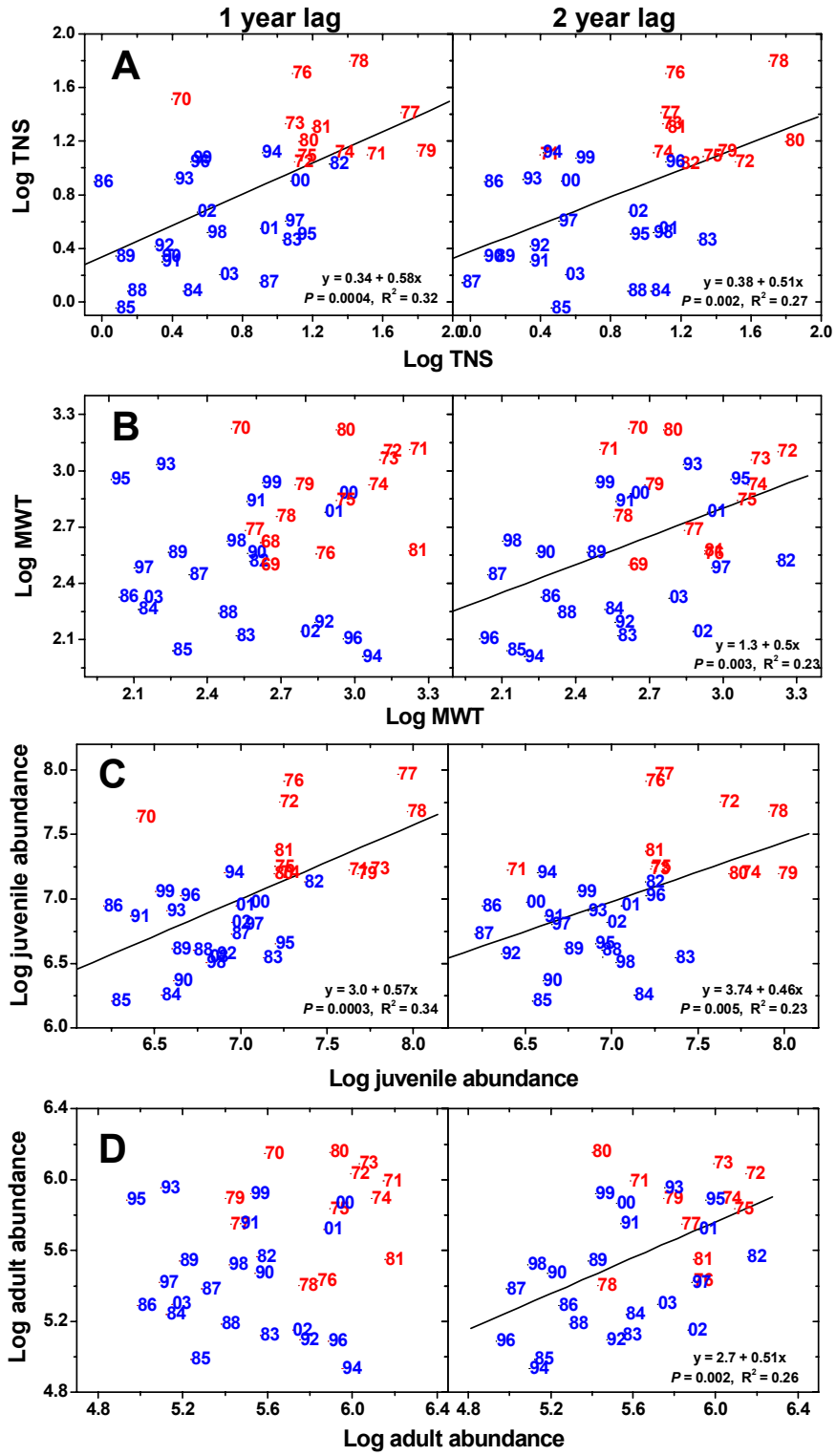


Figure 14. Auto-correlation relationships for juvenile (TNS) and pre-adult (MWT) delta smelt abundance indices (A, B) and abundance estimates (C, D) at years lagged one and two years. Fitted lines are linear regressions. Plotted numbers represent years before (<1982, red) and after (>1981, blue) the decline in delta smelt.

below, few exogenous factors are closely tied to delta smelt abundance. Thus, the autocorrelation at a two-year lag may reflect a small or intermittent, but important, influence of two-year-old females.

The number of two-year-old females in a given year may reflect variability in the timing and duration of the spawning season in the previous year: one possible alternative to a bet-hedging tactic. Delta smelt spawning success appears to be confined to water temperatures between about 15 to 20°C (Figures 10, 11). When a cool year is followed by a warm year, fish that are spawned late in the cool year may not reach reproductive maturity by the time water temperatures reach 20°C in the following warm year. These fish may then wait until year two to spawn. To explore this question, I estimated the number of two-year-old adults and the daily average temperature for Suisun Bay and the Delta during spring. The proportion of delta smelt over 80 mm FL in the MWT was used to represent two-year-old adults (Figure 15). Temperature data were then compiled from five DWR monitoring stations (1983–2002) and from the IEP zooplankton survey (1969–2002). Daily averages from the two data sources were highly correlated in overlapping years ($r = 0.85$, $P < 0.0001$), justifying use of both data sources in a single time series. The length of each annual spawning season for delta smelt was then estimated using the number of days water temperatures ranged from 15 to 20°C during spring. A plot of the range in days between 15 to 20°C shows that the timing and duration of the estimated spawning season has varied widely since the late 1960s (Figure 16). During the 1990s spawning seasons frequently extended into early June. During El Niño years, however, they can be constrained by rapidly rising water temperatures (e.g. 1983), and they are also typically preceded by an extended spawning season in the previous year (Figure 16). However, the estimated proportion of two-year-old fish is not associated with this spawning index. This analysis points to the need for field studies to determine the numbers and reproductive potential of two-year-old females during the spawning season to understand their potential importance for delta smelt population dynamics.

Stock-Recruit Relationships and Density Dependence

Stock-recruit analysis is a traditional approach for exploring the relative influences of density-dependent and density-independent limitations on population size. Density dependence occurs when population vital rates (per capita birth, death, fecundity) vary with the density of individuals. Organism density is expressed in units of the numbers of individuals per a measure of habitat, or space, and can only be equated with abundance if the amount of suitable habitat remains constant. Thus a population may experience density-dependent limitation at the same or lower abundance if the amount of suitable habitat shrinks. Density dependence is considered compensatory if population growth rate is negatively related to population density, meaning the population is limited at high density and a resilient growth response occurs at low densities. Density independent effects result from environmental influences on populations irrespective of their density; that is, with no feedbacks exerted at high densities to limit the population. Although density dependence would eventually provide an ultimate constraint on populations, its effects can be subtle and difficult to identify in many cases amidst high variability induced by environmental effects and sampling error (Strong 1986; Shepard and Cushing 1990; Dennis and Taper 1994). As a result, stock-recruit relationships typically exhibit considerable variability (see Myers and others 1995 for a catalogue of 274 relationships). Despite these inherent problems, identifying if and when density dependence occurs in a life cycle can have important implications for management and restoration. For example, compensatory density-dependent responses are a necessary condition for sustainable fishing (Sissenwine 1984; Shepard and Cushing 1990; Rose and others 2001).

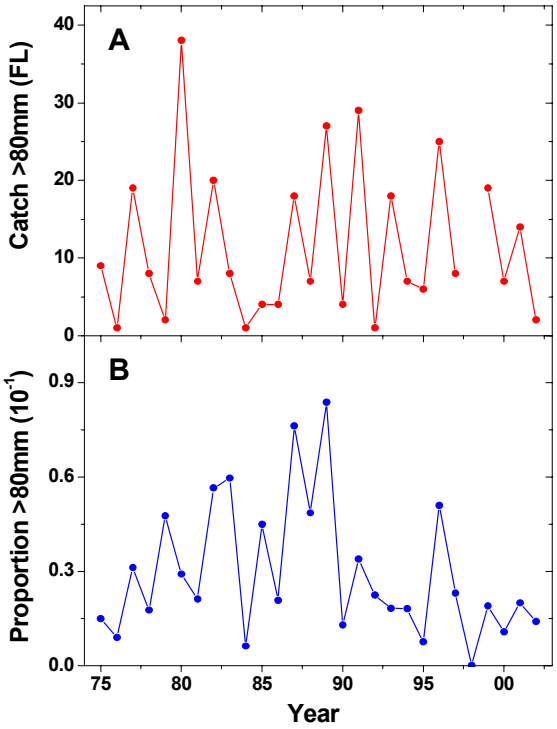


Figure 15. Annual catch (A) and proportion (B) of >80 mm delta smelt from the Midwater Trawl Survey.

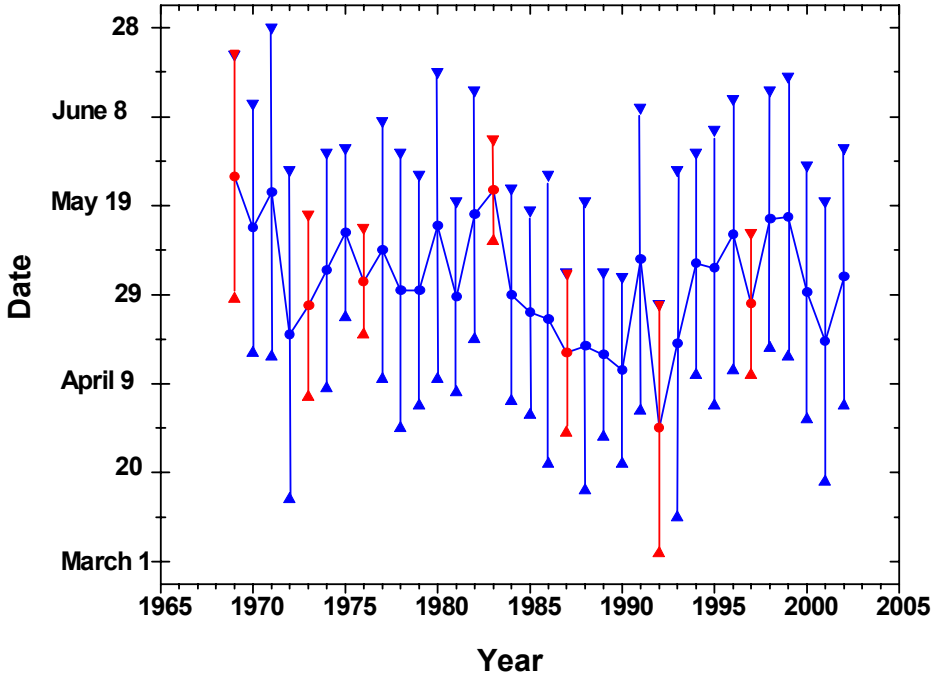


Figure 16. Range in daily of water temperature between 15 to 20°C averaged over Suisun Bay and the Delta during spring from 1969–2002. Red bars indicate El Niño years. Data for years 1983–present are from five DWR monitoring stations. Data for prior years are from the IEP Zooplankton Survey.

Previous attempts to evaluate density dependence in delta smelt examined relationships between the abundance of spawning stock and recruits using a traditional Beverton-Holt (1957) model (Moyle and others 1992; Sweetnam and Stevens 1993; DWR–USBR 1993; Miller 2000):

$$\text{Recruits} = \frac{1}{a + (b/\text{Spawners})} \quad \textbf{(1)}$$

where 1/a is the initial rate of increase, and 1/b is the asymptote of a curve, often interpreted as the carrying capacity (K) for the recruits. In these investigations coefficients of determination (R^2) were used to measure goodness of fit for relationships between MWT (spawning stock) and the MWT (recruits) in the following year (Moyle and others 1992; Sweetnam and Stevens 1993), as well as the MWT (spawning stock) and the TNS (recruits) in the following year (Miller 2000). Overall, the fitted models only explained about 25% of the variability in the data leading to the conclusion that environmental (or density-independent) factors regulated the delta smelt population (Moyle and others 1992; Sweetnam and Stevens 1993; DWR–USBR 1993; Miller 2000). This result was generally accepted, because density dependence seemed unlikely in a population with an annual life cycle at very low abundance: a conclusion assuming the amount of suitable habitat had remained constant.

Here, I re-evaluate density dependence using longer time-series for the MWT and TNS indices as well as the abundance estimates. Using stock-recruit analyses, I compare the relative fit of the Beverton-Holt (non-linear) model with a linear model that reflects density-independent processes (Quinn and Deriso 1999). Typically, comparing the relative fit of models with different conceptual interpretations is more appropriate for evaluating alternative hypotheses rather than examining the fit of any single model (Hilborn and Mangel 1997; Quinn and Deriso 1999). The fit of each model is assumed to pass through the origin because zero abundance of spawning stock would be expected to produce zero recruits. Because the appropriateness of this assumption using the abundance indices is uncertain, I also examine relationships using the abundance estimates. A variety of different stock-recruit scenarios was examined for delta smelt, but here I focus on four that encompass the range of life-history possibilities and model results (Figure 17):

- Intra-annual: juvenile to pre-adult stage in the same year.
- Inter-annual: pre-adult to juvenile stage in the following year.
- Inter-annual: pre-adult to pre-adult stage in the following year.
- Biannual: pre-adult to pre-adult stage two years later (the potential maximum generation time for delta smelt).

Instead of comparing coefficients of determination (R^2) model fits were evaluated using the residual sum of squares (RSS) and the Akaike Information Criterion (AIC) (Burnham and Anderson 1998; Quinn and Deriso 1999). For linear models with a zero intercept the R^2 statistic is inappropriate, because it is artificially inflated relative to the actual amount of variance explained by the model (Venables and Ripley 1997). Instead, the RSS measures the amount of residual variation unexplained by each model, and the AIC is a log-likelihood measure of the RSS penalized by the number of fitted parameters (Burnham and Anderson 1998). Thus, best-fit models have lower RSS and AIC values. In this instance, AIC is a conservative measure because the Beverton-Holt model has one more parameter than the linear model.

The results of the stock-recruitment modeling support the possibility that density dependence may limit the number of juveniles that reach the pre-adult life stage in some years. The Beverton-Holt model provides a better fit (lower RSS and AIC) than the linear

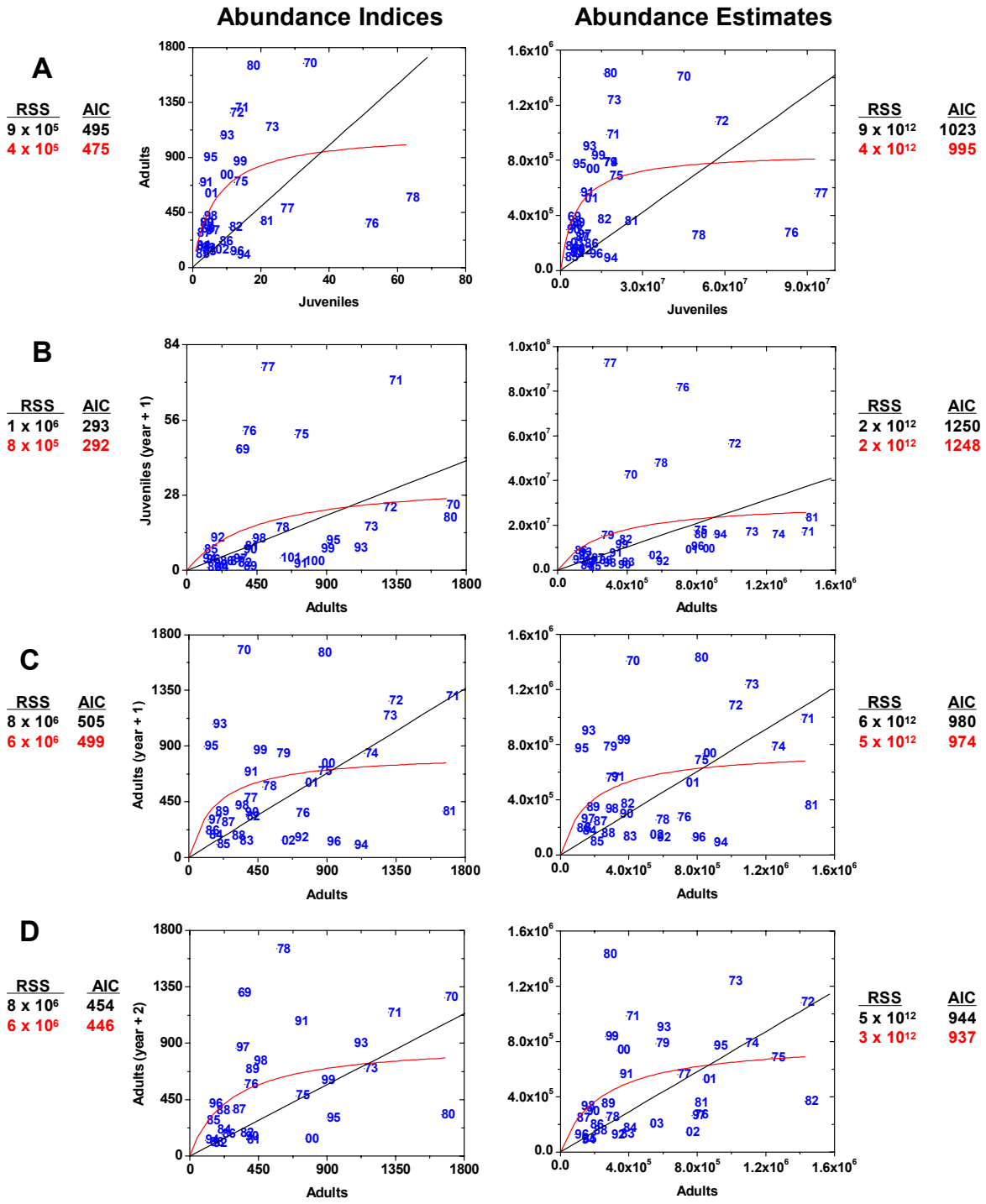


Figure 17. Stock recruitment relationships comparing a Beverton-Holt with a linear model using the abundance indices and abundance estimates for the juvenile to pre-adult stage (A), pre-adult to following juvenile stage (B), pre-adult to pre-adult stage in the following year (C) and from the pre-adult to pre-adult stage two years later (D). Model fits are compared using the residual sum of squares (RSS) and Akaike's Information Criterion (AIC). Plotted numbers represent years.

model for the intra-annual relationship between the TNS and MWT as well as a similar relationship using abundance estimates (Figure 17A). In contrast, model fits are equivalent for the scenario using the MWT and TNS in the following year (Figure 17B), suggesting that environmental factors dominant during the spawning and larval rearing stages. In the inter-annual and biannual scenarios, the Beverton-Holt model again explains a higher proportion of the variation between pre-adults (spawning stock) and pre-adults (recruits) one or two years later (Figures 17C, 17D). By using scenarios that reflect different periods in the entire life-cycle, it appears that density dependence may occur in some years during late summer when juveniles are recruiting to the pre-adult stage.

Although use of the entire data-record suggests density dependence may have occurred mostly during the 1970s, it is still detectable in recent years. High juvenile abundances, primarily in the 1970s, are a strong influence on the stock-recruit relationships; subsequent years tend to fall below the inflection point of model fits (Figure 17A). To address this issue, the previous analyses were repeated separating the data into pre- and post-decline periods, with 1969–1981 reflecting the pre-decline and 1982–2002 representing the post-decline period. Comparisons of model fits for each period indicate that the density-dependent models again have lower AIC values than the density-independent models (Figure 18). Therefore, these analyses support the possibility that density dependence also may have limited abundance in recent years. Moreover, comparison of Beverton-Holt model fits between the pre- and post-decline periods indicate that carrying capacity may have declined by about one-half between the two time periods (Figure 18). In the pre-decline period, the fitted curve begins to asymptote at MWT values between 600 to 800 and abundance estimates of about 8 x 10^6 fish, whereas in the post-decline period the curve asymptotes somewhere between 400 and 450 and an abundance estimate of about 4 x 10^6 fish (Figure 18). Thus, density dependence may be occurring in some recent years at lower levels of abundance than before the population declined. The potential occurrence of density dependence for delta smelt seems unlikely because a straightforward mechanism is not apparent for how a threatened fish could be limited by feedbacks on density. Although delta smelt are relatively rare, the population may still be limited by a critical resource, or suitable habitat may have declined over time. Habitat loss is a reasonable possibility for delta smelt given our limited knowledge of the ecology and the dramatic hydrological and food web changes that have occurred within its range over the past several decades. Overall, evidence for density dependence is most clearly observed in spatially-limited systems; for example, where abundance overwhelms available spawning habitat or territories (e.g. salmonids, Elliot 1994; Rose and others 2001). This is a possibility for delta smelt that appear to have specific spawning habitat requirements (see “Spawning and Egg Stages”), however, the various stock-recruit scenarios examined above imply that density dependence most likely occurs in the juvenile stage during the late summer: a pattern observed in a variety of other fish species (Cowan and others 2000). This issue is further addressed in the section describing “Carrying Capacity.”

While somewhat preliminary, the evidence for density dependence outlined above begs the question regarding mechanisms of population regulation. Further understanding of this mechanism is essential because density dependence implies a surplus of juveniles may occur in years of relatively high abundance. Thus it has major implications for assessing and managing the influences of human activities on the population, particularly losses of fish to the water export facilities. In addition, density dependence also has important implications for determining restoration options, especially if the capacity of low-salinity habitat to support delta smelt has declined in recent years. However, measuring the magnitude of density dependence is not easy, and will require field measurements of fish

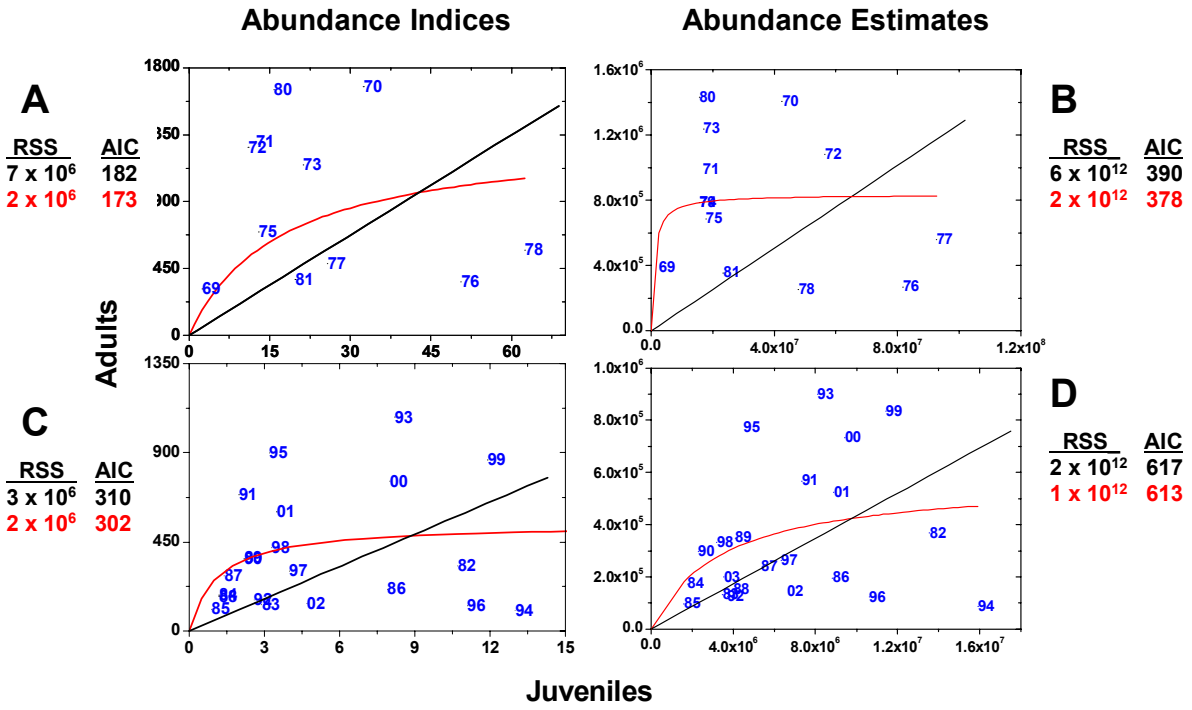


Figure 18. Stock recruitment relationships for the juvenile to pre-adult stage comparing a Beverton-Holt with a linear model for the period before the population decline (1967–1981) using the abundance indices (A) and abundance estimates (B). Similar relationships are also shown for the post-decline period (C,D).

condition, food resources, with detailed information on the physical environment to measure habitat suitability.

Environmental Factors

A variety of environmental factors influences delta smelt mortality. The Delta Native Fishes Recovery Team (Moyle and others 1996) and Estuarine Ecology Team (1997) listed several, including water project operations and entrainment, exotic species, food supplies, habitat loss and degradation, contaminants, and retention in the low salinity zone. Although typically treated as alternative mechanisms, their effects are not mutually exclusive. In reality, complex pathways of biological, environmental, and anthropogenic processes contribute to regulate abundance (Bennett and Moyle 1996). There is also a large stochastic component with effects operating sporadically in episodes or as subtle processes over time (Houde 1989). Bender and others (1984) described these environmental influences as “pulse” or “press” effects on population dynamics. Press effects, such as prolonged changes in food supplies, can influence carrying capacities of populations. In contrast, populations tend to rebound to former levels following a pulse effect, such as a major toxic spill or predation event. However, several different pulses or presses can occur simultaneously. I begin this section by discussing physical and anthropogenic factors and then alterations to the food web. Finally factors possibly determining carrying capacity are addressed.

Habitat Volume. Delta smelt habitat extends from the tidal freshwater reaches of the Delta seaward to about 19 psu salinity at water temperatures lower than 25°C. The volume and shape of this habitat is determined by climate, anthropogenic regulation of freshwater discharge, tidal forcing, and bathymetry. Inter-annual abundances of various biota are explained by the amount of freshwater outflow as indexed by X2, defined as the average distance (km) of 2 psu bottom salinity from the Golden Gate Bridge (Stevens 1977; Jassby and others 1995; Kimmerer 2002, 2004). Numerous mechanisms may underlie these relationships (Kimmerer 2002). However, unlike many other species, the abundance of delta smelt is not easily explained by this indicator or its analogue, freshwater flow (Figure 11, Stevens and Miller 1983; Kimmerer 2002).

Overall, delta smelt recruitment success is poor during drought and flood years, and highly variable during intermediate flow years when low salinity habitat is located in Suisun Bay (Figure 19A, Moyle and others 1992). This observation was first formalized by Obrebski (1993) who identified a significant relationship between the MWT index and the position of the low salinity zone in Suisun Bay. Herbold (1994) then found a significant relationship between the number of spring days X2 was located in Suisun Bay and adult abundance; a relationship that underlies the logic for the current salinity standards. However, this correlation no longer holds for the MWT index ($r = 0.30$, $P = 0.08$) or adult abundance ($r = 0.31$, $P = 0.06$, Figure 19C). In several recent years (since 1993) adult abundance remained fairly low even though X2 frequently was located in Suisun Bay (Figure 19C). Although recent abundances have been lower than anticipated, adult abundance is always low when X2 is located in the lower Sacramento and San Joaquin rivers (Figure 19A).

One possibility driving the confusion may be that delta smelt are responding differently to X2 since the population declined, or that other changes to the physical habitat have overridden the influence of freshwater discharge. Recently, Kimmerer (2002) found a positive relationship between juvenile smelt abundance and X2 position before the decline occurred in 1982, and a negative trend (recalculated here including 2003 data; $r = -0.39$, $P = 0.07$) since that time (Figure 19B). Similarly dividing the data into pre- and post-decline years for juvenile abundance and the number of days X2 was located in Suisun Bay, does not improve these relationships (Figure 19D). While these findings are puzzling, the differences in the trends suggest that spawning or rearing habitat in the lower rivers and Delta may have been more favorable for delta smelt before the 1982 than over the last two decades.

The importance of spawning and rearing habitat in Suisun Bay is also suggested by the analyses of Unger (1994). He showed that the overall surface area of habitat bounded by 0.3 to 1.8 psu was maximized with X2 positioned in Suisun Bay. When this habitat measure was weighted by the average monthly occurrence of larval and juvenile smelt he found a significant correlation with adult abundance. This finding is provocative, although it is preliminary and based on a fairly loose definition of delta smelt habitat. Changing habitat volume may be a key mechanism underlying density dependence. MacCall (1990) formalized this process using habitat selection models for pelagic fish. Larger habitat volume reduces crowding and provides opportunities to avoid localized sources of mortality, allowing for the “spreading-of-risk” over space (den Boer 1968). A potential change in habitat volume may underlie the observation that juvenile delta smelt are now rarely caught in the south Delta (DWR–USBR 1993, Sweetnam and Stevens 1993). Thus, it would be worthwhile to revisit this idea using current knowledge of the delta smelt habitat and newer modeling capabilities.

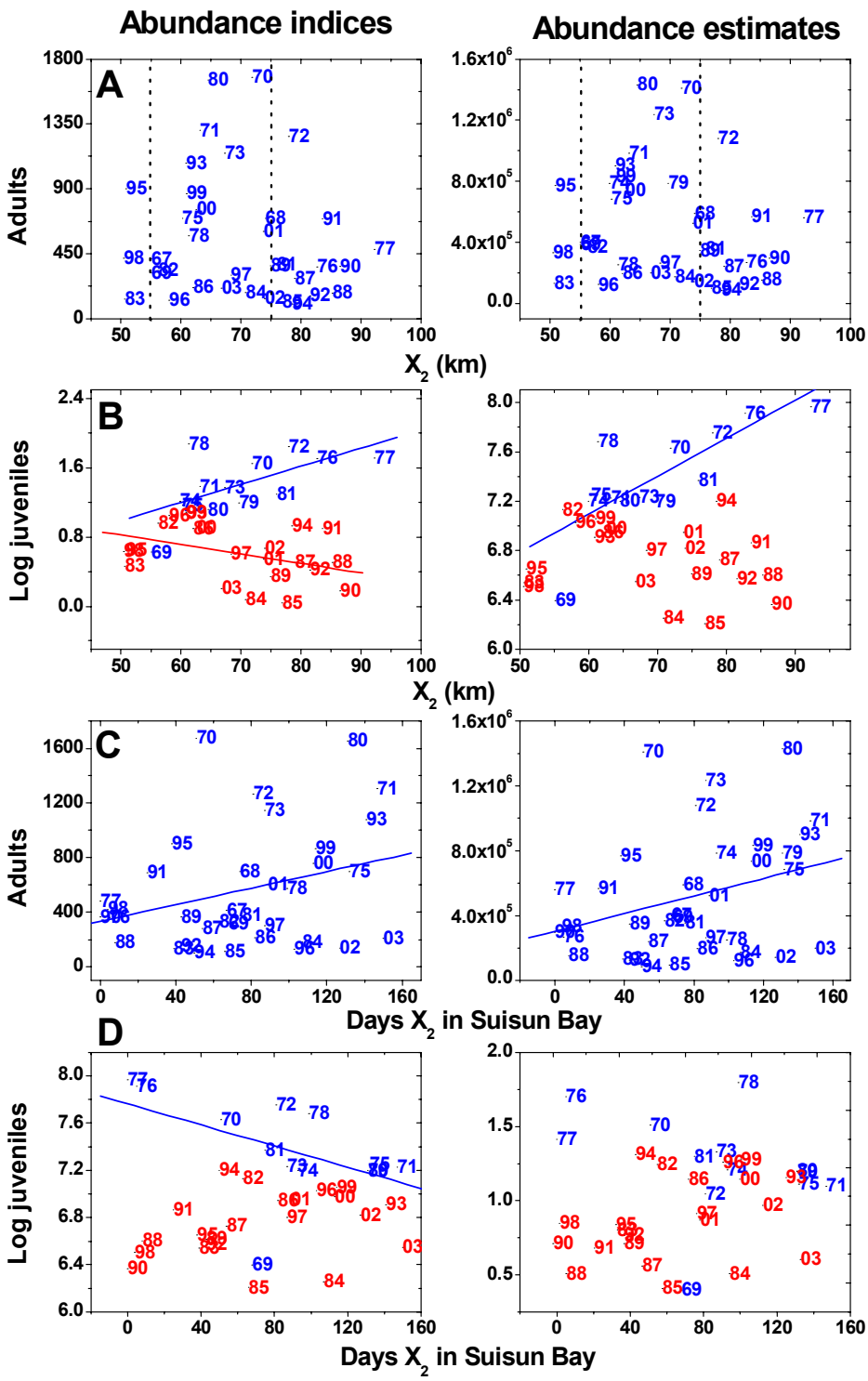


Figure 19. Various relationships between delta smelt abundance and position of the low salinity zone as indexed by X2. Delta smelt pre-adults (MWT index and abundance) with the average position of X2 during spring (A, X2 positions within vertical dotted lines reflect Suisun Bay), and for juveniles (TNS) by dividing the time series into before (1967–1981) and post-decline periods (B). Similar relationships are shown using the number of days during spring that X2 is located in Suisun Bay (C, D).

Indeed, habitat within Suisun Bay is not of the same quality. Moyle and others (1992, 1996) originally suggested that low salinity habitat distributed over shoal areas was more productive and provided better rearing conditions than habitat confined to deeper channels. This idea is appearing to hold true. In the low salinity zone studies, delta smelt were 8 times more abundant in northern Suisun Bay and adjoining shallows in Honker Bay and Grizzly Bay than in the deeper Ship channel to the south (Bennett and others 2002). Recent evaluations of these samples are also showing that post-larvae were on average larger and had higher feeding success in the north shoal area than in the Ship channel (Hobbs and others 2004). Therefore, several lines of evidence indicate that maintaining low salinity habitat in Suisun Bay during spring can be beneficial for delta smelt. This does not guarantee recruitment success, but may increase its probability.

Climate Change and Spawning Success. Longer spawning seasons can also increase the potential for high recruitment success. More opportunities for spawning can result in more cohorts (Figure 11), spreading the risk from various sources of mortality over time (den Boer 1968). The potential benefits of longer spawning seasons may be also enhanced if delta smelt spawn more than once in a single season (see "Generation Time"). Several mechanisms affecting recruitment have a temporal component (e.g. co-occurrence with food supplies, predators, or pulses of toxic chemicals) thus the probability of encountering an adverse condition will differ for fish spawned at different times. Estimated spawning season durations (Figure 16) show a positive trend with post-larval (20 mm) abundance, although only seven data points were available, and they do not explain juvenile abundance (Figure 20). However, they are significantly associated with adult abundance, especially since the decline occurred (Figure 20). This demonstrates that spreading cohorts in time may increase the probability of high adult abundance.

Duration of the spawning season is a function of climate and thus may be affected by extreme climatic events. As shown before (Figure 16), many spawning seasons appear to have ended relatively early in spring, especially during El Niño episodes. To examine this, I developed an index of climate change calculated as the first principle component of three environmental variables, sea surface temperature and sea level at Fort Point (entrance to the SFE at the Golden Gate Bridge) and the Pacific Decadal Oscillation (PDO), an index of inter-decadal climate regimes (Mantua and others 1997). The derived index is negatively associated with the last day of spawning season (Julian date water temperature reaches 20°C, Figure 21A), indicating that the delta smelt habitat warms faster during El Niños. The climate index is also negatively associated with juvenile and adult abundance (Figures 21B and 21C). Thus, spring water temperatures may provide an early indication of when to expect good versus poor recruitment success. Moreover, long-term climatic warming may be expected to have negative effects on delta smelt abundance by marginalizing spawning in the future.

Water Exports. Water project operations are by far the most conspicuous and controversial factor contributing to mortality in delta smelt. Overall, however, their impact on the population is a fundamental gap in knowledge. Large numbers of smelt are lost to the CVP and SWP water export facilities located in the south Delta, various smaller facilities (e.g. North Bay Aqueduct, PG&E powerplant), as well as about 2,200 agricultural diversions in the Delta (Herren and Kawasaki 2001). Relative to other factors, reasonably accurate estimates of delta smelt

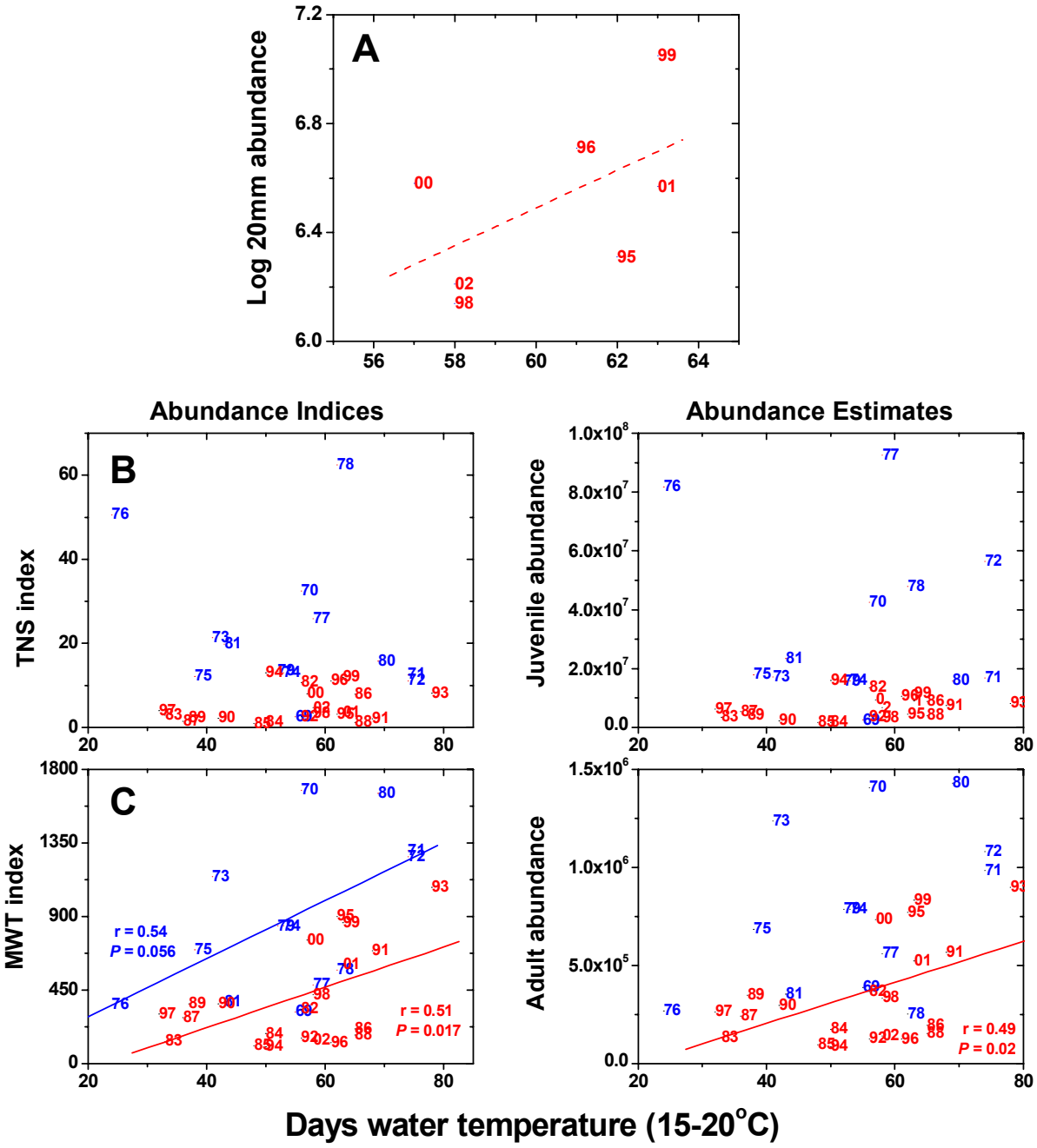


Figure 20. Relationships between delta smelt abundance and duration of spawning season as indexed by water temperature (15 to 20°C) for 20 mm post-larvae (A), juveniles (TNS, B), and pre-adults (MWT, A) as well as abundance estimates. Fitted solid lines are significant linear regressions, and the fitted dotted line shows a trend, for periods before (blue) and after (red) the decline in delta smelt. Numbered points are years.

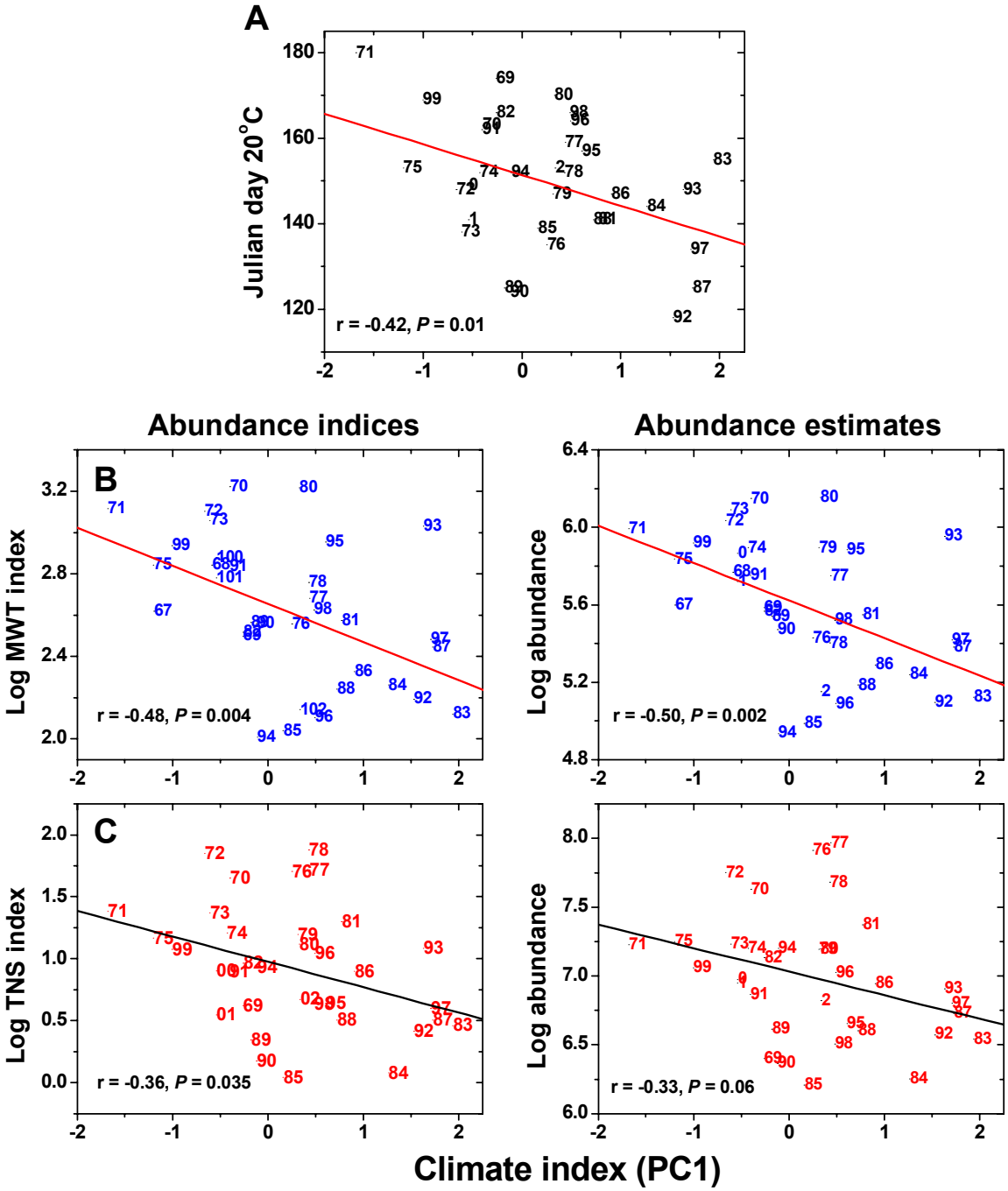


Figure 21. Relationships between the end of the annual spawning season (A), pre-adult (B) and juvenile (C) abundance, with an index of climate change. End of the spawning season is represented as the Julian day water temperatures in Suisun Bay and the Delta reach 20°C. The index of climate change is the first principal component using sea surface temperature, sea level at the Golden Gate Bridge, and the Pacific Decadal Oscillation index (Mantua and others 1997). Fitted lines are general linear regressions.

lost to the major facilities are recorded for fish larger than about 20 mm FL (Figure 2). Although there has been an effort to salvage these fish and return them to the system, delta smelt are very fragile and most of them die druing the salvage process. Losses of fish smaller than about 20 mm (larvae) can not be determined and are a key uncertainty for evaluating the effects of water operations. In addition, the numbers of fish entrained in the many smaller, mostly agricultural, diversions are also unknown. Understanding total entrainment losses is essential. For example, juvenile abundance (TNS) is positively associated with the salvage of fish >20 mm, but negatively associated with total water exported from the south Delta water facilities (Figure 22). Thus, the number salvaged merely tracks the abundance of juveniles, but total water exported may serve as a proxy describing losses of larvae <20 mm, as well as juveniles. In several respects, losses to the water export facilities are analogous to harvest in a fishery, with the main exception that "harvest" in this case includes all life stages (except eggs).

As first step, assessing the potential impacts of the water project operations on delta smelt requires estimating the proportion lost relative to population abundance. Initial attempts to examine proportional losses were sparked by high entrainment of juveniles in May–June 1999. Entrainment at the CVP and SWP exceeded the Federal incidental takelimits by nearly seven-fold (Nobriga and others 1999). (Incidental take limits are specified by the USFWS to avoid jeopardizing the persistence of the species.) Ensuing restrictions on freshwater export pumping may have curbed further mortality, but raised serious questions over the potential impacts to the delta smelt population. As a result, three abundance estimates were independently commissioned for delta smelt located in the vicinity of the pumping facilities' intakes by the USFWS, DWR, and stakeholders (Z. Hymanson, DWR, and C. Hanson, pers. comm.). These approaches similarly extrapolated densities of fish from the monitoring surveys to the volume of habitat in the south Delta region, and provided estimates of abundance ranging from 4 to 7 million individuals. Although the relative merits of each estimate were subsequently debated, they all fell within an order of magnitude indicating some degree of precision with the extrapolation approach (similar to the one employed here, Figure 3).

Recently, an alternative analysis suggested that water exports can have high impacts on post-larval and juvenile delta smelt. Kimmerer (San Francisco State University, pers. comm.) calculated the flux of post-larvae from the south Delta as a fraction of the total daily catch in the 20-mm Survey. Estimates of the percent of post-larvae exported per day from the Delta and Suisun Bay were generally negligible ranging from 0 for most days to about 4.5% in the peak episode during 1999 (Figure 23A). At first glance this suggests that impacts on post-larvae may have been very low since the survey began in 1995. Kimmerer then estimated the daily number of juveniles exported from the south Delta as a proportion of total caught in the TNS (Figure 23B). Although these estimates also suggest daily export rate is minor (ranging from about 0 to 0.6% per day), the percent lost can be quite large if they accumulate over the duration of each survey. For example, estimated cumulative impacts of exports have ranged from 0 in 1995 to about 60% in 1999 for post-larvae. For juveniles, average daily export rates were about 0.4% during 1985, however over a 60-day period the cumulative impact on juveniles would about 24% (Figure 23B). Yet, losses of this magnitude have been intermittent and primarily during the early part of the time series. In addition, they also decline abruptly during each season as the population distribution shifts away from the south Delta, indicating that losses have been higher for earlier spawned fish (Figure 23). However, these results should be viewed as speculative considering the large uncertainties associated with the sampling efficiencies of the monitoring surveys (see "Population Abundance").

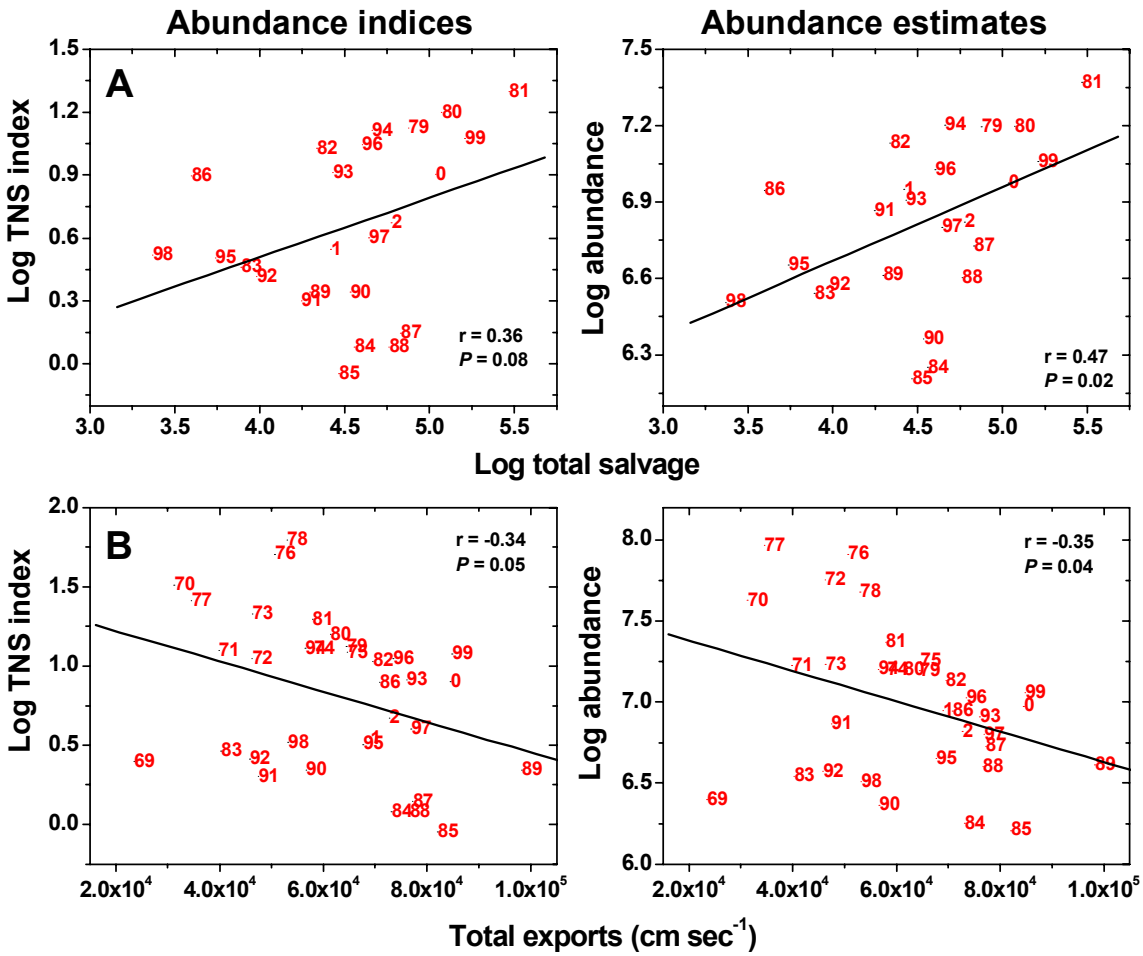


Figure 22. Relationships between juvenile abundance (TNS) with the estimated number of fish lost in water project operations (salvage) (A) and total water exported by the California State Water Project (SWP) and Federal Central Valley Project (CVP) (B). Fitted lines are linear regressions.

In reality, however, estimating the proportion lost to exports misrepresents their actual impact on the population, especially during years if and when other sources of mortality (e.g. density dependent effects) are important at later life stages. As in many fisheries, estimates of "harvest" by the water export facilities also need to be evaluated in the context of other sources of mortality. In years of high juvenile abundance, density dependent effects may minimize the impact of export losses. For example, even though an estimated 73,380 juveniles were lost during spring 1999 (Nobriga and others 1999), adult abundance later in the year (MWT = 864) was one of the highest recorded since the population declined. Thus, fish lost to entrainment in export facilities in some years may not have survived anyway. Conversely, in years when few cohorts are spawned (e.g., during warm years such as 1983; Figures 11, 16), entrainment losses may severely affect year-class success. However, even in years of low abundance it is possible that many fish lost in the water exports were weak and destined to die after exposure to toxic chemicals or low feeding success. Thus it is unlikely that losses of young fish to the export facilities consistently reflect a direct impact on recruitment success later in the year. These issues cannot be resolved without a comprehensive program to investigate the delta smelt population.

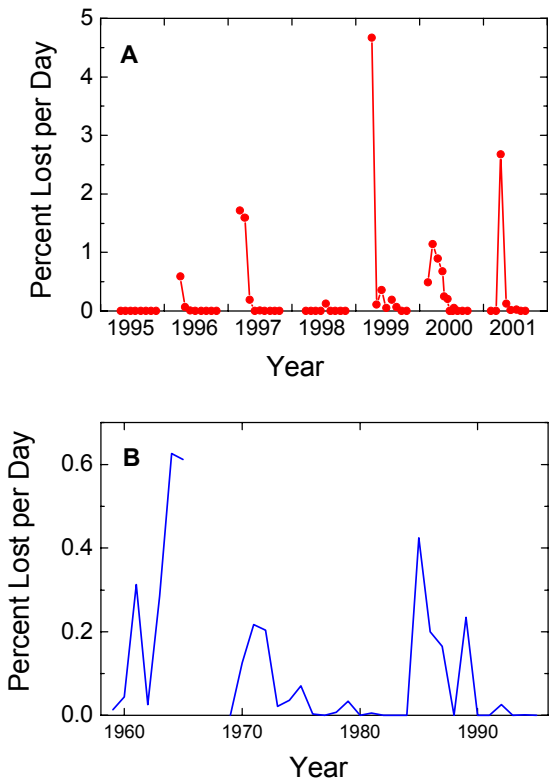


Figure 23. Flux of post-larval delta smelt from the south Delta in exported water as a percent of the total daily catch in the 20-mm Survey (A), and the number of juveniles lost to water exports as a percent of the daily total catch in the TNS (B). Graphs courtesy of W. Kimmerer, SFSU.

Tracking cohorts using growth over time demonstrates how export losses can affect recruitment success (Bennett and others, in prep.). In 1999, an extended spawning season produced several cohorts that then appeared in the 20-mm post-larval survey (Figure 11). Birth dates were estimated from daily growth increments in juvenile otoliths, and then forecasted using a mean growth rate (Figure 6B) to estimate which cohorts were salvaged at the pumping facilities (Figure 24). A cohort of fish hatched during the end of March (red bars, Figure 24A) made up 73% of the May–June losses (Figure 24B), but then comprised only about 6% of the TNS (Figure 24C). While losses from that cohort appear significant, recruitment success may have remained fairly high because several other cohorts were produced that year. This result compares well with Kimmerer's analysis (Figure 23), in that most effects were on the cohort spawned early in the season. Although this approach is currently limited by our knowledge of the efficiencies of the various sampling nets and monitoring of fish losses at the export facilities, tracking cohorts can significantly improve our understanding of recruitment success for delta smelt.

Information for smaller diversions is less available. Two studies have examined the effect of agricultural diversions on fish (Cook and Buffaloe 1998; Nobriga and others 2004). In both studies catches of delta smelt were low. Nobriga and others 2004 quantified these effects by evaluating flow rate as well as tidal and diel influences on the vulnerability of juvenile delta smelt. Water withdrawn by a screened and a nearby unscreened diversion pipe were monitored in 70, approximately hourly, samples in 2000 and 2001 when the catches of post-larval delta smelt in the 20-mm Survey were high in the adjacent Sacramento River. No smelt were entrained in the screened diversion, whereas in the unscreened pipe losses were intermittent and low compared to other fishes (e.g. inland silversides) with peaks (4 to 5 fish 10^{-4} m^3) occurring near dusk and dawn. Overall, delta smelt remained primarily offshore in the main river channel reducing their vulnerability. Although the use of channel habitat may reduce the delta smelt's vulnerability to agricultural diversions, it was the most abundant species entrained during a more qualitative study of a larger diversion in Suisun Marsh (Pickard and others 1982), suggesting that at certain times and locations smaller diversions may take larger numbers.

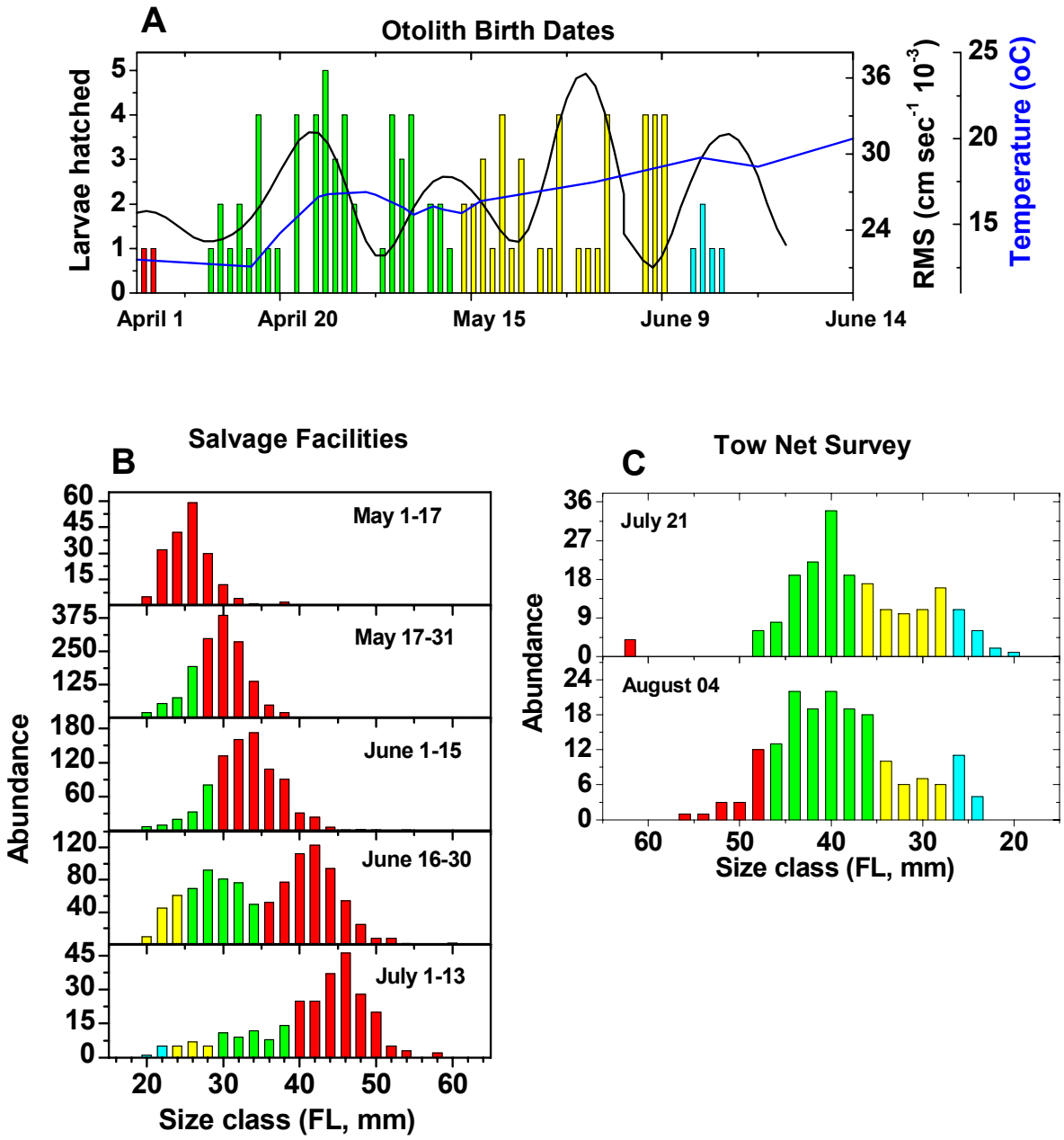


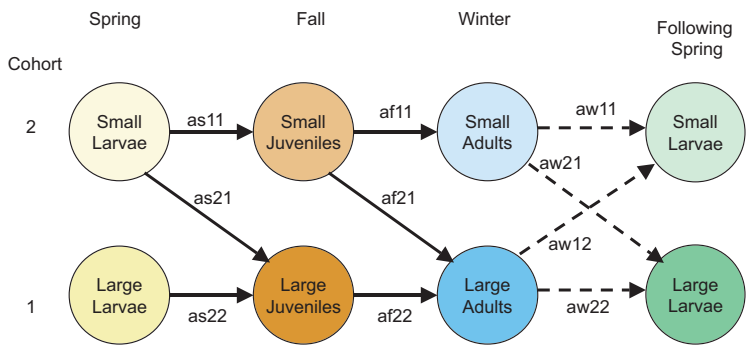
Figure 24. Potential loss of juvenile cohorts to the water export facilities in 1999. (A) Birth dates back-calculated from juvenile (TNS) otoliths (colored bars) with RMS tidal velocity (black line) and water temperature (blue line) during spring 1999. (B) Size-frequency distributions of fish lost to the water export facilities (salvage) and that subsequently appear in the (C) juvenile TNS.

If juveniles are vulnerable to many sources of mortality, should adults be given higher priority for protection? Intuitively it makes sense that adults would be worth more to the population because they have successfully avoided many risks. Previous analyses identified significant relationships between losses of pre-spawning adults in winter salvage and subsequent year class success, suggesting it may be beneficial to reduce water project impacts on this life stage (Bennett, unpublished analyses). However, relationships between pre-spawning adults and winter salvage no longer hold with more recent data included in the analyses.

Population modeling may be the best way to evaluate the potential impacts of water export operations relative to other sources of mortality. Here, I develop a stage-structured population model to examine potential tradeoffs among sources of mortality acting on different cohorts and life stages (Bennett, in prep.). These deterministic linear models incorporate relative survival and fecundity among life stages, assuming that all individuals in an age-class are identical and that the vital rates remain constant over time (Caswell 2001). Because delta smelt is primarily an annual species where seasonal processes dominate, I developed a periodic-stage model (Caswell 2001) that projects population abundance among years based on the dynamics of several seasonal matrices. I then use this modeling approach as a heuristic tool to analyze (1) model sensitivity (elasticities) as measured by the proportional contribution of each cohort and life stage to population growth (intrinsic rate of growth, *r*), and (2) simulations of the effect of changing key parameters on "*r*" for models with and without mortality due to water exports.

The model is composed of three seasonal matrices that roughly represent spring (March–June), summer (July–September), and fall-winter (October–February). Because this is a stage-model it is not necessary for each season to be of equal length (Caswell 2001). Among each season the model tracks the relative survival of two cohorts of individuals that were born early versus late in spring (Figure 25). The cohorts are represented as large (early-spawned) and small (late-spawned) individuals because at the time of transition to the next season (June 30) many fishes spawned early would be larger than those born later. Survival estimates were calculated as the average slope of fitted regression lines from catch curves between the abundance estimates for eggs, larvae (20-mm abundance), juveniles (TNS abundance), and adults (MWT abundance) from 1995–2003 (Figure 26). Egg abundances were calculated by weighting adult abundance by the average fecundity of females <80 mm FL from aquaculture (2,100 eggs, Figure 9; B. Baskerville-Bridges, UCD, pers. comm.) assuming a 50:50 sex ratio. Apparent size-selective bias of post-larvae by the sampling gear early in the season produced abundance estimates that were lower than those for juveniles in the TNS survey: a biological impossibility that would severely bias survival estimates. To help account for this, post-larval abundances were calculated using only surveys in which the mean length of fish was >20 mm FL, but even with this adjustment the estimates still contain size-selective bias.

The model requires two fecundity and five survival parameters to estimate the transition probabilities between successive seasons (Table 2). Large larvae are assumed to transition into large juveniles and adults, whereas small larvae transition as 25% large and 75% small juveniles and adults. Large adults are then assumed to spawn primarily early in the season producing 75% large and 25% small larvae, whereas small adults spawn evenly throughout the season producing 50% large and 50% small larvae. These proportions were chosen to reflect the potential that large



$$\begin{pmatrix} as11 & 0 \\ as21 & as22 \end{pmatrix} \cdot \begin{pmatrix} af11 & 0 \\ af21 & af22 \end{pmatrix} \cdot \begin{pmatrix} aw11 & aw12 \\ aw21 & aw22 \end{pmatrix} = A$$

Figure 25. Periodic stage-bases population model composed of three seasonal matrices that follows the fate of two cohorts. The model projects a small and large cohort of larvae to the following spring by multiplying the individual seasonal matrices into an aggregate matrix.

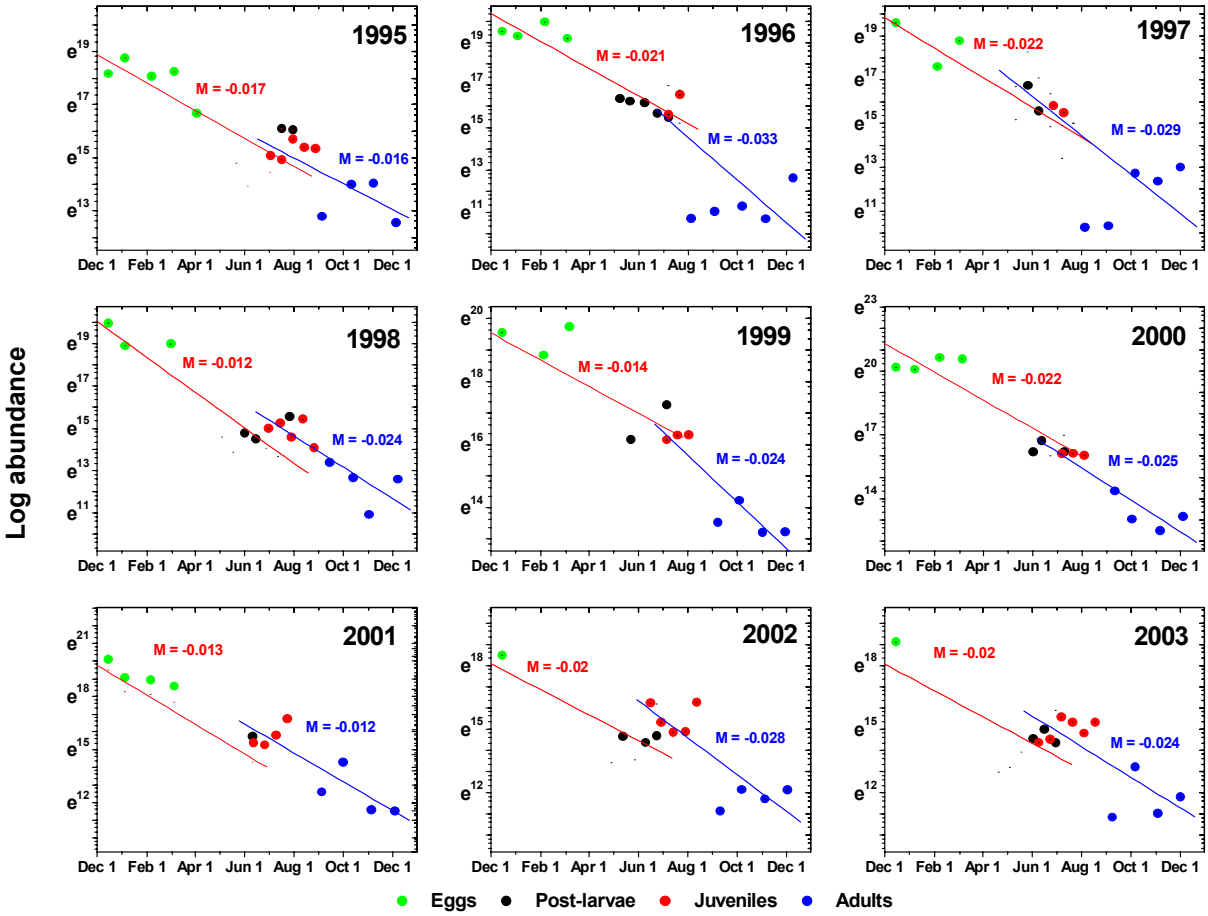


Figure 26. Delta smelt catch curves showing instantaneous mortality rates among life stages (M) calculated as the slope of linear regressions.

adults may mature earlier in the season than small adults. In the future, model sensitivity to changes in these proportions would be worthwhile to examine, but for this example they remain fixed. Large adults were also assumed to produce more eggs (median = 3,283; 77 to 93 mm FL) than small adults (median = 1,870; <75 mm FL) again based on Baskerville-Bridges' relationship (Figure 9). Export losses of fish were assumed to affect only large (early-spawned) post-larvae and were calculated from estimated losses per day in spring 1999 (Figure 23A, W. Kimmerer, San Francisco State University, pers. comm.).

Separate models, with and without export mortality, project the numbers of large and small larvae from spring to the following spring by calculating the product of the three seasonal

Table 2. The definition and estimates of parameters and transitions used in the periodic stage model for the delta smelt population

Transitions / Definition	*Estimate*
Parameters	
Fecundity small female eggs	1870/2 = 935
Fecundity large female eggs	3283/2 = 1642
Survival	
Fall adult to spring adult	0.59
Spring egg abundance to larvae	0.018
Larvae to juvenile	0.83
Exports during larval stage	0.40
Juvenile to fall adult	0.09
Spring	
as11 – Probability of small larvae becoming a small juvenile	0.83 x 0.75 = 0.62
as21 – Probability of small larvae becoming a large juvenile	0.83 x 0.25 = 0.21
as22 – Probability of large larvae becoming a large juvenile	0.83
as22 – Probability of large larvae becoming a large juvenile with export mortality	0.83 x 0.40 = 0.332
Fall	
af11 – Probability of small juvenile becoming a small adult	0.09 x 0.75 = 0.067
af21 – Probability of small juvenile becoming a large adult	0.09 x 0.25 = 0.023
af22 – Probability of large juvenile becoming a large adult	0.09
Winter	
aw11 – Number of small larvae produced by small adults	935 x 0.018 x 0.59 x 0.5 = 4
aw21 – Number of large larvae produced by small adults	935 x 0.018 x 0.59 x 0.5 = 4
aw22 – Number of large larvae produced by large adults	1642 x 0.018 x 0.59 x 0.75 = 13
aw12 – Number of small larvae produced by large adults	1642 x 0.018 x 0.59 x 0.25 = 4

matrices (Figure 25). Elasticities reflect the proportional change in population growth rate (r) given a small change in each matrix parameter, and thus can identify the relative importance of each cohort or life stage on population growth (Figure 26A, Caswell 2001). Elasticities calculated for the aggregate matrices show that the population growth rate is primarily influenced by factors influencing large larvae (Figure 26A). Including mortality induced by water exports does not change the overall pattern in elasticities, only slightly reducing the influence of large larvae on "*r*", and increasing the importance of small larvae (Figure 26A). This result reflects the structure of the model in which transitions and fecundities were chosen to favor large larvae (Houde 1987). However, because even apparently excessive losses in spring 1999 do not markedly influence the model elasticities, these results imply that export impacts may be difficult to detect on delta smelt population dynamics.

Simulating the influence of model parameters on population growth rate also suggests that impacts from losses to the export facilities may be difficult to detect. Estimates of cumulative export mortality during the post-larval (20 mm) season ranged from 0 in 1995 to about 60% in 1999 (Figure 23A). Projected population growth rates are relatively insensitive to changes in export mortality but highly sensitive to small changes in juvenile-adult and adult-larval mortality (Figure 27B). In addition, population growth rates remain positive when export losses are less than about 20%. These results show how export mortality could be easily offset or masked by very small changes in mortality at other life stages. For example, maximum export losses in 1999 were followed by relatively high survival between the juvenile-adult and then adult-larval stage in the following year. Because the overall range in mortality rates at these stages is only about 0.2, small differences in mortality may dramatically influence the numbers of adults or larvae in the following spring. More importantly they may also be logistically difficult to measure accurately, precluding an effective evaluation of mortality due to water export operations.

While these results are illustrative of how export effects may influence the delta smelt population, they are premature for management purposes. The model presented here is only one of many possible stage-structured forms and modeling approaches that should be investigated before useful management options can be developed. This would also require considerable refinement of the assumptions and vital rates used to develop model parameters. Simulations of a wider variety of such models can identify key areas of robustness and sensitivity that would have more direct relevance for management.

Toxic Chemicals. The importance of exposure to toxic chemicals on the population is highly uncertain. Numerous toxic chemicals from a variety of sources enter the delta smelt habitat (Thompson and others 2000). Pesticides from urban and agricultural run-off enter the system in large pulses during late winter and continue through the larval rearing period when delta smelt are most vulnerable (Kuivila and Foe 1995). However, time-series of chemical concentrations in the spawning habitat are lacking and impractical to obtain considering the potential for synergisms among chemicals, and rapid evolution of chemical use by agricultural and urban interests (Bennett 1996; Moon and others 2000). Pesticides have been shown to affect larval striped bass that co-occur with larval delta smelt, although a decrease in these effects was observed after agricultural practices were modified (Bennett and others 1995). Bioassays also regularly detect effects on aquatic test organisms (Thompson and others 2000); while the species used in tests are typically not found in the system, results from these tests may reflect an important but largely undocumented problem. Assessing the extent of this problem will be difficult especially because effects from toxic chemicals need to be distinguished from other processes affecting fish condition and population abundance.

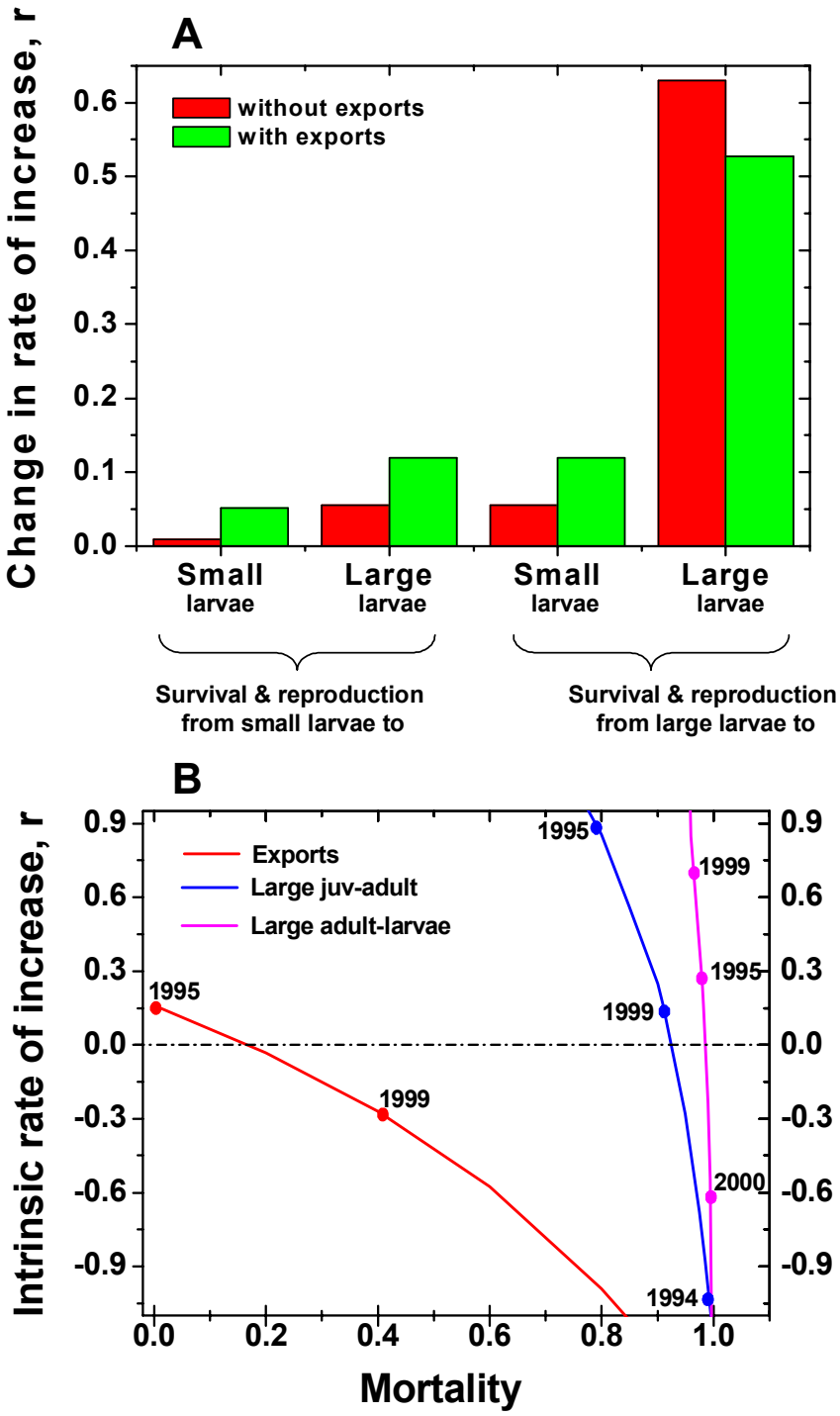


Figure 27. (A) Model sensitivity as represented by the elasticities, or proportional contribution of small and large larvae to the intrinsic population growth rate, using the aggregate matrices for models with and without mortality due to exports. (B) Influence on the population growth rate of variations in mortality due to exports, as well as between the juvenile to adult, and adult to larvae in the following spring. Years represent the range mortalities observed since 1994 as well as 1999.

Recent investigations demonstrate that an integrated application of toxicological and ecological techniques can be useful for evaluating chemical effects on delta smelt (Bennett and others, in prep.). Numerous pesticides were found to occur where post-larval delta smelt were collected in 1998–2000 (Moon and others 1999; Kuivila and Moon 2002, 2004; Figure 28A). Examinations of these specimens using two biomarker approaches, the "comet" assay and histopathology, indicated that about 10% had fragmented DNA in blood cells (Figure 28B), as well as cancerous cells and abnormalities in the organelle structure of livers (Figure 28C). These biomarkers can reliably detect exposure and organ damage that can impair reproductive success and survival (Anderson and Wild 1994; Teh and others 1997). Furthermore, the liver biomarkers indicated that 30% of the individuals were undernourished but were not affected by the pesticides (Figure 28C). Laboratory experiments show that undernourished individuals lack glycogen in their livers, whereas those damaged by toxic chemicals also have a variety of other abnormalities (Bennett and others, in prep.). Although the extent of impairment due to toxic exposure appeared minor using these techniques on samples taken in 1999–2000, the high variability in toxic exposure among years suggests this may not always be the case. Current applications of pyrethroid pesticides pose an important threat, because they are known to cause DNA fragmentation and interfere with endocrine development in fishes exposed to very low doses (in the $\mu g\ L^{-1}$ range, Capana and others 1999). Methods to detect concentrations of pyrethroid pesticides in the delta smelt habitat are currently under development (K. Kuivila, USGS, pers. comm.).

Larval Feeding Success and Exotic Species. As discussed previously, delta smelt consume copepods almost exclusively throughout their life history. Dramatic changes have occurred in the composition and abundance of delta smelt food resources particularly following invasions by exotic species. *E. affinis* was historically the dominant food resource for all life stages of delta smelt. Following the invasion of the overbite clam, *Potamocorbula amurensis*, in 1987–1988, several copepod species declined sharply, with *E. affinis* bring replaced over much of its distribution by the exotic copepod, *P. forbesi*. (Moyle and others 1992; Kimmerer and others 1994; Kimmerer and Orsi 1996). Seasonally, *E. affinis* is abundant during early to mid-spring and declines in late spring apparently from recruitment failure (W. Kimmerer, SFSU, pers. comm.) and is soon replaced by *P. forbesi*. This transition period results in a seasonal low in total copepod abundance.

It is reasonable to expect that a decline in overall food supplies would affect delta smelt. Several relationships indicate the declining abundance of *E. affinis* is associated with delta smelt abundance. For example, Stevens and others (1990) found a significant correlation between total copepod and delta smelt abundance in the MWT. A decade later, Miller (2000) identified a similar relationship between the abundance of *E. affinis* and the residuals from a stock-recruitment model encompassing the period between the MWT and the following TNS. Average lengths of delta smelt also dropped sharply following the changes in abundance and composition of copepods (Figure 29; Sweetnam 1999). Fish size may have been compromised by an overall reduction in food supplies, or because fish were younger due to shifts of the spawning season into June (Figure 16). However, declines in overall densities of *E. affinis* are significantly associated with mean lengths in both the MWT and Bay Study surveys (Figure 30), but similar relationships with the estimated end of the spawning season (date of water temperature = 20°C) are not significant. Nonetheless, without information on fish size-at-age derived from otoliths or the efficiencies of the sampling nets we cannot distinguish between these potential reasons for declining fish size.

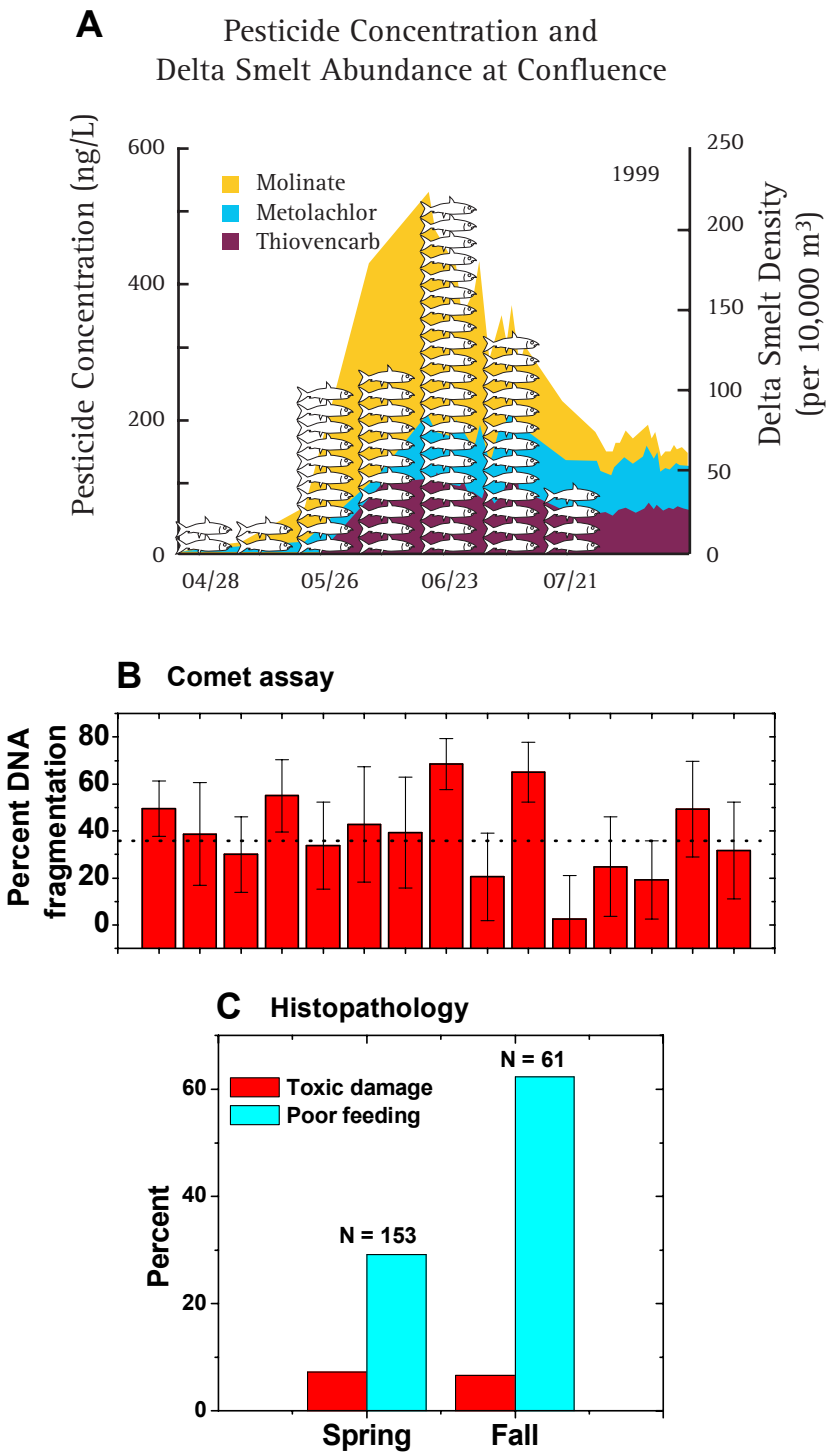


Figure 28. Evaluations of exposure to pesticides in 1999 (Bennett and others, in prep.). Water chemistry results showing elevations in concentrations of pesticides at stations where delta smelt were collected in the 20-mm and TNS surveys (A) (Original graph courtesy of K. Kuivila, USGS). Comet assay results indicating five individuals had a higher than average percent of DNA fragmentation in 50 blood cells (B) (S. Anderson, UCD). Results from histopathology of juvenile livers showing percent damaged by pesticides versus poor nutrition (C) (S. Teh, UCD).

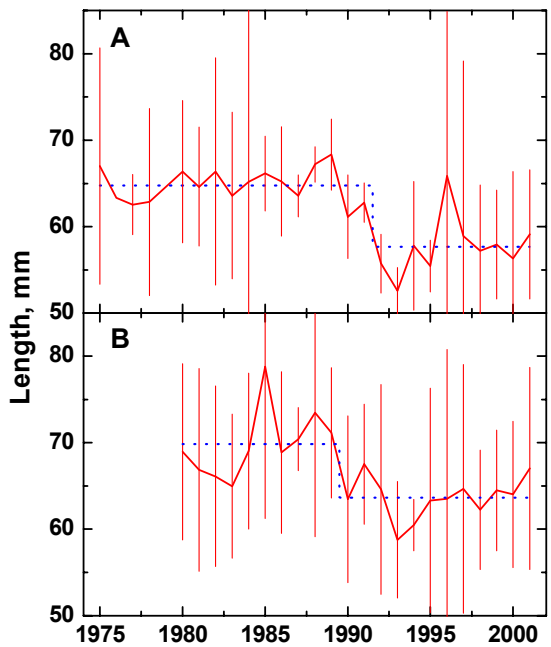


Figure 29. Mean lengths (red line) for adult delta smelt caught in the Fall Midwater Trawl Survey (A) and the Bay Study (B). Vertical lines are 90% confidence limits and the blue dotted line shows long-term change in mean length before and after the decline in the early 1990s. Graph courtesy of W. Kimmerer, SFSU.

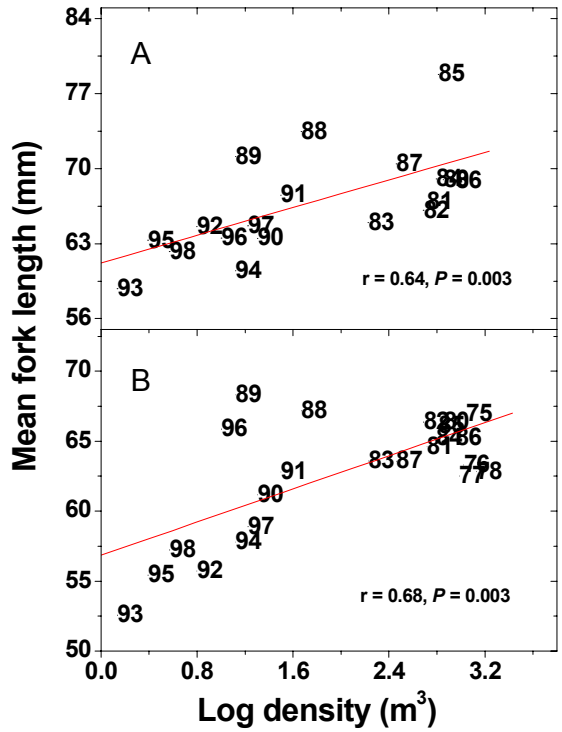


Figure 30. Relationships between mean length of delta smelt from the Bay Study (A) and Fall Midwater Trawl Survey (B) with the overall density of *Eurytemora affinis*. Numbers are years. Fitted lines are linear regressions.

Recent work suggests the seasonal low in copepod densities during late spring is associated with poor feeding success in larval delta smelt (Figure 31, Kimmerer and Bennett, unpublished data). In June 1999 the transition period produced an overall decline in food that lasted about 2 weeks (Figure 31A; W. Kimmerer, SFSU, pers. comm.). Otolith and histopathological investigations indicated that larval delta smelt during this period grew slowly and developed liver abnormalities consistent with poor feeding success (Figures 28, 31B; Bennett and others, in prep.). Depressed food abundance, therefore, can influence the probability of survival for cohorts that begin to feed at this time. The adverse effect of a seasonal low in copepod abundance may be enhanced because larvae also appear to be slow to switch from *E. affinis* to *P. forbesi* than abundance of the latter would suggest (Nobriga 1998).

Tracking of delta smelt cohorts also suggests that intermittent food shortages may lead to lower survival operating as a subtle process over time (Houde 1987, 1989; Cowan and others 1993, 1996). As previously described (see “Water Exports”) cohorts were tracked in time from back-calculated birth dates to size frequency distributions in the TNS and fish salvage data (Figure 24). The cohort most likely to have initiated first-feeding during the seasonal decline of *E. affinis* (cyan shading, Figure 24) comprises only a minor proportion of the salvage and TNS samples later in the season. This implies that they may have experienced higher predation or advection as a result of slower growth during the intervening period, or that the sampling gear did not adequately sample the younger cohorts.

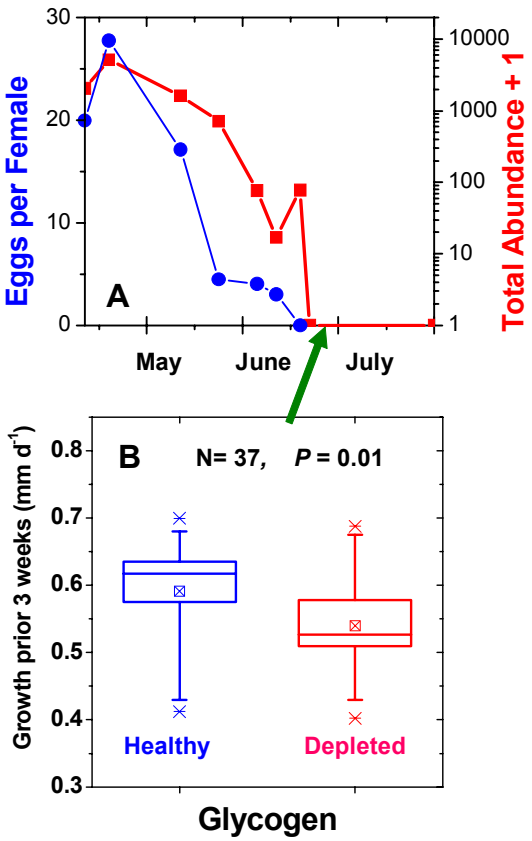


Figure 31. Trends in *Eurytemora affinis* abundance and fecundity during spring 1999 (A). Relative growth during the three weeks prior to capture for healthy and undernourished juvenile delta smelt that had begun to feed exogenously when *E. affinis* declined in abundance (B). Arrow shows date of fish capture. Diagnosis of feeding condition was by histopathological evaluations of glycogen content in liver cells (Bennett and others, in prep.).

Feeding, particularly for larval delta smelt has a substantial stochastic component and operates at very small scales. Successful feeding requires co-occurrence of larvae with patches of suitable zooplankton at scales much smaller than can be observed by monitoring (Okubo 1988; Cowan and others 1993; Bennett and Moyle 1996). For example, intensive sampling by Kimmerer and others (1998, 2002) and Bennett and others (2002) was able to describe only the meso-scales of this patchiness (i.e., at the scale of meters and hours). In addition, because larval abundance is so low and the co-occurrence with food patches largely stochastic, feeding success is more of a density independent, or density vague process (Strong 1986; Laurence 1990). However, Nobriga (2002) was able to find a relationship between food supply and feeding success using fish and zooplankton sampled in the 20-mm Survey. Nonetheless, these concepts may underlie the density independent stock-recruit relationship encompassing the larval feeding period (Inter-annual: adult-juvenile, Figure 17B).

Interactions with Exotic Species. The impact of exotic fishes on native species is well documented (Moyle 1996). Several potential fish predators on delta smelt have either invaded the SFE or increased in abundance over the last few decades, including largemouth bass (*Micropterus salmoides*), threadfin shad (*Dorosoma petenense*) and inland silversides (*Menidia berrylina*). Delta smelt, however, do not constitute an important prey item in the gut contents of the exotic piscivore, striped bass (Stevens 1966), possibly because they are somewhat cryptic due to their translucent body and unique swimming behavior, or they are relatively rare compared to other prey items.

Inland silversides, in particular, could have had a dramatic impact by preying on eggs and larvae and then competing with juvenile delta smelt. This interaction, referred to as intra-guild predation, is often associated with declines in native species (Polis and others 1989). Inland silversides became established in the SFE Delta in 1975–1976 (Meinz and Mecum 1977). Catch data from the USFWS Beach Seine Survey indicate silversides have increased dramatically in abundance over the last two decades (Figure 32A). They are effective colonizers and competitors elsewhere in the US. (McComas and Drenner 1982), and are perfect candidates for intra-guild interactions with delta smelt (Bennett 1995; Bennett and Moyle 1996). The two species are ecologically

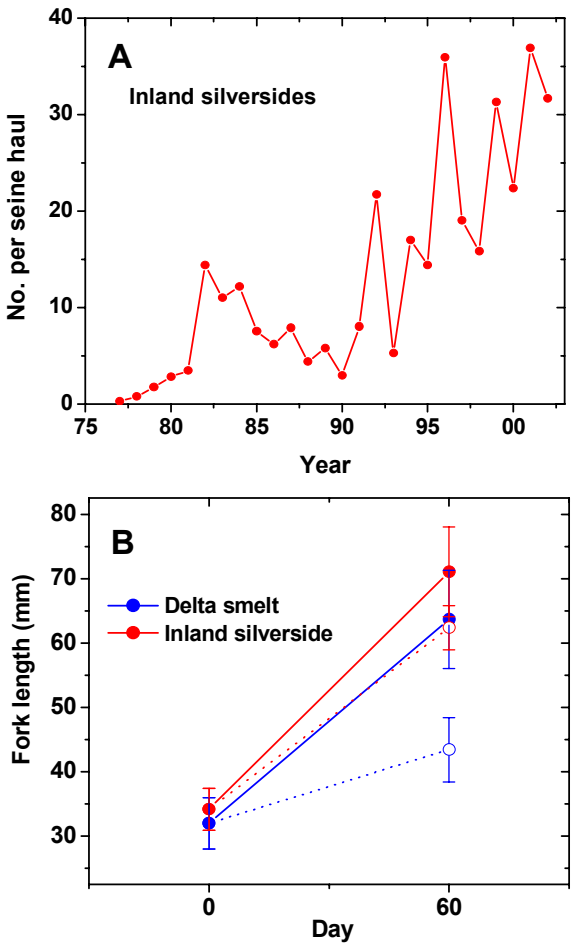


Figure 32. Trend in the abundance of inland silversides from beach seine surveys by USFWS (A). Data are from five stations sampled consistently in the lower Sacramento River. Results of a laboratory experiment on the relative feeding success of 40 inland silversides and 40 delta smelt held separately (solid circles), and 20 of each species in the same aquaria (open circles and dotted lines) over a two-month period (B).

very similar in morphology, diet, and life span. Silversides, however, have a broader diet, feed nocturnally as well as during the day, and spawn repeatedly from late spring through the fall. Thus the delta smelt niche is included within the silverside niche, a pattern that can provide a competitive advantage to a species with a wider niche (Rozensweig 1985; Polis and others 1989).

Delta smelt are at high risk if eggs or larvae co-occur with schools of foraging silversides. Dense aggregations form in the shoal-shoreline habitats of the SFE and Delta where delta smelt spawn. Silversides readily consume delta smelt larvae in laboratory aquaria (Hobbs and Bennett, unpublished data), and were very efficient predators of striped bass larvae in field experiments using large enclosures (Bennett 1993).

Recent work demonstrates that silversides can be efficient competitors with delta smelt. Competition for food resources may occur in the late summer and fall when planktivorous fishes are at peak abundance. This situation was simulated in laboratory aquaria using juvenile delta smelt and inland silversides (Hobbs and Bennett, in prep.). Fish in all treatments were fed 2,500 artemia nauplii L^{-1} daily. In separate aquaria 40 silversides grew an average of 0.61 mm d^{-1} and 40 delta smelt 0.53 mm d^{-1} over 2 months (Figure 32B). In contrast, when they were held together 20 silversides grew 0.47 mm d^{-1} whereas six delta smelt died and the survivors grew only 0.19 mm d^{-1} over the two-month period (Figure 32B). Although caution should taken when extrapolating laboratory experiments to field situations, this experiment clearly demonstrates the potential for silversides to be effective competitors with delta smelt.

Interbreeding with the exotic wakasagi has been another important concern for delta smelt. Wakasagi were established in California in 1959 and arrived in the SFE Delta region by as early as 1974. Because they closely resemble delta smelt they were frequently mis-identified. Records of delta smelt over 100 mm FL recorded from beach seines near Sacramento in the early 1980s were almost certainly wakasagi (Bennett, pers. obs.). However, the abundance of wakasagi in the Delta apparently increased in the mid-1990s most likely due to fish spilling out of several reservoirs upstream of the Delta (Wang 1995;

Aasen and others 1998). Subsequent concerns of introgression between wakasagi and delta smelt arose after Wang (1995) identified hybrids between the two species, which were later confirmed by genetic analyses (Moyle 1995). Fortunately, the probability of wakasagi undermining the genetic integrity of delta smelt appears small, because only F1 hybrids have been found and the two species are not closely related genetically (Stanley and others 1995; Trenham and others 1998). However, if abundances increase substantially in the delta smelt habitat, introgression and competition with wakasagi may again be a cause for concern.

Carrying Capacity

All populations are ultimately limited by the capacity of ecosystems to support additional individuals. The stock-recruit relationships (Figures 17 and 18) suggest that density dependence may limit the number of juveniles recruiting to the adult stage in some years during late summer. The asymptotes of the stock-recruit relationships portray long-term average carrying capacities (Figures 17 and 18). Residual values from the fitted lines reflect inter-annual variation in carrying capacity as well as density-independent effects on abundance and sampling error. A variety of prolonged perturbations to the ecosystem may fluctuate in intensity over time to alter carrying capacity for delta smelt, including climate change, water export operations, changes in food resources, and invasions of exotic species.

Density dependence has been most frequently observed in populations where space is limited for reproduction or living space (Elliot 1994; Rose and others 2001). Food limitation is also a likely mechanism for density dependence and may be associated with declining habitat space to define carrying capacity (Cowan and others 2000; Rose and others 2001). Typically, food shortages result in reduced condition, growth rate, or fecundity. Limited evidence for this in delta smelt was observed in 1999–2001, when juvenile abundance was near the inflection point in the stock-recruit relationship spanning the entire date record (Figure 17), and higher than this level during the post-decline period (Figure 18), i.e. approaching and exceeding carrying capacity. Histopathology and otolith investigations from this time showed that about 60% of 61 juveniles were undernourished with poor glycogen reserves and had slow growth at this time (Figures 28 and 33; Bennett and others, in prep.).

The extent to which delta smelt habitat volume decreases during late summer and fall, however, is unknown. One possibility is that seasonally low outflow and warm water temperatures contribute to concentrate delta smelt in habitat with other planktivorous fishes that are at peak abundance during late summer. The combined effects of all planktivorous fishes on food supplies (i.e. diffuse, or community competition) may then exert density dependent effects and define carrying capacity for delta smelt during late

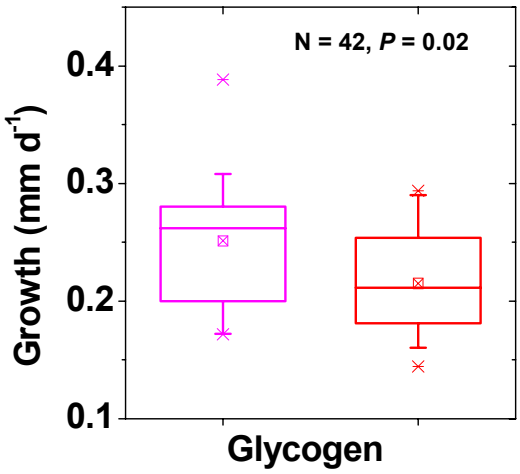


Figure 33. Relative growth during the 3 weeks prior to capture for healthy and undernourished juvenile delta smelt in August and September 2000. Diagnosis of feeding condition was by histopathological evaluations of glycogen content in liver cells (Bennett and others, in prep.).

summer. Droughts may further reduce food availability and heighten these effects. Although this is speculation, it may be worth further examination because the cumulative effects of common species on rare ones can be strong, as was shown by the seminal studies of Zaret and Rand (1971) for fishes in Panamanian streams, as well as in plant communities (Goldberg and others 2001).

Overall, the stock recruit analyses suggest that carrying capacity may currently limit the delta smelt population at lower levels of density than before the population declined in the early 1980s (Figures 17 and 18). This has important implications for restoring the population to historic levels of abundance (see Tables 17-19 in Errkila 1950; Radtke 1966). Given the complex and dramatic changes that have occurred in the food web over the last several decades (Nichols and others 1986; Hollibaugh 1996) this is a reasonable possibility. Unfortunately, there are currently few tools available to management for enhancing carrying capacity. A first step would require investigating potential processes producing density dependence and defining carrying capacity during late summer as juveniles recruit to the pre-adult life stage.

Probability of Extinction

Underlying any decision to remove a species from threatened ESA status is a basis for claiming the probability for further decline, or even extinction, has been reduced since the species was originally listed. A variety of tools has been developed to estimate this potential, collectively called population viability analyses (PVA, Morris and Doak 2002). Here, I provide an analysis of extinction probability for delta smelt using the method developed by Dennis and others (1991). The method assumes that abundance over time in a stochastically changing environment will have a lognormal distribution. For such a population, the time until a defined threshold of abundance will be reached can then be determined by two parameters. The parameter μ determines the rate at which the mean of the distribution increases, whereas Φ^2 is a measure of how fast the variance increases over time. Dennis and others (1991) outlined a straightforward method for estimating these parameters using linear regression with zero intercept and a simple transformation of count data that describes the relative amount of change in abundance between successive years:

$$x = \sqrt{t_2 - t_1} \quad \textbf{(2)}$$

$$y = \ln(N_2/N_1)/\sqrt{t_2 - t_1} \quad \textbf{(3)}$$

The slope of this regression then is an estimate of μ and the mean squared residual is an estimate of Φ^2. From these parameters a variety of measures of population viability can be estimated, particularly the average growth rate, and the median time until abundance will reach an extinction threshold. Typically, these are summarized in the cumulative distribution function (CDF) of the times to extinction at a specified abundance level. Thus, the CDF describes the probability that a population at a particular abundance level in year, *t*, will hit a specified extinction threshold at a certain time in the future (Dennis and others 1991; Morris and Doak 2002).

Using the abundance estimates for pre-adult delta smelt, I calculated μ and Φ^2 using regression (as above) over the entire time series (1967–2003, Figure 34A), as well as for the post-decline period (1982–2003, Figure 34B). I then specified three extinction levels 80,000, 8,000, and 800, chosen because the lowest MWT index on record (102 in 1994) corresponds to a calculated abundance level of 86,203 fish. I then calculated the CDFs using these three extinction thresholds for the entire and post-decline time series as well as bootstrap estimates of 95% confidence limits using 1000 iterations (Figure 35). From each CDF plot, I then obtained the median time in years to which 50% of the extinction probabilities would be realized, as well as the probability that a particular extinction level would be reached within 20 years (Morris and Doak 2002).

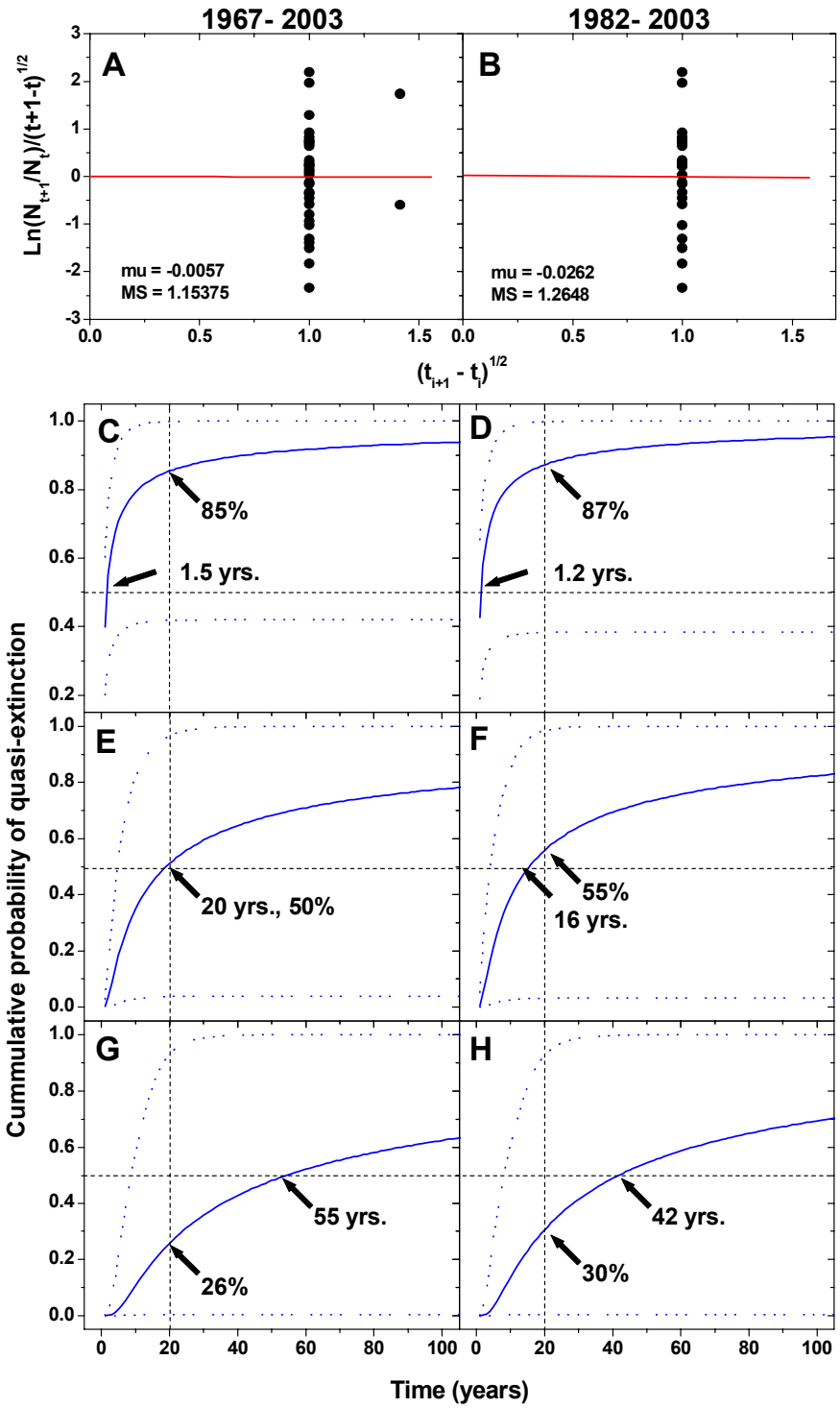


Figure 34. Population Viability Analysis using delta smelt abundance estimates for the entire data record and post-decline period (1982–2003). (A) Regressions used to estimate the rate (μ) and variance (MS) parameters for projecting the probability of future population levels reaching three quasi-extinction levels. (B) Cumulative Probability Distributions of times to quasi-extinction at 80,000, 8,000, and 800 fish. Arrows show the number of years within which 50% of the extinction probabilities occur, or the percent probability of extinction within 20 years.

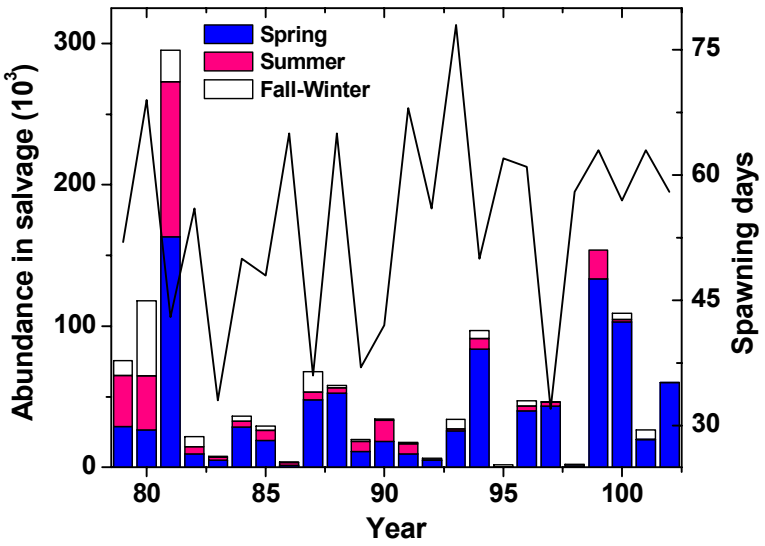


Figure 35. Trends in seasonal loss of delta smelt >20 mm to water export facilities (salvage) and estimated duration of spawning seasons.

Overall, the results using each extinction level were similar using either the entire time series or the post-decline period (Figure 34). The median time to when 50% of the extinction probabilities fall below the lowest calculated level recorded for delta smelt (about 80,000 fish) was only 1.2 to 1.5 years from the present, whereas 85% to 87% of these probabilities would be realized within 20 years (Figure 34C, 34D). Confidence limits on these estimates do not change the time to 50% extinction, but show a 40% to 100% probability that this level would be reached within 20 years (Figure 34C, 34D). Lowering the extinction level naturally decreases extinction risk as well as the levels of confidence associated with those estimates. However, lowering by one order of magnitude (8,000 fish) predicts that the median time to 50% extinction would occur in only 20 years (Figures 34E, 34F), whereas lowering by an additional order of magnitude (800 fish) extends this time to 42 to 55 years, with a 26% to 30% probability of encountering such low abundance within 20 years (Figures 34G, 34H).

The Dennis and others (1991) method for assessing population viability has become a standard conservation tool widely applied to a variety of organisms worldwide; the results rest on two main assumptions (Morris and Doak 2002). First and foremost is that estimates of abundance accurately reflect population size. Given that the estimates used here represent a first-order attempt to evaluate abundance for delta smelt suggests that these extinction probabilities be revised based on future refinements of this, or an alternative method. Second, the model assumes that abundance is not influenced by population density. This further indicates the importance of understanding the potential for density dependent processes to influence delta smelt abundance.

Overall, however, the results of this PVA indicate that ESA listing of delta smelt is justified under the extinction criteria adopted by the International Union for Conservation of Nature and Natural Resources (IUCN). The IUCN (2001) has adopted the use of such quantitative criteria where it exists over semi-quantitative assessments for evaluating extinction risk for a variety of organisms. Listing a species as Endangered under IUCN criteria requires a quantitative analysis

showing a probability of extinction that is at least 20% within 20 years or five generations, whereas Vulnerable status (similar to the USFWS Threatened status) requires a 10% chance within 100 years. Given these criteria, the results from the PVA indicate delta smelt qualifies for Endangered rather than Vulnerable status, and thus provides quantitative support for upholding the ESA listing for delta smelt.

Scenario of Population Decline

What caused the decline of the delta smelt population? Because abundance dropped suddenly some sort of episodic event may be responsible, yet the following years of prolonged low abundance implies some combination of "press" environmental influences has been responsible. Entrainment in water exports and sea surface temperatures appear to be the most conspicuous extreme events during 1981–1983 and may have contributed to the sudden drop in abundance observed at that time (Figure 36). High entrainment of all life stages occurred in 1981, and was immediately followed by the extreme El Niño of 1982–1983. Some have speculated that young delta smelt were washed out of the system during the flood produced by the El Niño (DWR–USBR 1993). Instead, it is more likely that the spawning season, which was constrained by warm water to only one month in 1983, allowed few opportunities for spawning (Figure 16). Although the decline could have been caused by a variety of other factors, it is reasonable to propose it was produced by some combination of these extreme events. The factors responsible for the ensuing years of low abundance have been the topic of much of this review, and continue to be a critical uncertainty for delta smelt.

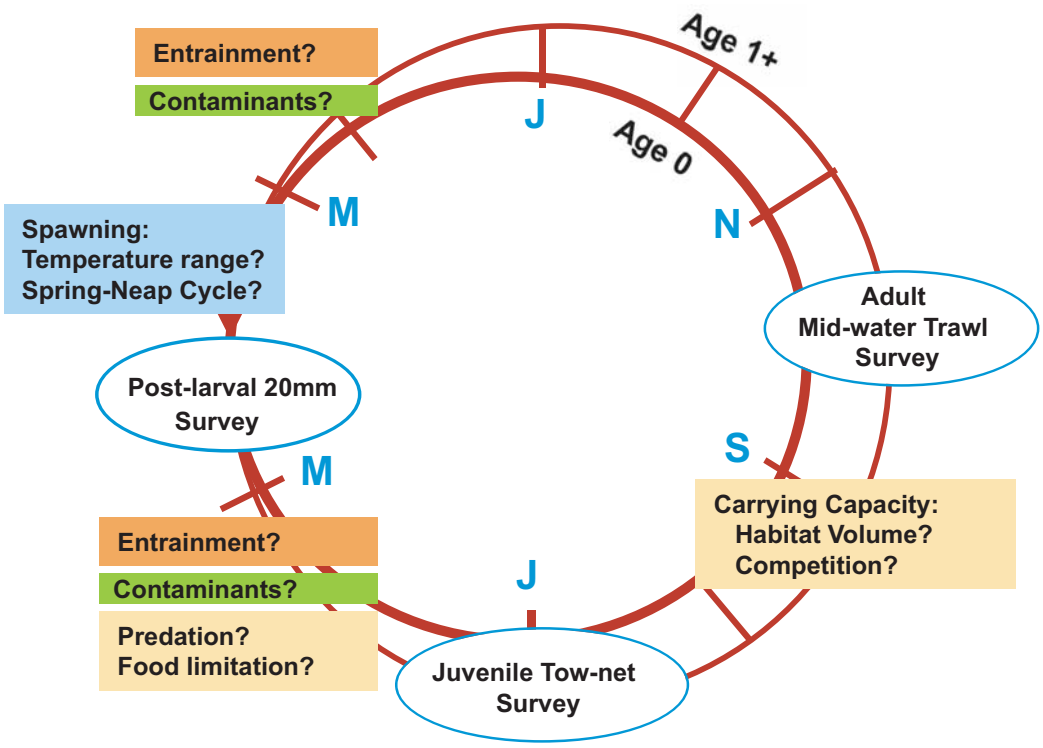


Figure 36. Conceptual model of factors influencing abundance (boxes) at key periods in the life cycle. Thick red circle represents one-year cycle, and thin red circle reflects the small proportion of adults that survive two years. Ovals show the timing of the primary monitoring surveys.

Implications and Uncertainties: A Conceptual Model

Numerous uncertainties underlie the previous sections summarizing the factors limiting the delta smelt population. Here these are organized with those outlined under previous sections describing biology and life history using a conceptual model that points to key periods in the life cycle where these occur (shown in boxes on the life-cycle diagram, Figure 36). Overall, the ecology of delta smelt appears unusual compared with many fishes. Persistence of the population occurs by maintaining growth, survival, and reproductive competence within a primarily annual life cycle in a fluctuating environment. Throughout this process a diverse array of limiting factors appear to interact episodically or as subtle processes (Houde 1989) among seasons, various geographical locations, and years in the delta smelt habitat. A fundamental uncertainty is whether the few fish that survive two years constitute a key life history tactic to ensure population persistence after years of poor recruitment success (Figure 36).

The period between winter and summer appears to be dominated by environmental factors operating in a density independent fashion (Figure 17B). Spawning success during this period appears to be driven by water temperatures between about 15 to 20°C. Longer spawning seasons in cooler years produce more cohorts (Figure 11) and on average higher annual recruitment (Figure 20). Within this temperature range, spawning in aquaculture is coordinated with lunar periodicity such that spawning occurs at or near spring tidal phases. Cohorts spaced in time have different probabilities of encountering favorable food supplies as well as various sources of mortality including entrainment in water export facilities, pulses of toxic pesticides, and predation (Figure 36). Threats posed by water project operations are highly uncertain with losses of fish under 20 mm FL largely unaccounted for, but appear greatest during early spring given the limited information available from the 20 mm survey (Figure 23). Simulations of these losses in a population model, however, imply that their influence on annual abundance may be difficult to detect compared to small changes in survival during late summer as juveniles advance into the pre-adult life stage. Overall, extended spawning seasons during spring provide better opportunities for recruitment success (Figure 20).

Between late-summer and fall, the transition of juveniles to the pre-adult stage may be limited by density dependence in years when abundance exceeds population carrying capacity, as well as from toxic chemicals, or other mechanisms operating in a density independent fashion. Although speculative, carrying capacity during late summer may be defined by declining size in suitable habitat and seasonally high abundances of planktivorous fishes.

Overall, annual variability in delta smelt recruitment success appears to be induced by the prevailing climate during the spawning season, combined with various environmental and anthropogenic factors during spring and early summer. During late-summer some of this variation appears to be dampened in years of high juvenile abundance relative to the prevailing carrying capacity of the delta smelt habitat. In years of poor recruitment success the small proportion of fish that survive two years may help the population to persist, thus providing some insurance to prevent extinction. Clearly, this conceptual model is based on numerous uncertainties and leaps-of-faith. At this point in our level of knowledge, this was deemed necessary to bring together somewhat disparate fragments of information into a working blueprint to serve as a guide for future investigations of the delta smelt population.

Implications for Restoration

Currently, humans have only four options for delta smelt restoration, reflecting our limited ability to control the ecosystem. These include controls on the amount freshwater discharge,

quality of estuarine water, amount of water exported, and physical rejuvenation of shoreline and shallow-water habitats. The question for restoration, therefore, is how to devise ways to use these options to the benefit of the delta smelt population?

Freshwater Discharge

Freshwater discharge to the estuary is currently managed in an environmentally friendly manner using the X2 standard. This action assumes that maintaining the low salinity zone in Suisun Bay during spring will benefit delta smelt (see Kimmerer 2002, 2004). Although there is no statistical relationship justifying its usefulness (Figure 20, Kimmerer 2002), the X2 standard remains a worthwhile management action, because the abundance of delta smelt is elevated only in years when the low salinity zone is located in Suisun Bay; and, from an ecosystem perspective, the abundances of a variety of organisms are enhanced with X2 in Suisun Bay (Jassby and others 1995; Kimmerer 2002, 2004).

Water Quality

Numerous toxic chemicals, primarily pesticides from urban and agricultural run-off enter the delta smelt habitat (Thompson and others 2000). Considerable vigilance is required to monitor water quality and diagnose the large variety of chemicals, their concentrations, and potential harm to the biota including delta smelt (Kuivila and Foe 1995). However, these efforts are very difficult and expensive. Population level effects from exposure to toxic chemicals are possible (Kuivila and Moon 2002, 2004), but with the limited information available they have not been shown to occur (Figure 28; Bennett 1995; Bennett and others, in prep.). Given the potential for population level effects, however, monitoring pesticide concentrations in the delta smelt habitat is necessary. Monitoring is especially needed considering the increasing applications of a new type of pesticide, pyrethroids, known to cause endocrine disruption in fishes at very low concentrations.

Water Export Operations

Actions to reduce the losses of delta smelt in water export operations are the most controversial. The export incidental “take” limits clearly provide benefits to individual delta smelt, yet there does not appear to be a defensible biological basis for the levels chosen. Over the past five years, the take limits have become an integral part of the California Bay-Delta Authority’s (CBDA) Environmental Water Account (EWA) designed to alleviate the uncertainty of water use, as well as to provide benefits to delta smelt and other fishes of special concern. Environmental water is acquired and “banked” and used for fish protection, primarily by reducing water exports at critical times when delta smelt “take” at the major facilities is elevated. For delta smelt, however, it has never been established that reducing water exports at the critical times has any benefit for the population. In the future, successful use of EWA water will rely on a better understanding of the overall impacts of the water exports on delta smelt, as well as a process-oriented understanding of the mechanisms influencing entrainment at and near the facilities. For example, fish saved by EWA action in one week may remain vulnerable to exports soon after the protective measure has been relaxed.

A related tactic has been to devise effective fish screens and handling procedures. By many, the perception is that more effective screening and fish handling capabilities would augment EWA expenditures to provide benefits for delta smelt. Unfortunately, there is no scientific evidence supporting this expensive proposition. What is clear, however, is that delta smelt caught in the wild are extremely fragile and many do not survive even the most well prepared attempt to handle them in the laboratory (Swanson and others 1996, Bennett, personal observations). Moreover, it is currently unclear if losses to the water projects are a major impact on their abundance. Further evaluation of these losses and the processes influencing entrainment should be carefully examined before a major

effort to "improve" the fish screening and salvaging operations at the facilities is undertaken. Similarly, there has been a consistent effort to install fish screens on the numerous small agricultural diversions in the Delta. Again, however, the benefits of fish screening have never been established for delta smelt, and the added structural complexity to these diversions may provide habitat harboring predatory fishes. What little is known indicates their effect is small (Nobriga and others 2004). Moreover, the installation of fish screens involves significant capitol investment that is then unavailable to other environmental uses.

Two relationships emerging from this review may provide additional opportunities for guiding the use of water as a management and restoration option. The first is the length of the spawning season. Although this relationship only crudely predicts delta smelt abundance overall, it is a very reliable predictor of recruitment success in years with either very wide or narrow spawning seasons (Figure 20). Spawning seasons spanning less than 60 days, or ending before Julian day 160 are likely to result in lower abundance, in which case protective measures such as use of EWA may be of higher value. Unfortunately, releases of environmental water are insufficient to maintain appropriate spawning temperatures. In the future, the duration of the spawning season may be a significant concern for the persistence of delta smelt, because of the trend in climate toward earlier snow melt and warmer air temperature during spring (Dettinger and Cayan 1995). The second, carrying capacity may limit adult recruitment in years of high juvenile abundance. However, it is less obvious how to alleviate density dependence, especially by using controls on fresh water discharge, considering that we need to learn much more about how often and why it occurs. Density dependence deserves further examination because it may preclude the benefits of current restoration actions.

Shallow-Water Habitat and Marshes

Increasing delta smelt habitat by rehabilitation or creation of shallow habitat is an intuitively appealing notion, and several projects are currently underway to provide benefits to delta smelt, perceived as spawning and rearing habitat. Studies of the Yolo Bypass clearly show the benefits of flooding shallow areas for Sacramento splittail (*Pogonichthys macrolepidotus*) and Chinook salmon (*Oncorhynchus tshawytscha*) smolts (Sommer and others 2001), thus delta smelt may also receive benefits from additional spawning habitat and rearing areas of high productivity. For example, delta smelt in northern Suisun Bay adjacent to shoal habitats have higher feeding success (Hobbs 2004). However, what constitutes spawning habitat for delta smelt is currently uncertain, and there is little monitoring associated with such restoration projects to ascertain whether they have any benefit to the population. One can speculate that the cumulative influences of many restored habitat areas may help to raise overall system productivity and potential carrying capacity for delta smelt. However, the vast uncertainties of these perceived benefits need to be weighed against the high cost of rehabilitation, and the potential for constructed habitats to foster exotic species (Grimaldo and others 1998) as well as re-mobilize toxic chemicals (Suchanek and others 1999).

Research Needs

I began this review by posing three questions for which numerous data gaps impede progress toward answering:

1. Should the species continue to be listed under the ESA, or what is the probability of extinction?

2. What is the impact of human activities, particularly water export operations, on population abundance?

3. Are there potential avenues for restoration and recovery?

This synthesis of the available information cannot answer these vital management questions, but it is hoped that some insight or progress toward their resolution has been achieved. The most compelling observation from this review is the large number of fundamental data gaps and fragmented progress research has made in the decade since the species was listed under the ESA. To provide the types of options needed to simultaneously manage California's water supply and ensure the persistence of delta smelt, there is an urgent need for a significant and comprehensive program of research. Such a program needs to address the many gaps in knowledge in an organized fashion so that it may be effectively synthesized into tools for management and restoration. This could be effectively accomplished as part of an ambitious series of whole-system experiments in which freshwater discharge and export operations are systematically and dramatically altered. Although such experiments are improbable, significant research programs are routinely commissioned worldwide to investigate major fishery stocks that are arguably worth less in terms of dollars than California water. This section addresses some of the key research areas that such a program should target. Many of these recommendations have not received adequate attention since initially posed in the first Delta Smelt Study Plan (Sweetnam and Stevens 1991), and are also in accord with a more recent IEP Delta Smelt Research Strategy (see Brown and Kimmerer 2002). Similar views were also expressed by an independent group of experts forming the CBDA Environmental Water Account Technical Review Panel (http://science.calwater.ca.gov/pdf/EWAReviewFinal_1-27-03.pdf).

Monitoring and Abundance

A trustworthy measure of delta smelt abundance is probably the most critical information gap as noted throughout this review. However, quantifying abundance for delta smelt is not a straightforward task (Herbold 1995). Two options appear worth pursuing. The first would be to continue investigating statistical estimates based on raw catch and effort records as used in this paper. To achieve this, size-selective biases associated with each of the sampling gears need to be estimated with field-based measurements, and work is needed to better quantify the volume of suitable habitat for delta smelt. Second, novel technologies may facilitate development of mark-recapture or hydroacoustic protocols that can be routinely applied. A program integrating these options would provide the best results.

Life History

As also noted under the section on delta smelt biology, there are several aspects of the life history that remain uncertain or unknown. For example, spawning areas and microhabitats, size-specific fecundity and within-season reproductive strategies are all poorly known and critical for developing population models and identifying potential habitat areas for restoration. A key uncertainty is longevity, and the potential importance of bet-hedging as a tactic for provisioning reproduction; such a strategy could be fundamental to how delta smelt avoid extinction.

Effective Population Size

At what level of abundance is the population unable to recover? Understanding risk of extinction also requires a quantitative measure defining effective population size, or the abundance at which significant genetic diversity is lost due to inbreeding (Falconer and Mackay 1996). Various genetic tools are available and should be applied to this important gap in knowledge.

Growth and Mortality

Estimates of stage-specific growth and mortality are fundamental for understanding, and predicting recruitment success in fishes. Currently little is known of these important vital parameters and the fish caught during the course of monitoring provide an economy of

effort to estimate birth dates and locations, growth, as well as mechanisms of potential mortality. Synthesizing this information with effective abundance measures will be required to estimate these parameters for the population.

Density Dependence and Carrying Capacity

Evidence for density dependence identified in this paper is not by itself convincing. Density dependence is important because it regulates abundance, and has major implications for understanding the impacts of human activities on the population. Further study is needed to measure the potential strength, and identify the underlying mechanisms of density dependence before useful management and restoration options can be devised.

Interactions with Exotic Species

Exotic species are an ever increasing component of the delta smelt habitat, influencing the abundance and composition of the delta smelt food supply, potential predators, and competitors, at several life stages. The mechanisms by which exotic species interfere with delta smelt recruitment are complex and will continue to be an uncertainty into the future as new species invade at rates faster than research can unravel their effects.

Toxic Chemicals

As long as human land use occurs, concern over chemicals washing into the delta smelt habitat will remain important. However, identifying and understanding the impacts of toxic chemicals, and primarily pesticides, is costly and difficult to assess at the population level. Limited work to date has not shown a significant impact of toxic chemicals on delta smelt, however, the threat is real especially considering the rapidly evolving development and use of new pesticides. One way to approach this complex problem is to use various biomarkers (Anderson and Wild 1994; Bennett and others 1995; Teh and others 1997) as screening techniques to identify effects on individual fish caught during routine monitoring before embarking on a comprehensive effort. Water quality monitoring is also useful in this regard to narrow down the choices of specific biomarkers to be applied to individual fish.

Water Project Operations

As stated several times before, little is known about the impacts of water export operations on the delta smelt population. The uncertainties range from limited knowledge of the numbers of larvae lost in exported water, and impacts of predators near the facilities, to the conditions promoting significant entrainment events at all life stages. A better understanding of the interactions among the local hydrodynamics, fish behavior, and design of the pumping facilities would provide managers with potential options for project operations or design modifications that may reduce export losses. Studies would require intensive monitoring of hydrodynamics and fish distribution over tidal time scales at key locations near the facilities. However, even with better knowledge of these factors, their impacts need to be evaluated in a similar context with other known sources of mortality in population models. Numerous data gaps will need to be filled before we can understand the impacts of water export operations on the delta smelt population.

Delta Smelt in Our Future?

In several regards, the uniqueness of delta smelt as a species, and as an environmental concern constitutes a critical test case, or “canary in the coal mine,” for environmental issues in California and beyond for the future. The institutional infrastructure associated with managing and marketing California water is immense with increasing pressures from a rapidly growing human population and world class economy. The “Achilles heel” in this scenario are the environmental impacts to ESA listed species, and primarily delta smelt, due to the CVP and SWP in the south Delta that

transfer a significant portion of the State water supply from northern to central and southern California. The current state of knowledge suggests a high probability that delta smelt abundance will decline in the future; as this paper enters publication the population is currently at record low abundance. Considering the rate at which water demands have intensified, relative to the rate at which scientific understanding of delta smelt has advanced over the last decade, it will interesting to observe whether we will be able to answer the questions posed here in time to circumvent an environmental catastrophe.

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UNITED STATES DISTRICT COURT
EASTERN DISTRICT OF CALIFORNIA

THE CONSOLIDATED SALMON CASES: SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. LOCKE, *et al.* STOCKTON EAST WATER DISTRICT v. NOAA, *et al.* STATE WATER CONTRACTORS v. LOCKE, *et al.* KERN COUNTY WATER AGENCY, *et al.* v. U.S. DEPARTMENT OF COMMERCE, *et al.* OAKDALE IRRIGATION DISTRICT, *et al.* v. U.S. DEPARTMENT OF COMMERCE, *et al.* THE METROPOLITAN WATER DISTRICT OF SOUTHERN CALIFORNIA v. NATIONAL MARINE FISHERIES SERVICE, *et al.*	**LEAD CASE NO: 1:09-cv-1053-OWW-DLB** Consolidated With: 1:09-cv-1090-OWW-DLB 1:09-cv-1378-OWW-DLB 1:09-cv-1520-OWW-SMS 1:09-cv-1580-OWW-DLB 1:09-cv-1624-OWW-SMS **CORRECTED DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF METROPOLITAN WATER DISTRICT'S JOINDER IN MOTION FOR TEMPORARY RESTRAINING ORDER** Date: February 2, 2010 Time: 1:00 p.m. Ctrm: 3 Judge: Oliver W. Wanger

I, Dr. Richard B. Deriso, declare:

1. I have reviewed the National Marine Fisheries Service's ("NMFS") 2009 biological opinion for the Sacramento River winter-run Chinook salmon, Central Valley spring-run Chinook salmon, Central Valley steelhead, Southern Distinct Population Segment of North American green sturgeon, and Southern Resident killer whales ("BiOp"). In the BiOp, NMFS determined that the Central Valley Project ("CVP") and State Water Project ("SWP") jeopardize the continued existence of these listed species and adversely modify their critical habitat. Accordingly, the BiOp includes Reasonable and Prudent Alternatives ("RPAs") that purport to avoid jeopardy and benefit the species. The RPA that is the subject of the motion for a temporary restraining order is Action IV.2.3.

2. Action IV.2.3 is one of the Delta Division RPAs, prescribed to "[c]ontrol the net negative flows toward the export pumps in Old and Middle rivers to reduce the likelihood that fish will be diverted from the San Joaquin or Sacramento River into the southern or central Delta" and entrained at the pumps. BiOp at 630. Specifically, Action IV.2.3 reduces exports to limit negative Old and Middle River ("OMR") flows to -2,500 to -5,000 cfs from January 1 through June 15, depending on the presence of salmonids. BiOp at 648.

3. Action IV.2.3 is based on the Effects of the Proposed Action section of the BiOp at pages 313-432, and particularly the analysis of the relationship between OMR flows and salvage on pages 352-374. The BiOp includes two figures which depict the relationship between monthly older juvenile loss at the CVP and SWP facilities and monthly average December-April OMR flows. BiOp at 361-62 (Figures 6-65 and 6-66). Based on these figures and the results of particle tracking modeling, NMFS concluded that there is a significant relationship between OMR flows and salvage. The RPAs reduce exports in order to reduce salvage and thereby purportedly avoid jeopardy to the species. Figures 6-65 and 6-66 are shown below.

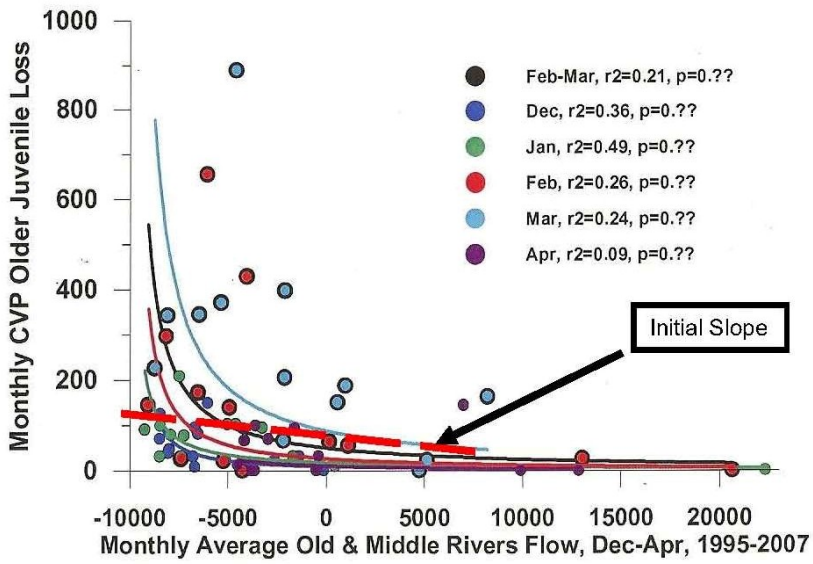


Figure 6-65. Relationship between OMR flows and entrainment at the CVP, 1995-2007 (DWR 2008).

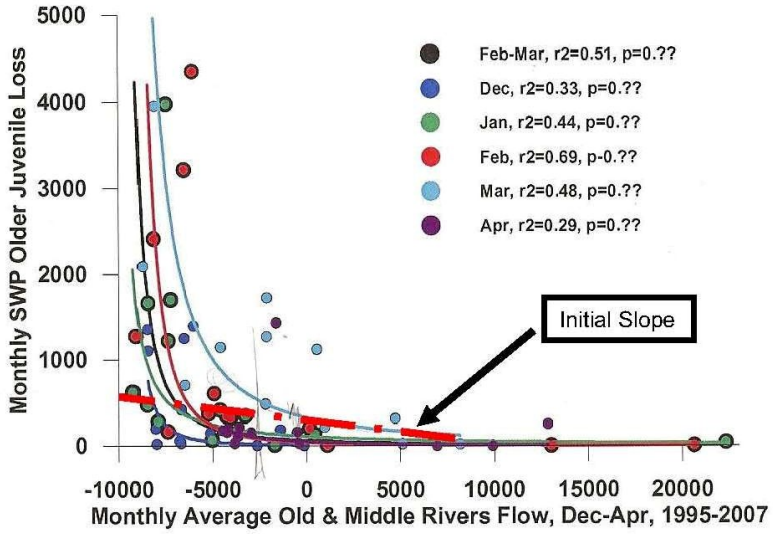


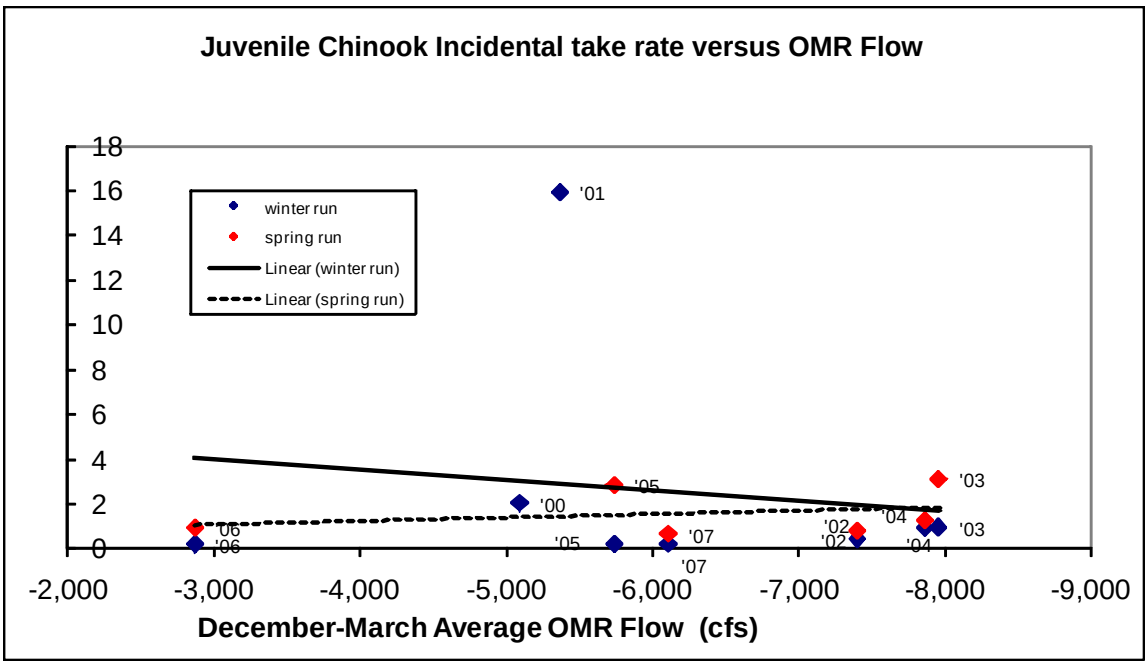
Figure 6-66. Relationship between OMR flows and entrainment at the SWP, 1995-2007 (DWR 2007).

4. In Figures 6-65 and 6-66, NMFS relied on raw salvage numbers as a measure of salmonid loss, rather than a cumulative salvage index or incidental take index. Raw salvage numbers in isolation do not provide a measure of effects to a population. Such an analysis must take into account the overall size of the population and the *proportion* of the population that is lost to salvage.

5. Using an incidental take index instead of raw salvage numbers is the proper approach to analyzing population effects. This approach accords with standard principles of

fisheries population assessment. *See* Declaration of Dr. Richard B. Deriso, Docket #401, *The Delta Smelt Cases*, No. 1:09-cv-407-OWW (E.D. Cal.) at ¶¶ 14-15, 55-57 (explaining the application of this approach). An incidental take index represents the raw number salvaged divided by the total size of the population. It is the appropriate measure of the significance of a mortality event on an overall population.

6. I modeled the relationship between the juvenile incidental take index and December-March average OMR flows. The analysis shows that there is no statistically significant relationship between the take index and OMR flows. This means that OMR flows do not have a significant effect on salmonid abundance. The results are depicted in the figure below.



Juvenile Chinook salmon incidental take index is the incidental take divided by escapement.
The estimates are made separately for the winter-run and spring-run. Incidental take does not include tagged hatchery fish.
Escapement estimates are given for naturally spawning salmon and years 2000-2007, except incidental take estimates were not available for 2000-2001 for spring Chinook salmon on the web site below (#2).
OMR flow axis is reversed so that more negative values occur as one moves progressively left to right.
Best fit regression lines are shown. Note that neither regression line has a slope that differs statistically significantly from a horizontal line.
Data sources:
1. http://www.calfish.org/IndependentDatasets/CDFGFisheriesBranch/tabid/157/Default.aspx
2. http://www.usbr.gov/mp/cvo/fishrpt.html
3. Digitized OMR flow data from Figure E-2 (page 248) of the delta smelt biological opinion.

7. I repeated the analysis using December-March average OMR flows for winter-run salmon and March-May average OMR flows for spring-run salmon, which are better representative months for the two runs. In addition, I used OMR flow data provided by the United States Fish and Wildlife Service ("FWS") pursuant to a Freedom of Information Act ("FOIA") request from Metropolitan, rather than digitizing the data from the delta smelt biological opinion as I did in my first analysis (see notes to figure above). This analysis shows the same result—there is no statistically significant relationship between the take index and OMR flows. This means that OMR flows do not have a statistically significant effect on salmonid abundance. The results are depicted in Figure X below.

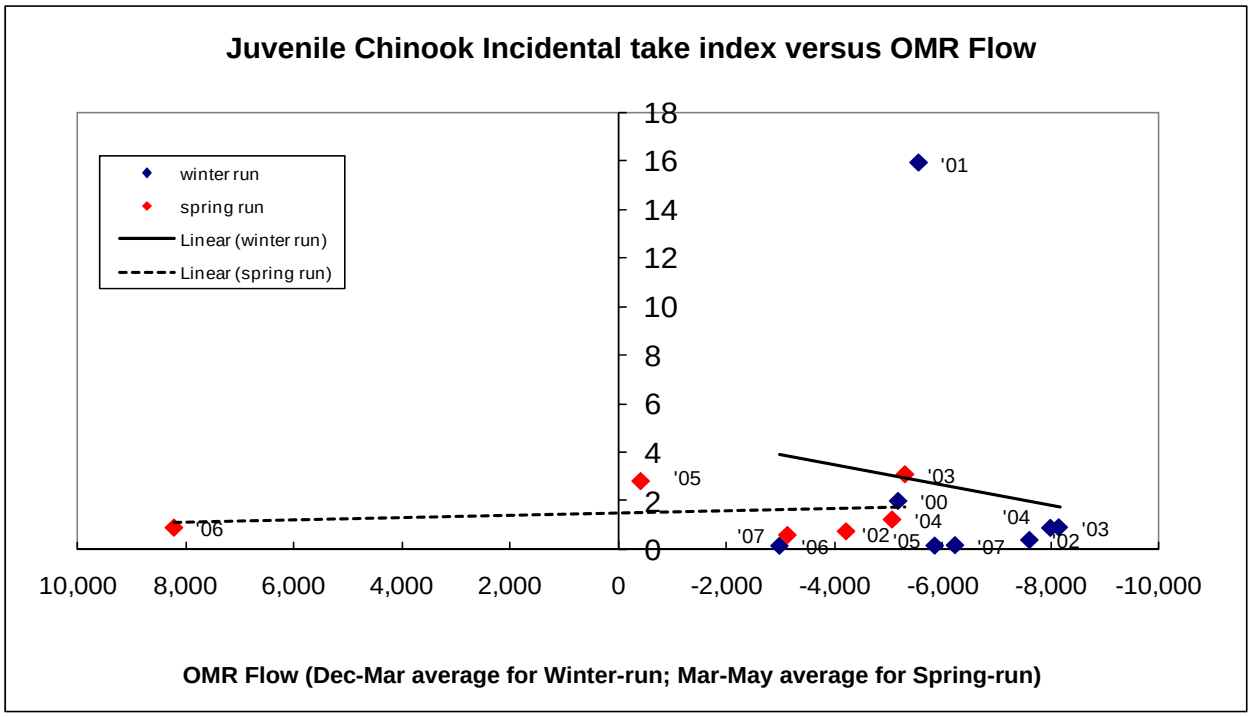
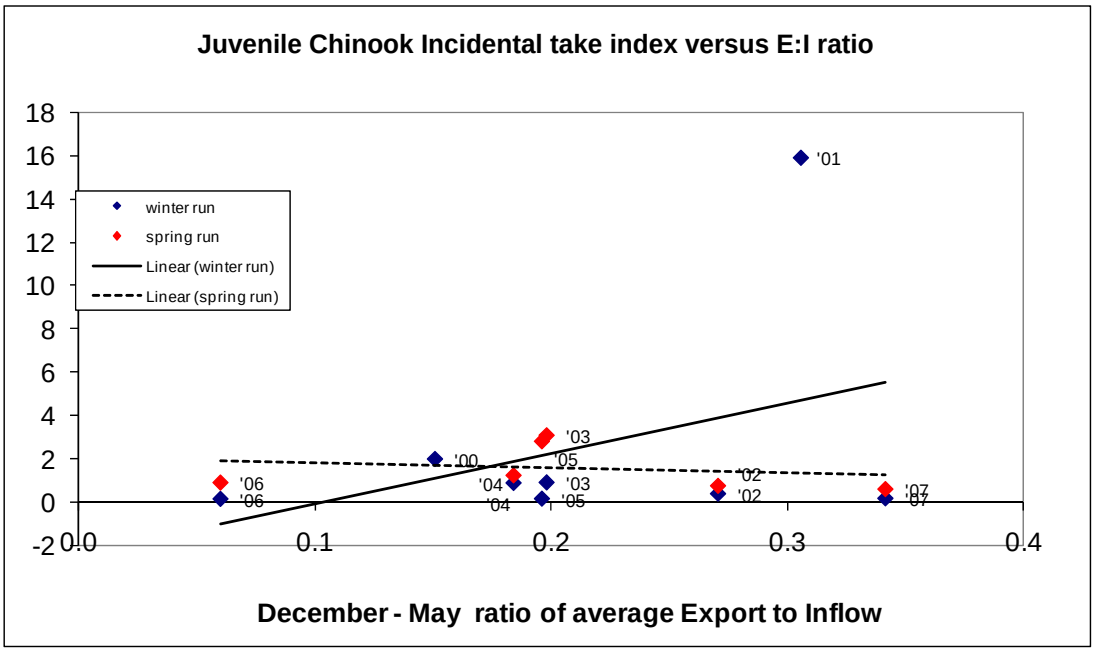


Figure X. Juvenile Chinook salmon incidental take index is the incidental take divided by escapement. The estimates are made separately for the winter-run and spring-run. Incidental take does not include tagged hatchery fish.
Escapement estimates are for naturally spawning salmon and years 2000-2007, except incidental take estimates were not available for 2000-2001 for spring Chinook salmon.
Best fit regression lines are shown. Note that neither regression line has a slope that differs statistically significantly from a horizontal line.
Months chosen for winter- and spring-run Chinook salmon are based on dates for movement into Delta (Table 6-34 BiOp)
Data sources: grandtab in http://www.calfish.org/IndependentDatasets/CDFGFisheriesBranch/tabid/157/Default.aspx
http://www.usbr.gov/mp/cvo/fishrpt.html
OMR flow data provided by FWS per a FOIA request from MWD

8. I also modeled the relationship between the juvenile incidental take index and the export-to-inflow ratio ("E:I ratio") for December-May. The analysis shows that there is no statistically significant relationship between the take index and the E:I ratio. This means that the E:I ratio does not have a significant effect on salmonid abundance. The results are depicted in the figure below.



Juvenile chinook salmon incidental take index is the incidental take divided by escapement (data source #1). The estimates are made separately for the winter run and spring run. Incidental take does not include tagged hatchery fish. Escapement estimates are given for naturally spawning salmon and years 2000-2007, except incidental take estimates were not available for 2000-2001 for spring chinook salmon on the web site below (data source #2). E:I ratio is the ratio of exports to inflow (data source #3). Best fit regression lines are shown. Note that neither regression line has a slope that differs statistically significantly from a horizontal line.
Data sources:
1. Grandtab at http://www.calfish.org/IndependentDatasets/CDFGFisheriesBranch/tabid/157/Default.aspx
2. http://www.usbr.gov/mp/cvo/fishrpt.html
3. http://www.iep.ca.gov/dayflow/output/index.html

9. I repeated the analysis using the December-March average E:I ratio for winter-run salmon and the March-May average E:I ratio for spring-run salmon, which are better representative months for the two runs. I also used OMR flow data provided by FWS pursuant to the FOIA request from Metropolitan. This analysis shows the same result—there is no statistically significant relationship between the take index and the E:I ratio. This means that the E:I ratio does not have a significant effect on salmonid abundance. The results are depicted in Figure Y below.

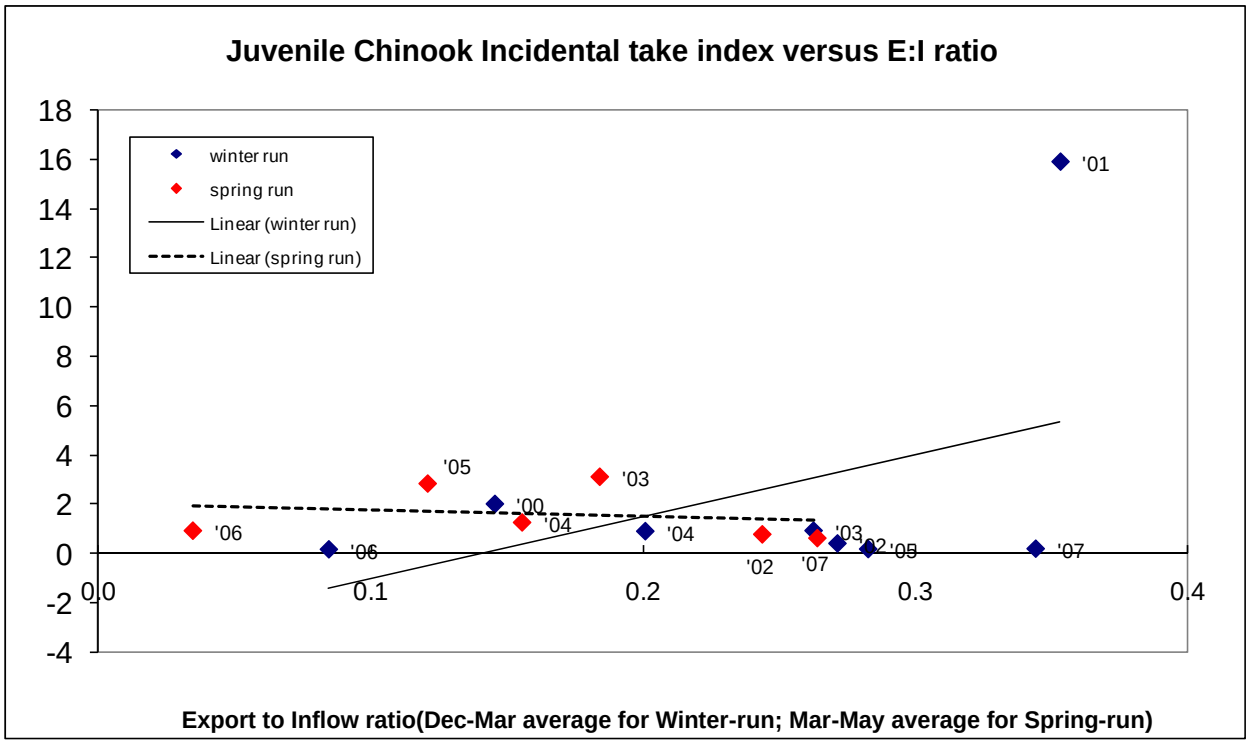


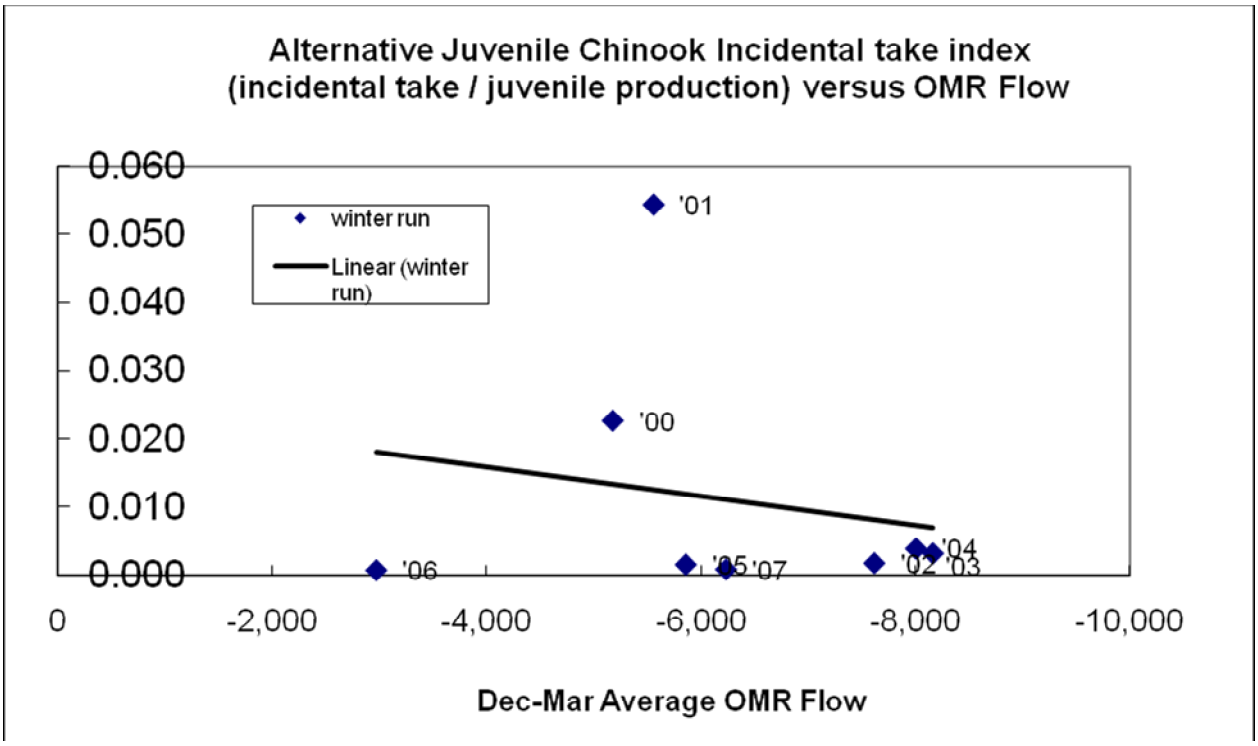
Figure Y. Juvenile Chinook salmon incidental take index is the incidental take divided by escapement. The estimates are made separately for the winter-run and spring-run. Incidental take does not include tagged hatchery fish.
Escapement estimates are for naturally spawning salmon and years 2000-2007, except incidental take estimates were not available for 2000-2001 for spring Chinook salmon. Salmon salvage data for winter- and spring-run naturally spawned Chinook salmon were not shown for years prior to 2000 on the web site below and they are not provided in the BiOp, as best I can tell.
Best fit regression lines are shown. Note that neither regression line has a slope that differs statistically significantly from a horizontal line.
Months chosen for winter- and spring-run Chinook salmon are based on dates for movement into Delta (Table 6-34 in BiOp).

Data sources: grandtab in
http://www.calfish.org/IndependentDatasets/CDFGFisheriesBranch/tabid/157/Default.aspx
http://www.usbr.gov/mp/cvo/fishrpt.html
Export and inflow data provided by FWS per FOIA request from MWD

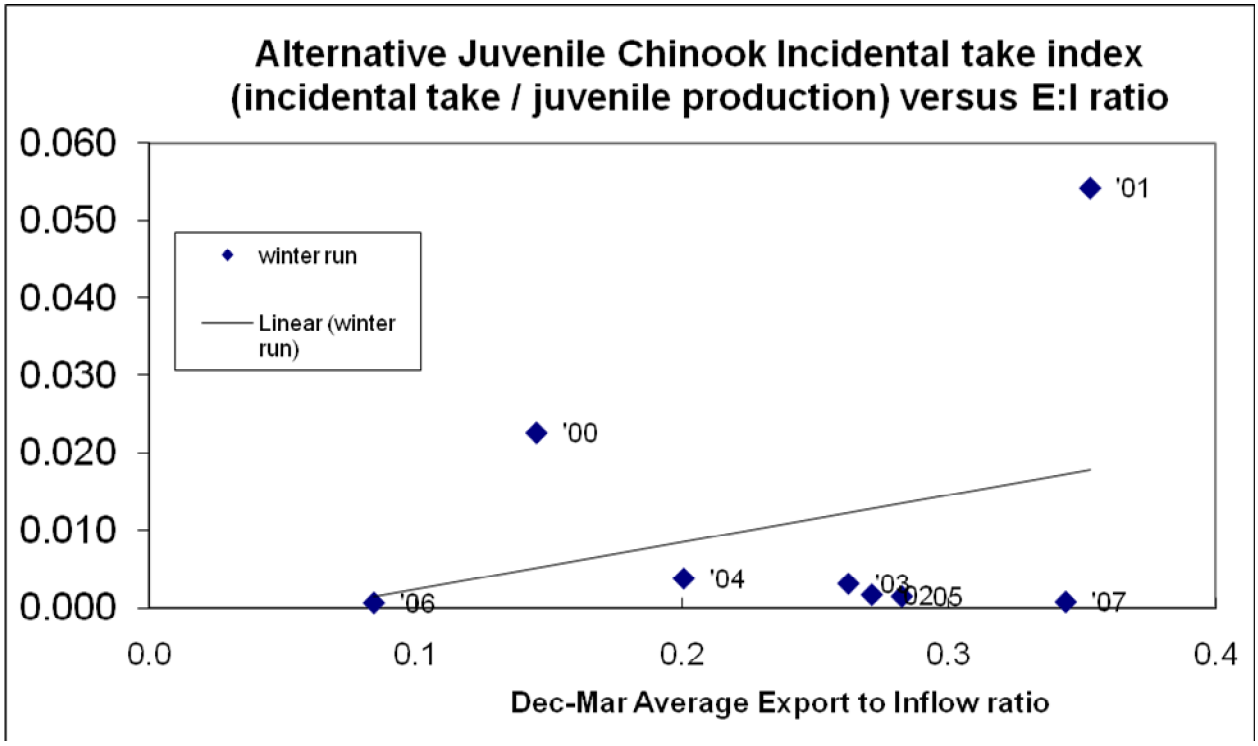
10. The above Figures X and Y are based on the following data:

Year	E:I ratio Dec-Mar	E:I ratio Mar-May	OMR Dec-Mar	OMR Mar-May	Winter-Run Chinook Salmon Incidental Take Index	Spring-Run Chinook Salmon Incidental Take Index
2000	0.145	0.112	-5178.42	-2802.45	2.008	
2001	0.353	0.228	-5558.68	-3370.64	15.912	
2002	0.271	0.244	-7615.35	-4220.59	0.406	0.769
2003	0.262	0.184	-8161.14	-5310.83	0.927	3.111
2004	0.200	0.155	-8004.52	-5071.68	0.902	1.255
2005	0.282	0.121	-5858.41	-417.315	0.177	2.834
2006	0.084	0.034	-2975.74	8221.25	0.166	0.919
2007	0.344	0.264	-6234.28	-3135.6	0.192	0.616

11. It is possible to construct an alternative winter-run incidental take index using abundance data taken solely from the BiOp, rather than using other public sources (see notes to figures above for listing of data sources used). Incidental take is divided by the juvenile production estimates given in Table 4-2 of the BiOp on page 83 to create an alternative take index. Juvenile production estimates are a more direct estimate of abundance than escapement. Repeating the above analyses with the alternative take index reaches the same conclusion as reached with the original incidental take index, namely, that there is no statistically significant correlation between the alternative index and either December-March average OMR flows or the December-March average E:I ratio. The results are shown visually in the figures below.



Alternative juvenile Chinook salmon incidental take index is the incidental take divided by juvenile production (table 4-2 of BiOp).
Incidental take does not include tagged hatchery fish.
Escapement estimates are for naturally spawning salmon and years 2000-2007.
Best fit regression line is shown. Note that the regression line has a slope that does not differ statistically significantly from a horizontal line.
Months chosen for winter and spring-run Chinook salmon are based on dates for movement into Delta (Table 6-34 BiOp)
Data sources:
http://www.usbr.gov/mp/cvo/fishrpt.html
OMR flow data provided by FWS pursuant to
FOIA request from MWD



Alternative juvenile Chinook salmon incidental take index is the incidental take divided by juvenile production as estimated in BiOp Table 4-2.
Escapement estimates are for naturally spawning salmon and years 2000-2007.
Best fit regression line is shown. Note that the regression line has a slope that does not differ statistically significantly from a horizontal line.
Months chosen for winter- and spring-run Chinook salmon are based on dates for movement into Delta (Table 6-34 BiOp)
Data sources:
http://www.usbr.gov/mp/cvo/fishrpt.html
Export and inflow data provided by FWS pursuant to FOIA request from MWD

12. My evaluation of the analysis and modeling underlying the OMR flow restrictions in Action IV.2.3 reveals that NMFS did not utilize the best available scientific methods. When I applied standard principles of fish population dynamics and conducted the same analysis using the incidental take index, the results were fundamentally different from those reached in the BiOp. The modeling shows that there is no statistically significant relationship between OMR flows and abundance or between the E:I ratio and abundance.

I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on March 15, 2010, at La Jolla, Ca.

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UNITED STATES DISTRICT COURT

EASTERN DISTRICT OF CALIFORNIA

THE DELTA SMELT CASES, SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. SALAZAR, *et al.* (Case No. 1:09-cv-407) STATE WATER CONTRACTORS v. SALAZAR, *et al.* (Case No. 1:09-cv-422) COALITION FOR A SUSTAINABLE DELTA, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-480) METROPOLITAN WATER DISTRICT v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al*. (Case No. 1:09-cv-631) STEWART & JASPER ORCHARDS, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-892)	1:09-cv-407 OWW GSA 1:09-cv-422 OWW GSA 1:09-cv-631 OWW GSA 1:09-cv-892 OWW GSA PARTIALLY CONSOLIDATED WITH: 1:09-cv-480 OWW GSA **DECLARATION OF DR. RICHARD B. DERISO** Date: March 23, 2010 Time: 8:30 a.m. Ctrm: 3 Judge: Hon. Oliver W. Wanger

I, RICHARD B. DERISO, declare:

1. The facts and statements set forth in this declaration are true of my own knowledge and if called as a witness, I can testify competently thereto. Any opinions expressed in this declaration are based upon my knowledge, experience, training and education, as set forth in section I.

2. My declaration is set forth in the following manner:

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I. INTRODUCTION

3. In July of this year, I prepared a preliminary declaration that set forth a general explanation of the statistical analysis contained in the 2008 Delta Smelt Biological Opinion ("BiOp") prepared by the United States Fish and Wildlife Service ("FWS"). In that declaration, I focused on three areas of analysis performed by FWS—(1) the relationship between Old and Middle River ("OMR") flows and salvage, (2) the effect of Fall X2 on population survival, and (3) the establishment of incidental take levels. In each of these areas, FWS employed statistics, data analysis, and/or statistical modeling—tools that require technical training to understand. The equations, the statistical, mathematical and fishery population dynamic principles, and the modeling exercises involved in the BiOp are highly complicated. Someone without the proper background and training would be unable to thoroughly review what FWS did in a meaningful way.

4. It is my understanding that the Court has authorized the submittal of this declaration so that I may address and explain in detail the issues I identified in my prior declaration. Since my prior declaration, I have been able to complete my review of the BiOp, as well as the relevant publications relied on by FWS and cited in the BiOp. This declaration sets

forth my comprehensive explanation of the statistical modeling and analysis that FWS performed, including its clear, fundamental errors, focusing again on OMR flows, Fall X2, and the incidental take levels. Below, and in the accompanying appendix, I explain what FWS purported to do, and the mistakes they made in reaching their conclusions. I have also provided the information and equations that I used in conducting my review in an appendix so that my statements and explanations can be critically reviewed by others.

II. BACKGROUND AND EXPERIENCE

5. I am the Chief Scientist of the Tuna-Billfish Program at the Inter-American Tropical Tuna Commission ("IATTC"), and I have held this position since 1989. *See* Summary Professional Vitae, attached hereto as Exhibit A. I supervise a scientific staff of approximately 20 scientists and our primary responsibilities are: (1) to collect statistics on the fisheries that operate in the eastern Pacific Ocean, such as tuna and tuna-like species, and (2) to conduct stock assessments annually on the principal tropical tuna species as well as periodically other species such as turtles, sharks, and billfish species. My work involves advising the Commission on the current status of the populations and making conservation recommendations that can permit stocks to be maintained at a level of abundance that will support maximum sustainable yields.

6. IATTC has a long history of successful management of the tuna stocks in the eastern Pacific Ocean. The largest fishery historically has been yellowfin tuna. Yellowfin tuna is currently at a level of abundance above that which would support maximum sustainable yield.

7. I have a Ph.D. in Biomathematics (Quantitative Ecology) from the University of Washington, a Master's of Science in Mathematics from the University of Florida, and a Bachelor's of Science in Industrial Engineering from Auburn University. I have been teaching courses in fish population dynamics, quantitative ecology, and related areas for over twenty years. I was an Associate Adjunct Professor at the Scripps Institution of Oceanography, University of California, San Diego, from 1990 to 2006 and an Affiliate Associate Professor of Fisheries at the University of Washington from 1987 to 2006. Among the graduate courses I have taught are "Theoretical Models of Exploited Animal Populations" at the University of Washington; "Decision Analysis for Exploited Populations" at the University of Washington; and

"Quantitative Theory of Populations and Communities" at Scripps Institution of Oceanography. I have additional professional experience through a current membership on the Scientific and Statistical Committee of the Western Pacific Regional Fisheries Management Council and a past membership on the Ocean Studies Board which governs the U.S. National Research Council, where I served as co-chairman of the Committee on Fish Stock Assessment Methods. I was also formerly a Population Dynamicist for the International Pacific Halibut Commission. I have been a consultant to several agencies and institutions, both public and private.

8. I have authored or co-authored over 50 peer reviewed publications and technical reports, including Deriso, R., Maunder, M., and Pearson, W, *Incorporating covariates into fisheries stock assessment models with application to Pacific herring*, Ecol. App. 18(5): 1270-1286 (2008); Deriso, R., Maunder, M., and Skalski, J., *Variance estimation in integrated assessment models and its importance for hypothesis testing*, Can. J. Fish. Aquat. Sci. 64: 187-197 (2007); and Quinn, T. and Deriso, R., *Quantitative Fish Dynamics*, Oxford University Press (1999). *See* List of Publications, attached hereto as Exhibit B.

9. I have been retained to evaluate the effects of entrainment on fish populations in many circumstances throughout the United States. I have consulted on the environmental review of once-through cooling systems of the Indian Point nuclear power plants on the Hudson and Delaware Rivers, focusing on impingement and entrainment of fish, with a particular emphasis on their impacts to population. For this analysis, I was retained by ESSA Technologies Ltd. through a contract with the New York State Department of Environmental Conservation. This analysis included modeling, and reviewing models of, the impacts of entrainment and impingement on fish populations. I am a member of the Estuary Enhancement Program Advisory Committee that reviews the mitigation measures for losses of fish through impingement and entrainment at the Salem Nuclear Power Plant on the Delaware River in New Jersey. I have evaluated both the mortality and related impacts of hydroelectric dam operations on Chinook salmon populations on the Columbia and Snake Rivers.

10. I am familiar with, understand, and am able to explain to the Court the concepts and techniques used in the 2008 Delta Smelt Biological Opinion to evaluate the impacts of the

Central Valley Project and the State Water Project operations on the delta smelt population. My testimony and opinions are offered in the context of explaining the standard practices and statistical methods that are used in fish population dynamics to evaluate impacts to fish populations, and the practices and statistical methods employed by the FWS in the BiOp.

III. GENERALLY ACCEPTED PRINCIPLES OF FISH POPULATION DYNAMICS THAT APPLY TO AN ANALYSIS OF IMPACTS TO FISH SPECIES

11. In the BiOp, FWS sought to evaluate the effects of the Central Valley Project and State Water Project on the threatened delta smelt. When looking at potential impacts of a project to fish species, the standard of practice is for qualified professionals to employ certain well-established principles of fish population dynamics.

A. Principle 1: Quantitative Analysis Should Be Conducted

12. The fundamental approach to assessing fish population dynamics is through quantitative statistical analysis (mathematical models) of population dynamics. "Quantitative analysis" involves the use of actual measured data and the testing of relationships between that data. The nature and degree of project impacts on a species must be determined using quantitative methods where quantitative data is available. Similarly, measures designed to benefit the species and avoid harm must be based on a quantitative approach. Only in this way can impacts and benefits be measured for proper evaluation of their effect on the species.

13. By contrast, a qualitative approach may be appropriate where no quantitative data or measurements are available. Qualitative analysis consists of a more subjective evaluation of the degrees of importance of particular factors and circumstances for which quantitative data and measurements are not appropriate or do not exist.

B. Principle 2: Impacts to the Total Population Should Be Evaluated

14. Population dynamics also involve a qualified scientist conducting an evaluation of project impacts to a threatened fish by focusing on impacts to the total population. Measuring effects on a single fish, or a limited group of fish, does not lead to reliable conclusions about population level effects. Such population level conclusions are essential when evaluating a project's impacts on the species as a whole and its ability to survive and recover.

15. Population level effects are properly evaluated using rates and proportions. This means that a given impact or variable cannot be taken as significant on its own without accounting for the *relative* impact on the total population. The population growth rate is an appropriate and reliable measure of population increases and decreases from year to year.

C. Principle 3: Models Should Be Reliable and Biologically Plausible

16. The standard of practice for a fish population dynamicist requires that any statistical models that are utilized must be reliable and biologically plausible. Such statistical models are based on mathematical formulas that assign numeric values to biotic and abiotic variables to explain the relationships among them. To be biologically plausible means that the mathematical formulas used must reflect the reality that the "variables" are reflective of the biology of the living organisms that are being assessed. For example, living organisms have a limited life span and limited reproductive capabilities that must be taken into account in any model used to evaluate their behavior and vulnerabilities. Thus, the models that are properly used are designed to attribute a quantitative value to those influential biological factors so that the model enables quantitative measurement of their interrelationships. Such models are designed to reflect biological realities and to evaluate the relationship between living stock and recruits.

D. Principle 4: Data Should Be Used Consistently

17. In performing a quantitative fish population analysis, generally accepted scientific standards require that the study be internally consistent in its use of data. Data that is rejected in one aspect of the analysis should not be relied upon elsewhere in the same study.

18. With these general principles in mind, I turn to the subject of this action, the 2008 Delta Smelt Biological Opinion for the Operations Criteria and Plan for the State Water Project and the Central Valley Project.

IV. THE BIOP'S EVALUATION OF PROJECT EFFECTS AND THE BIOP'S RPAS ARE BASED ON A "QUANTITATIVE" ANALYSIS

19. The core analyses and conclusions in the BiOp are contained in the sections entitled "Effects of the Proposed Action" (BiOp at 202-239 [Administrative Record ("AR") at 000217-000254]), "Reasonable and Prudent Alternative" ("RPA") (BiOp at 279-285, 324-81 [AR

at 000294-000300, 000339-000396]), and "Incidental Take Statement" ("ITS") (BiOp at 285-295 [AR at 000300-000310]). These sections define the effects of the water projects on the delta smelt and the restrictions which FWS imposed to avoid jeopardy.

20. In the section of the BiOp entitled "Effects Analysis Methods," FWS explains that the effects of the project pumps on entrainment (OMR flows and salvage, and incidental take levels) and the fall habitat suitability and its effect on population (Fall X2) "are quantitatively analyzed."

> The effects analyses range from qualitative descriptions and conceptual models of project effects to quantitative analyses. The effects of Banks and Jones pumping on adult delta smelt entrainment, larval-juvenile delta smelt entrainment, and fall habitat suitability and its predicted effect on the summer townet survey abundance index are quantitatively analyzed. The remainder of proposed action elements and effects are not analyzed quantitatively because data are not available to do so or it is the opinion of the FWS that they have minor effects on delta smelt.

BiOp at 208-209 (AR at 000223-000224). This representation is consistent with my review of the BiOp—FWS conducted a quantitative statistical analysis in order to (1) evaluate project effects on the smelt population and (2) develop RPAs designed to mitigate and avoid any such effects to the extent necessary to avoid jeopardy to the species and adverse modification of its critical habitat. As I would expect of most any scientific exercise, FWS relied on and used data when it was available, unless FWS concluded that the issue was too "minor."

21. Because the BiOp concludes that the projects jeopardize the species and adversely modify its critical habitat, it includes RPAs that restrict project operations in an attempt to avoid jeopardy and adverse modification. The RPAs address categories of effects to which FWS applied quantitative analyses: adult entrainment and larval/juvenile entrainment as related to OMR flows, and fall habitat. These are outlined in more detail below.

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22. **Actions 1 and 2 (Winter OMR Flows)**.[1] Actions 1 and 2 are designed to avoid jeopardy to adults from entrainment. These Actions restrict Old and Middle River ("OMR") flows to reduce adult salvage in the winter. Action 1 is triggered first and lasts for 14 days, followed immediately by Action 2, which is triggered if certain criteria are present and lasts until spawning begins or a certain water temperature is reached. Both of these Actions prescribe a similar range of OMR flows, but at different times of the year. The quantitative analysis presented in Attachment B to support the prescribed OMR flow levels in Actions 1 and 2 is set forth in the BiOp at 345-349 and is represented in two graphs labeled Figure B-13 and Figure B-14, which appear to share the same data. *See* BiOp at 348, 350 (AR at 000363, 000365). Figure B-13 depicts the BiOp's analysis of the relationship between winter OMR flows and adult salvage, concluding that as flows become more negative, salvage increases. Based on this relationship, Actions 1 and 2 set less negative flow levels to reduce salvage.

23. **Action 3 (Spring OMR Flows)**. Action 3 is designed to avoid jeopardy to larvae and juveniles from entrainment. This Action restricts OMR flows to reduce larval/juvenile salvage in the spring. FWS did not apply statistical modeling to evaluate whether or not reductions in OMR flows or X2 would reduce impacts to juveniles, because there is no actual data on larval and juvenile salvage for fish smaller than 20 millimeters. Instead, FWS relied on the assumption that larval and juvenile movement can be predicted using a particle tracking model. A particle tracking model is a theoretical simulation of the flow of neutrally buoyant particles through a water system, where particles are used as surrogates for actual fish. Similar to Actions 1 and 2, Action 3 sets less negative flow levels to reduce salvage.

24. **Action 4 (Fall X2)**. Action 4 is designed to protect fall habitat for adults. This Action prescribes Delta outflows to push X2 more seaward during the fall. The BiOp relies primarily on the quantitative analysis represented by the summary statistics for the stock-recruit

[1] The RPAs are divided into four "Components," which are supported by supplemental information in Attachment B to the BiOp. Attachment B breaks down the RPA Components into five "Actions," such that Component 1 is represented by Actions 1 and 2, Component 2 is supported by Action 3, Component 3 is supported by Action 4, and Component 4 is supported by Action 5. Because most of the technical analysis is contained in Attachment B, and for ease of reference, I will refer to the RPAs in terms of the Actions rather than the Components.

model set forth in Figure E-22 to establish that the location of Fall X2 has a significant effect on delta smelt abundance. *See* BiOp at 268 (AR at 000283). Based on this purported relationship, Action 4 sets Delta outflow levels to control the location of X2.

25. **Incidental Take Statement**. The BiOp also includes an Incidental Take Statement, which prescribes the acceptable level of take of larval/juvenile and adult delta smelt using quantitative methods. For each of larvae/juveniles and adults, FWS took the average salvage rate from certain prior years which it deemed to be representative of future conditions under the RPAs. The average salvage rate from the prior representative years was set as the maximum take level under the RPAs. *See* BiOp at 385-390 (AR at 000400-000405).

26. To summarize, FWS used quantitative methods to evaluate the effects of water project operations (OMR flows) on the species, on its fall habitat (as represented by Fall X2), and to establish incidental take levels. I will next explain the clear, fundamental errors I have identified in that quantitative analysis.

V. THE QUANTITATIVE ANALYSIS BY FWS DOES NOT FOLLOW STANDARD FISH POPULATION ASSESSMENT METHODS

A. Actions 1 & 2 (Winter OMR Flows): Use of Raw Salvage Numbers Instead of the Salvage Rate

27. Actions 1 and 2 prescribe OMR flow levels based on the BiOp's calculation of the relationship between OMR flows and adult salvage. This relationship is depicted in Figure B-13 and compares OMR flow levels to raw salvage numbers. The salvage numbers used are the total number of fish counted at the salvage facilities.

28. Raw salvage numbers do not represent the proportion of the total population that is lost to salvage, which is the salvage rate. For example, a raw salvage total of 100 adults has vastly different significance depending on whether the total population is 200 (salvage rate of 50 percent) or 10,000 (salvage rate of 1 percent). Thus, Figure B-13 does not show what effect OMR flows have on the total delta smelt population.

29. Use of raw salvage numbers, rather than the salvage rate, could be appropriate if the total delta smelt population was known and a model that incorporates every life stage of the

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species (a life-cycle model)[2] was being used. Salvage of delta smelt is a source of loss of individuals—it is analogous to using catch as a mortality loss to the population. If the total delta smelt population was known, then the salvage numbers themselves could be incorporated directly into a life-cycle model and would make it possible to determine the population effects of salvage. A simple version of such a model is explained in Hilborn, R. & Walters, C., *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*, Chapman & Hall (1992) at 298:

> The changes in a population's biomass from one time to the next can be simply written as
>
> next biomass = last biomass + recruitment + growth – catch – natural mortality.

Salvage would take the role of catch in a similar life-cycle model for delta smelt.

30. Here, however, the total population of delta smelt is unknown, although there have been recent attempts to provide such estimates. Because actual abundance is not known, raw salvage numbers cannot be used to show population level effects.

31. In the absence of actual adult abundance numbers, adult abundance is estimated by the Fall Midwater Trawl Survey ("FMWT"), which collects samples around the Delta. An index of the FMWT is used to track the relative increase or decrease in adult abundance from year to year. The survey counts the number of smelt captured in a net of known dimensions and multiplies it by the volume of water actually sampled. That number is then applied to the entire estimated volume of water where the smelt is believed to reside. From this data, an index is derived.

32. The FMWT index is scientifically reasonable and widely relied upon by scientists studying the delta smelt, though not without its technical flaws. It is a numerical scale used to compare variables derived from a series of observed facts with one another or with some reference number to reveal relative changes as a function of time. Because actual abundance is not known, raw salvage numbers cannot be used to show population level effects.

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[2] A life-cycle model is a well-accepted and reliable method of evaluating population dynamics from generation to generation (adults to adults), rather than focusing solely on one age group or the change from adults to juveniles.

33. For adult delta smelt, the scientifically accepted and reliable method is to use the cumulative salvage index to evaluate whether a relationship exists between OMR flows and adult salvage. The cumulative salvage index is equal to the raw number salvaged divided by the prior year FMWT index. *See* BiOp at 338 (AR at 000353). In this way, the cumulative salvage index represents an index of the proportion of abundance that is lost to salvage each year. In the absence of abundance figures, the prior year FMWT index stands as a usable denominator for a ratio that would reveal any population level effects from entrainment.

B. Actions 1, 2 & 3 (Winter and Spring OMR Flows): Failure to Evaluate the Smelt's Population Growth Over Time

34. The BiOp's failure to evaluate population level effects using the correct variable (salvage rate) is consistent with its more general failure to use the well-accepted, reliable statistical models typically used to evaluate population level effects. The BiOp did not employ life-cycle modeling**,** which, among other things, is used to estimate a population's growth.

35. Life-cycle modeling is a well-accepted and reliable method of evaluating population dynamics from generation to generation (adults to adults). It typically consists of the simple models known as biomass dynamic models and stock production models, or the more complex models such as age-structured models. *See* Quinn & Deriso (1999) at ch. 2, 6-8; Hilborn & Walters (1992) at 297.

36. In fisheries science, often the total number of fish in a population is unknown. It is standard practice that, given the data available, population level effects can be determined using surrogate methods such as the population growth rate and the salvage rate.

37. Similar to Actions 1 and 2, the BiOp omits any analysis of the effect of spring OMR flows (Action 3) on the delta smelt population growth rate. A standard life-cycle model could be applied to determine whether spring OMR flows, which would potentially affect larvae and juveniles, are affecting the change in total population from year to year. This kind of quantitative analysis would make it possible to reliably calculate population level effects for delta smelt.

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C. Action 4 (Fall X2): Use of a Linear Additive Model Instead of a Multiplicative Model

38. FWS's quantitative Fall X2 analysis for Action 4 of the BiOp is based on a stock-recruitment model. A stock-recruitment model is a model used to evaluate population level effects that quantitatively characterizes the relationship between the parental "stock" and the progeny it produces ("recruits"). In the BiOp, the parental stock is measured through the FMWT and the progeny is measured at the juvenile life stage through the Summer Townet Survey ("TNS").

39. There are many different stock-recruitment models. In selecting a model, one necessary criterion is that the model must be biologically plausible. This means that the mathematical formulas reflect biological reality and limitations, as described above.

40. FWS employed a linear additive stock-recruitment model when evaluating Action 4. A linear additive model adds several factors together to achieve a sum, without use of logarithms. A simple example is A + B = C. This type of model is not appropriate for stock and recruitment relationships, for two main reasons.

41. First, adding and subtracting factors can generate a positive sum, even if one of the factors is zero. This seems mathematically accurate, but it does not work in a situation where the factors are living organisms with certain non-mathematical properties. For instance, in an equation where various factors are added to adult abundance to determine the effect on their juvenile offspring, one can achieve a positive sum (number of juveniles) even if the factor representing the number of adults is zero. In terms of biological reality, zero adults cannot produce offspring. Thus, simply adding the factors does not reflect the manner in which populations grow.

42. Second, a linear additive model treats factors as having a fixed effect on the population, rather than a proportional effect. That is, by adding a factor, it will always increase or decrease the sum by the same absolute amount. While mathematically accurate, this does not work when the factors being added are habitat components that have a changing proportional effect on the sum (population abundance), not a fixed effect. When the total population is

smaller, a smaller number of individuals exist that can potentially be affected by a given factor. This is accounted for by using proportions and rates.

43. In contrast, multiplicative stock-recruitment models produce biologically accurate results and they are appropriate for fish population dynamics. Simply put, a multiplicative model reads as A x B = C. Two multiplicative models available to FWS are the Beverton-Holt and Ricker models. These models are typically used because they are well-accepted by the scientific peer community and are reliable.[3]

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[3] *See, e.g.*, Jorgensen, S. & Fath, B. (eds.), *Encyclopedia of Ecology*, Academic Press (2008); Knowler, D., Estimation of a Stock-Recruitment Relationship for Black Sea Anchovy (Engraulis encrasicolus) Under the Influence of Nutrient Enrichment and the Invasive Comb-Jelly, Mnemiopsis leidyi, 84:3 Fisheries Research 275-281 (May 2007); Owen-Smith, N., Introduction to Modeling Wildlife and Resource Conservation, Blackwell Publ'g (2007); Brauer, F. & Castillo-Chavez, C., Mathematical Models in Biology and Epidemiology, Springer-Verlag New York, Inc. (2006); Kritzer, J. & Sale, P. (eds.), Marine Metapopulations, Elsevier Academic Press (2006); Mangel, M., The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology, Cambridge Univ. Press (2006); Ferrier, R., et al. (eds.), Evolutionary Conservation Biology, Cambridge Studies in Adaptive Dynamics, Cambridge Univ. Press (2004); Hoff, M., Biotic and Abiotic Factors Related to Rainbow Smelt Recruitment in the Wisconsin Waters of Lake Superior, 1978-1997, 30 Journal of Great Lakes Research, Supp. 1 Exploring Superior, 414-422 (2004); Walters, C. & Martell, S., Fisheries Ecology and Management, Princeton Univ. Press (2004); Hart, P. & Reynolds, R. (eds.), Handbook of Fish Biology and Fisheries, 1 Fish Biology, Blackwell Publ'g (2002); Haddon, M., Modeling and Quantitative Methods in Fisheries, Chapman & Hall (2001); Jennings, S., et al., Marine Fisheries Ecology, Blackwell Publ'g (2001); Lorda, E. et al., Application of a Population Dynamics Model to the Probabilistic Assessment of Cooling Water Intake Effects of Millstone Nuclear Power Station (Waterford, CT) on a Nearby Winter Flounder Spawning Stock, 3 Envtl. Science & Policy, Supp. 1, 471-482 (Sept. 2000); McCallum, H., Population Parameters: Estimation for Ecological Models, Blackwell Publ'g (2000); Guenette, S. & Pitcher, T., An Age-Structured Model Showing the Benefits of Marine Reserves in Controlling Overexploitation, 39:3 Fisheries Research 295-303 (Jan. 1999); Quinn & Deriso (1999); Ricklefs, R. & Miller, G., Ecology, 4th ed., W.H. Freeman (1999); Hilborn & Walters (1992); Rothschild, B., Dynamics of Marine Fish Populations, Harvard Univ. Press (1986); Walters, C., Adaptive Management of Renewable Resources, MacMillan Publ'g Co. (1986); Mangel, M., Decision and Control in Uncertain Resource Systems, Academic Press (1985); Pauly, D., Fish Population Dynamics in Tropical Waters: A Manual for Use With Programmable Calculators, 8 ICLARM Studies & Reviews (1984); Fournier, D. & Archibald, C., A General Theory for Analyzing Catch at Age Data, 39 Canadian Journal of Fisheries & Aquatic Sciences 1195-1207 (1982); Pitcher, T. & Hart, P., Fisheries Ecology, Kluwer Academic Publ'g (1982); Walters, C. & Ludwig, D., Effects of Measurement Errors on the Assessment of Stock-Recruitment Relationships, 38 Canadian Journal of Fisheries & Aquatic Sciences 704-710 (1981); Clark, C., Mathematical Bioeconomics: The Optimal Management of Renewable Resources, Wiley (1976); Ricker, W., Handbook of Computation for Biological Statistics of Fish Populations, Bulletin 119 of the Canada Fisheries Res. Bd. (1958), issued again as Ricker, W., Computation and Interpretation of Biological Statistics of Fish Populations, Bulletin 191 of the Canada Fisheries Res. Bd. (1975); Weatherley, A., Growth and Ecology of Fish Populations, Academic Press (1972); Beverton, R. & Holt, S., On the Dynamics of Exploited Fish Populations, 14 Fishery Investigations Series II, Ministry of Agriculture, Fisheries & Food (1957).

44. For measuring population level effects, multiplicative or rate-based models such as Ricker and Beverton-Holt should be used to achieve scientifically accepted, reliable results. Additive models should not, because they generate inaccurate and unreliable results. These are the two most widely-used models in actual practice because they were designed to be biologically accurate and reflect the relationship between stock and recruits. A feature of a multiplicative model is that when there are zero adults on one side of the equation, there are zero young on the other side; i.e., zero adults yields zero offspring. This follows because any number multiplied by zero will always equal zero. As stated in Ricker (1975) at 281, the model is designed "so that when there is no adult stock there is no reproduction . . . ." The same result can be expected using other types of multiplicative models.

D. ITS: Use of Rejected Data Points Instead of Representative Data Points

45. The BiOp sets the adult incidental take limit based on the average salvage rate from the years 2006, 2007, and 2008, which FWS determined to be representative of future conditions under the RPAs. BiOp at 385-86 (AR at 000400-000401). According to the list of salvage levels contained in the ITS, salvage in 2007 was extremely low compared to other years and to 2006 and 2008 in particular. *See* BiOp at 386 (AR at 000401) (Table C-1). In another section of the BiOp, FWS itself had considered the salvage level in 2007 as unusable for purposes of analyzing salvage and OMR flows due to that year's low average water turbidity, a presence/absence indicator. *See* BiOp at 348 (AR at 000363) (Figure B-13, Note). Thus, FWS recognized that the unusual conditions in 2007 made it an unrepresentative year that would skew its analysis of salvage impacts. Use of an unrepresentative data point that was rejected elsewhere in the same study runs counter to basic principles of quantitative fish assessment. FWS does not attempt to justify why the data point would be used in one instance and not another, so one possible explanation is that it is simply a material error in the analysis.

46. To calculate the incidental take limit for larvae and juveniles, FWS largely followed the same methodology that it used for adults. BiOp at 389 (AR at 000404). The take limit is set based on the average monthly juvenile salvage index from four years – 2005, 2006,

2007, and 2008. According to data listed in the BiOp, the salvage in 2006 was extremely low compared to other years. *See* BiOp at 392 (AR at 000407) (Table C-4). I examined this year carefully and discovered through my review of OMR flow data obtained from a Freedom of Information Act ("FOIA") request to FWS[4], that in 2006, average OMR flow was strongly positive in April through June. When analyzing the effects of OMR flows on salvage in the Effects Analysis section of the BiOp, FWS explained that positive OMR flow yields zero or very low salvage. BiOp at 163 (AR at 000178). Thus, FWS's use of 2006 as a "representative" year for larval/juvenile salvage is internally inconsistent with its explanation elsewhere that positive OMR flow (which is what occurred in spring 2006) yields little or no salvage. The year 2006 was therefore not representative and should have been omitted, as it was elsewhere by FWS for other purposes.

VI. THE BIOP'S APPLICATION OF STATISTICAL MODELS AND INPUT VARIABLES IS INCONSISTENT WITH STANDARD PRINCIPLES OF FISHERIES POPULATION DYNAMICS

47. To decipher the models and methods that FWS used, I reviewed and interpreted the limited graphs and tables provided in the BiOp, along with similar information and studies in the administrative record.

48. I compared FWS's models against the standard models employed by the scientific community, and particularly those models that are commonly used in fish population modeling. My review and comparison revealed that the BiOp does not use the well-accepted models in more

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[4] My review of the BiOp and the administrative record revealed that FWS had not provided all of the underlying data that FWS relied on in performing its work on the BiOp. In my experience, a full scientific analysis is not possible without making the underlying data available so that the work may be checked and evaluated by others. This omission hinders the ability to conduct a standard peer review of the FWS analysis without estimating data point values from the graphs or searching for data in other sections. FWS's failure to include the data underlying its basic analyses and determinations is an inexplicable defect given the conclusions FWS reaches. After I identified the missing categories of data, the Metropolitan Water District of Southern California requested that data through a FOIA request. On October 29, 2009, more than ten weeks after the request was made, FWS provided a disc containing portions of the data underlying the BiOp. Included on that disc were daily OMR flow data. I used those data to calculate several average OMR flows, including monthly average flows, as noted in this declaration.

than one place, but rather relies on models that are not biologically sound and lead to erroneous results.

49. I evaluated the same data presented in the BiOp and input it into the standard models to determine whether the end result would be different. The results are fundamentally different from the results reached in the BiOp.

50. Based on the material I reviewed, the fundamental errors I have identified call into question the jeopardy and adverse modification conclusions in the BiOp and reveal that FWS had no reliable scientific basis for imposing the RPAs adopted.

A. FWS's Analysis of the Relationship Between Old and Middle River Flows and Adult Salvage Is Flawed

51. The BiOp's analysis of the effects of the projects on adult delta smelt and its conclusion that winter flow restrictions are necessary are based on a statistical model of the alleged relationship between OMR flows and adult salvage. The modeling and analysis are contained in the Effects of the Proposed Action section of the BiOp, pages 202-279 (AR at 000217-000294), and RPA Actions 1 and 2 in Attachment B to the BiOp, pages 329-356 (AR at 000344-000371). Actions 1 and 2 rely on Figure B-13 on page 348 (AR at 000363) and on various studies, including Kimmerer, W., *Losses of Sacramento River Chinook Salmon and Delta Smelt to Entrainment in Water Diversions in the Sacramento-San Joaquin Delta* (AR at 018854), and the work of Pete Smith, which is cited by Kimmerer.

(1) Improper Use of Total Adult Salvage Numbers Instead of Cumulative Salvage Index

52. FWS uses total adult salvage numbers to demonstrate an alleged relationship between OMR flows and adult salvage. *See* BiOp at 163-65; 347-50 (AR at 000178-000180; 000362-000365). The alleged relationship is derived from the graph in Figure B-13 which compares the number of adults salvaged each year to the corresponding OMR flow rate for that year. BiOp at 164, 348 (AR at 000179; 000363).

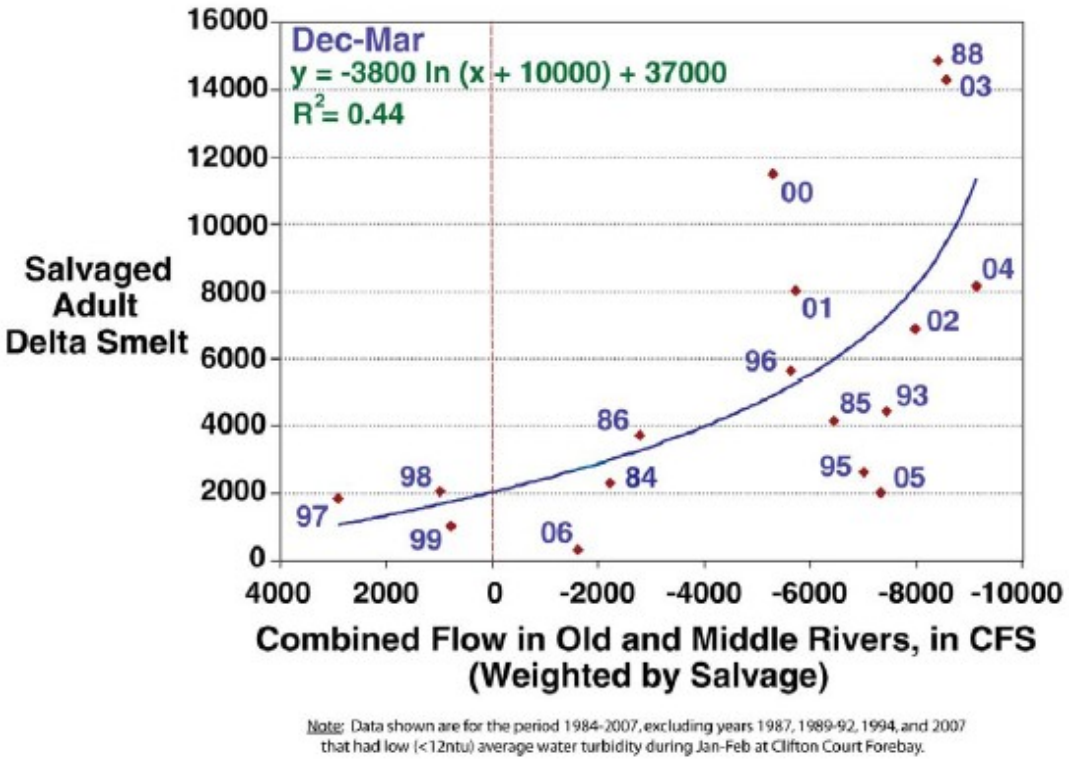

Figure B-13. OMR-Salvage relationship for adult delta smelt. (source, P. Smith). Data from this figure were the raw data used in the piecewise polynomial regression analysis.

53. FWS relied on this graph to conclude that OMR flows correlate to total salvage numbers—suggesting that as negative OMR flows increase, more adults are salvaged.

54. This conclusion by FWS is scientifically flawed because raw salvage numbers do not have a directly proportional effect on population and do not take into account the overall size of the population as determined by representative survey data. Nonetheless, FWS relied on Figure B-13 and Figure B-14 (which appear to share the same data) to set OMR flow levels in RPA Actions 1 and 2. In other words, FWS set OMR flow levels in Actions 1 and 2 without determining population level effects.

55. The scientifically appropriate approach would have been for FWS to use the cumulative salvage index to evaluate whether a relationship exists between OMR flows and adult salvage. FWS had already developed that index for other purposes. *See* BiOp at 386 (AR at 000401) (using the cumulative salvage index in another context, to calculate the incidental take). The cumulative salvage index represents an index of the salvage rate, taking into account data on the size of the population. This has long been recognized as appropriate for analysis of delta

smelt by those scientists actively studying the smelt. *See, e.g.*, Bennett, W., *Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California*, San Francisco Estuary & Watershed Science, Cal. Bay-Delta Auth. Science Program & John Muir Inst. of the Env't (2005) at 37 ("As first step [sic], assessing the potential impacts of the water project operations on delta smelt requires estimating the proportion lost relative to population abundance."). The cumulative salvage index is proportional to the fraction of adult fish that are lost due to water diversion.

56. The concept of dividing fish loss by abundance is well-accepted and reliable and is applied in other, similar applications, such as part of the procedure for estimating the impact of entrainment and impingement of fishes by water withdrawals of once-through cooling systems for nuclear power plants on the Hudson River.

> This approach is based on conditional mortality rates, or the fraction of an initial population that would be killed by some agent during the year if no other sources of mortality operated. Conditional entrainment mortality rates are used as estimates of the direct impact of power plants on individual year classes . . . . (2) Conditional mortality rates can be entered directly into life-cycle models for assessing potential long-term impacts on fish populations.

Barnthouse, L., et al. (eds.), *Science, Law, and Hudson River Power Plants: a Case Study in Environmental Impact Assessment*, Am. Fisheries Soc'y Monograph 4, Am. Fisheries Soc'y (1988) at 122.

57. Another example is biological reference points ("BRP") which can be used as targets for optimal fishing: "A BRP can be expressed as a fishing mortality rate (F) and/or as a level of stock biomass (B)." Comm. on Fish Stock Assessment Methods, Nat'l Research Council, *Improving Fish Stock Assessment Methods*, Nat'l Academy Press (1998) at 45. The fishing mortality rate (F) depends mathematically on the ratio of catch divided by biomass and it is similar to a cumulative salvage index in that both represent a ratio of losses to abundance.

58. Since total population data does not exist, the cumulative salvage index uses a survey index which gives a relative increase or decrease in annual survey numbers to monitor population levels. Use of the cumulative salvage index to evaluate the effects of OMR flows is

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scientifically accepted, reliable, and superior to using the raw salvage numbers themselves (as used in Figure B-13), for the following reasons:

59. The total number of adults salvaged does not indicate population level effects. *See* BiOp at 338 (AR at 000353) ("the total number salvaged at the facilities does not necessarily indicate a negative impact upon the overall delta smelt population"). Stated differently, to make sense of total adult salvage numbers, total adult abundance must be taken into account. For example, a salvage of 100 adults has vastly different significance depending on whether the total population is 200 or 50,000.

60. In contrast, the cumulative salvage index is an index of the *proportion* of adults salvaged from the total population, using the FMWT to relate salvage to population levels. The cumulative salvage index is equal to the number salvaged divided by the prior year FMWT index. *See* BiOp at 338 (AR at 000353).

61. Use of the cumulative salvage index, rather than total salvage numbers, was recommended by the Peer Review. *See Independent Peer Review of USFWS's Draft Effects Analysis for the Operations Criteria and Plan's Biological Opinion, 2008* at 6 (AR at 008818) ("The Panel suggests that the use of predicted salvage of adult smelt should be normalized for population size. . . . Expressing salvage as a normalized index may help remove some of the confounding of the temporal trends during the baseline period.").

(2) Use of the Cumulative Salvage Index Shows That There Is No Statistically Significant Relationship Between OMR Flows and Adult Salvage for Flows Less Negative Than -6100 Cubic Feet per Second at the Very Least

62. To assess FWS's methods, I plotted a graph of the relationship between the cumulative salvage index (salvage rate) and the OMR flows for each year that was analyzed in the BiOp. In developing this graph, I used the cumulative salvage index data provided in the BiOp. *See, e.g.,* BiOp at 386 (AR at 000401). Because Figure B-13 uses salvage weighted OMR flows, which are not listed anywhere in the BiOp, I visually estimated a magnified version of the OMR flow curve in Figure B-13 and interpolated the data points for each year.

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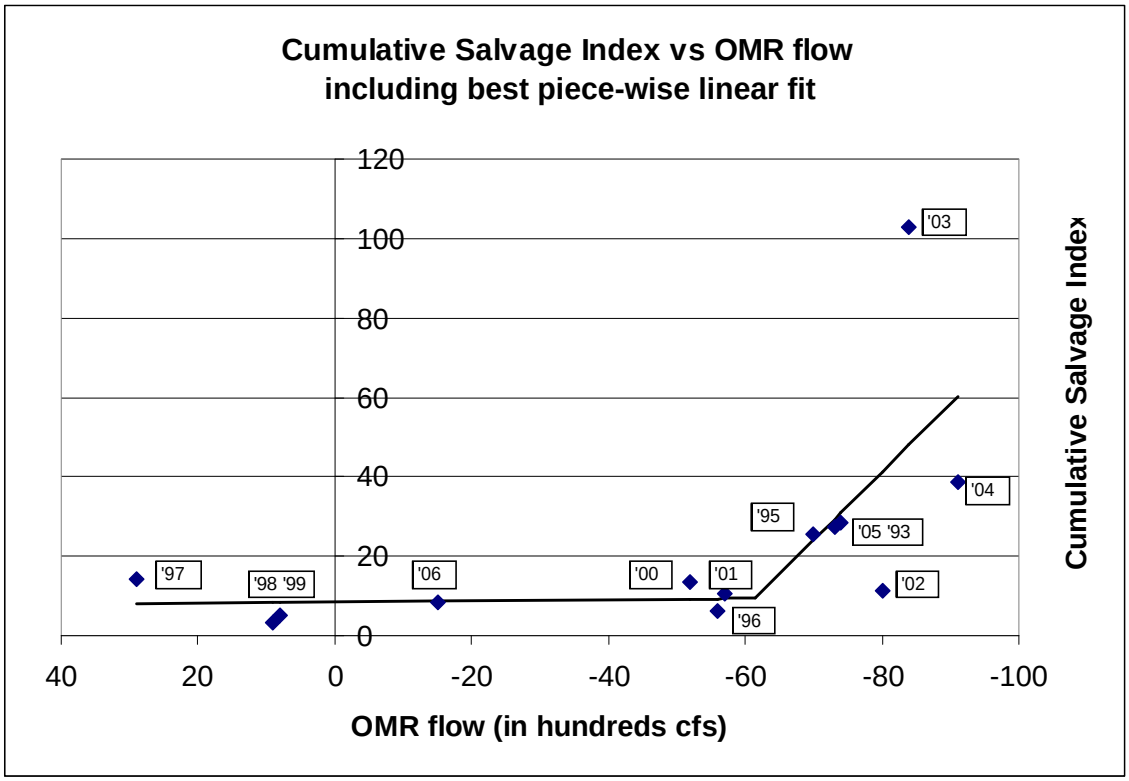

The Cumulative Salvage Index (Table B-2 & C-1) and corresponding Dec-Mar salvage weighted OMR (Figure B-13); note the salvage weighted OMR flows were visually estimated from Figure B-13. Years span 1993-2006 but exclude 1994 because that was also excluded in Figure B-13. A piece-wise linear model (the line on the figure) is also shown whose coefficients were obtained by the statistical procedure of maximum likelihood estimation.

63. The graph of salvage rate versus OMR flow shows that salvage rate remains flat as OMR flows increase until OMR flows reach -6100 to -7000 cubic feet per second ("cfs"). At -7000 cfs, salvage rate begins to increase as negative OMR flows increase. The graph demonstrates that OMR flows do not correlate to the salvage rate at flows less negative than -6100 cfs at the very least. I have determined that, based on the data available and using the appropriate reliable analytic method, there is no scientific basis for FWS's imposition of OMR flow restrictions at flows less negative than -6100 cfs (and potentially -7000 cfs). For additional technical detail, see Appendix 1 at Point 1.

64. As shown in the x-axis label on Figure B-13 (see ¶ 52 above), FWS used "Combined Flow in Old and Middle Rivers, in CFS (Weighted by Salvage)" to evaluate the relationship between OMR flows and salvage. "Weighted by Salvage" is not defined in the

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BiOp; however, a logical definition is that the salvage weighted average OMR flow is an average over several time periods, such as weeks, and the influence that a given week's OMR flow has on the overall average is set proportional to the salvage in that week.

65. FWS's October 29, 2009 FOIA response included daily OMR flow data (as opposed to the weighted average flows used in Figure B-13). I constructed December through March average OMR estimates based on the daily OMR flows provided by FWS. I modeled the relationship between the straight average OMR flows and the cumulative salvage index and confirmed that the results are consistent with those reached using the Figure B-13 weighted average flows. Using the straight average, the flows were not significant until a much more negative flow level (approximately -7943 cfs). The results are shown in Appendix 1 at Point 1.

B. The BiOp Fails to Evaluate Population Level Effects Using the Population Growth Rate – Interpreting the Data in This Way Shows That Salvage and OMR Flows Do Not Have a Statistically Significant Effect on the Population Growth Rate

66. Given the data in FWS's possession, and given its goal of evaluating the projects' effect on the total population, the appropriate analysis is to use that data to evaluate the effect on the population from year to year. This includes interpretation of the data to determine the effect of salvage (or more generally, population removals) on the population growth rate by application of a life-cycle model, as is standard practice in fisheries stock assessment. This approach is confirmed by the authors of widely read and accepted texts, which discuss the reliable methods of undertaking these analyses. *See, e.g.*, Quinn & Deriso (1999) at ch. 2; Hilborn & Walters (1992) at ch. 8. The population growth rate represents the relative increase or decrease in adults from one year to the next, which is a full life-cycle approach. Owen-Smith (2007) at 28. This approach is critical for evaluating the species' potential for recovery in that it measures the population's ability to rebound from year to year. *See, e.g.*, Bennett (2005) at 41 ("Population modeling may be the best way to evaluate the potential impacts of water export operations relative to other sources of mortality.").

67. Interpreting the data to evaluate the effect of salvage on the population growth rate is necessary because the survival of the species at one life stage cannot necessarily be the basis

for population level conclusions. To evaluate the effects of salvage, one must look beyond a single phase of life (i.e., FMWT only) or even adults to juveniles (i.e., FMWT to TNS). A complete analysis requires an evaluation of trends from one year's FMWT to the next year's FMWT because mortality in one life stage may be offset by mortality in another life stage or it may be affected by density dependence (described below in ¶ 68). As noted by Bennett (2005) at 44, when discussing simulation results of a hypothetical population model for delta smelt, "These results show how export mortality could be easily offset or masked by very small changes in mortality at other life stages." A generation-to-generation analysis eliminates or reduces the risk that population level conclusions will be drawn based on mortality effects in one life stage or the apparent change in mortality effects due to offsets in another life stage.

68. Delta smelt appear to exhibit reduced population growth when population abundance is high due to density dependence. Density dependence can occur through many mechanisms, as described by Ricker (1975) at 280: "Although cannibalism of young by adults is possible in many species, it is likely that the effect of parental stock density upon recruitment is usually exerted *via* the density of the eggs or larvae they produce, survival of the latter being affected by density-dependent competition for food or space, compensatory predation, etc." Thus, density dependent effects must be taken into account when evaluating the population growth rate. Density dependence terms are present in all major stock production, biomass dynamic, and stock-recruitment models, including the Ricker model. *See* Quinn & Deriso (1999) at chs. 2, 3.

69. Standard practice dictates that population level conclusions should not be based solely on raw salvage numbers. Rather, a fish population dynamicist should evaluate population level effects using the cumulative salvage index (salvage rate), and also evaluate the effect of the cumulative salvage index on the population growth rate, just as is typically done with harvest rates. As noted by Bennett (2005) at 37, "In several respects, losses to the water export facilities are analogous to harvest in a fishery, with the main exception that 'harvest' in this case includes all life stages (except eggs)." Harvest rates are routinely evaluated for their population level effects, and their consequence to population growth levels over time, in fisheries stock

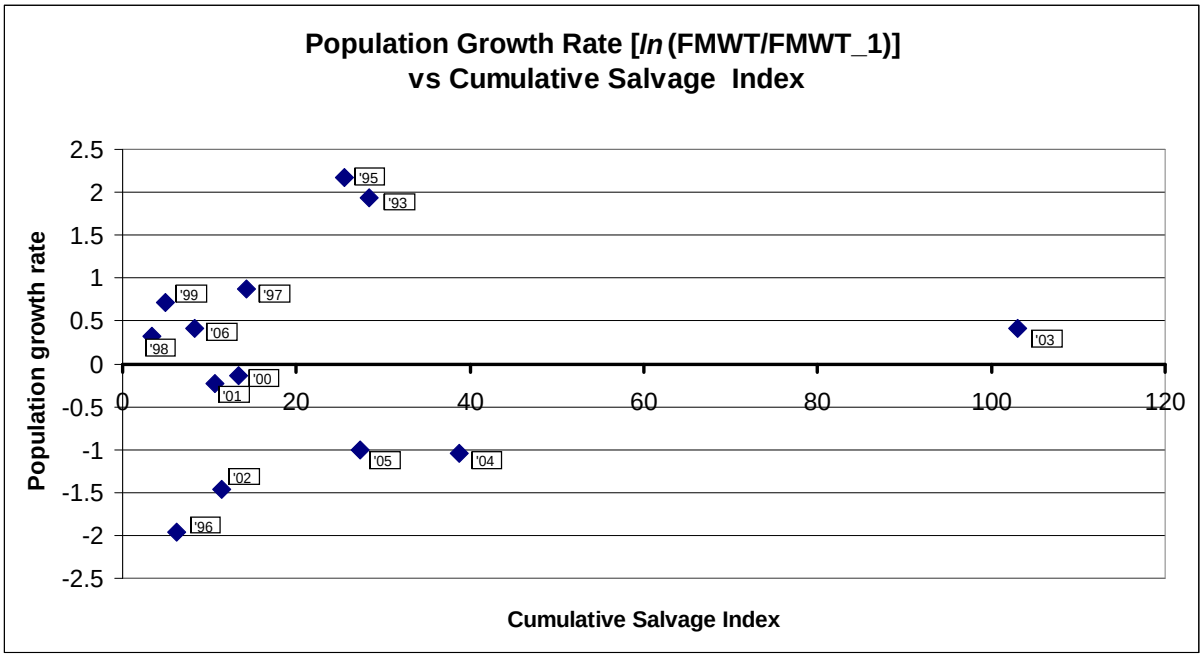
evaluations. *See, e.g.*, Quinn & Deriso (1999) at ch. 2; Hilborn & Walters (1992) at ch. 8. Only by looking at population level effects can it be determined whether salvage is impacting the delta smelt population and its ability to recover in a statistically significant way.

70. Through my review of the modeling and analysis in the BiOp, I determined that FWS did not apply a life-cycle approach in the BiOp. FWS did not attempt to evaluate the effect of the projects on the population growth rate. The BiOp completely omits any analysis or conclusions about project effects on the overall life cycle of the delta smelt and its ability to recover from year to year. However, the data to perform such an analysis is all available, and evaluating population growth rate effects is an elementary exercise. When I looked at the data for such effects, I readily recognized that there is no statistically significant relationship between salvage and the population growth rate.

(1) Adults – Salvage

71. Applying standard principles to calculate population level effects, and using the correct variable to determine those effects (the salvage rate), I modeled the relationship between the cumulative salvage index and the population growth rate. The life-cycle model used for this analysis is a standard Ricker stock-recruitment model in which consecutive year FMWT estimates take the role of stock and recruitment, respectively. I used the cumulative salvage index data taken from the BiOp itself. *See* BiOp at 386 (AR at 000401).

72. The output of this standard model shows that there is no statistically significant relationship between salvage and the population growth rate. This demonstration is based upon using 0.05 as the significance level—the standard benchmark in applied statistics for determining a significance level. *See, e.g.*, Sigler, S., *Fisher and the 5% Level*, 21:4 Chance, Springer New York (Dec. 2008). Statistical significance is found when the p-value is less than 0.05. The p-value is the probability that the result obtained in a statistical test is due to chance rather than a true relationship between variables. In the analysis that I performed, the p-value was 0.76, which is greater than the benchmark and thus not statistically significant. *See* Appendix 1 at Point 2 for additional technical detail. The population growth rate and cumulative salvage index are depicted in the graph below as a visual aid.

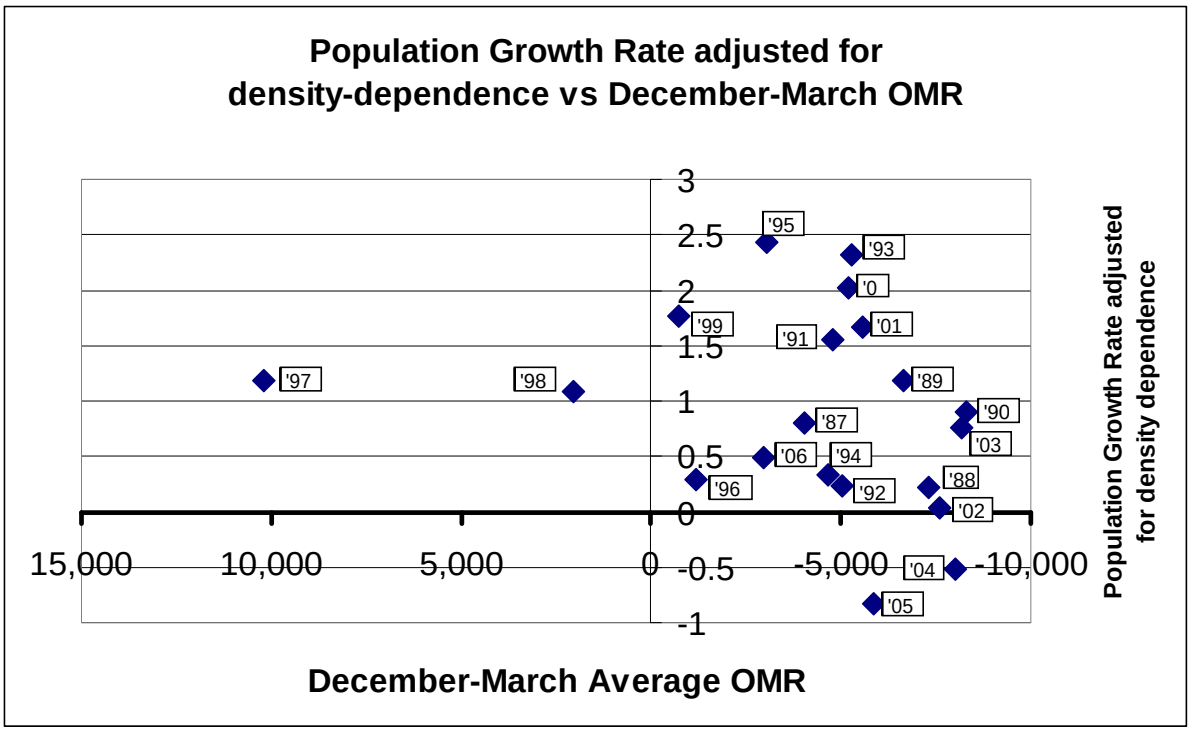


73. If the cumulative salvage index had a strong negative effect on population growth, the above graph would have been expected to show a pronounced negative slope. Instead, the graph shows no trend in population growth rate as the salvage rate increases. If the population has a growth rate of zero, then the population is neither increasing nor declining. A positive growth rate means the population is increasing on an annual basis, and a negative growth rate means the population is declining on an annual basis. Here, the population growth rate did not trend in a negative direction as the cumulative salvage index increased, so there is no statistical basis to conclude that cumulative salvage has a negative population level effect within the range of cumulative salvage index levels historically observed.

(2) Adults – OMR Flows

74. I conducted a second analysis to evaluate the relationship between December-March average OMR flows and the population growth rate. I calculated the average flows using the daily OMR flow data from the October 29, 2009 FOIA request. Using a standard Ricker stock-recruitment model and the standard 0.05 significance level, I found that the relationship between March-December OMR flows and the population growth rate is not statistically significant. The p-value is 0.321, which is above the significance level of 0.05. The modeling

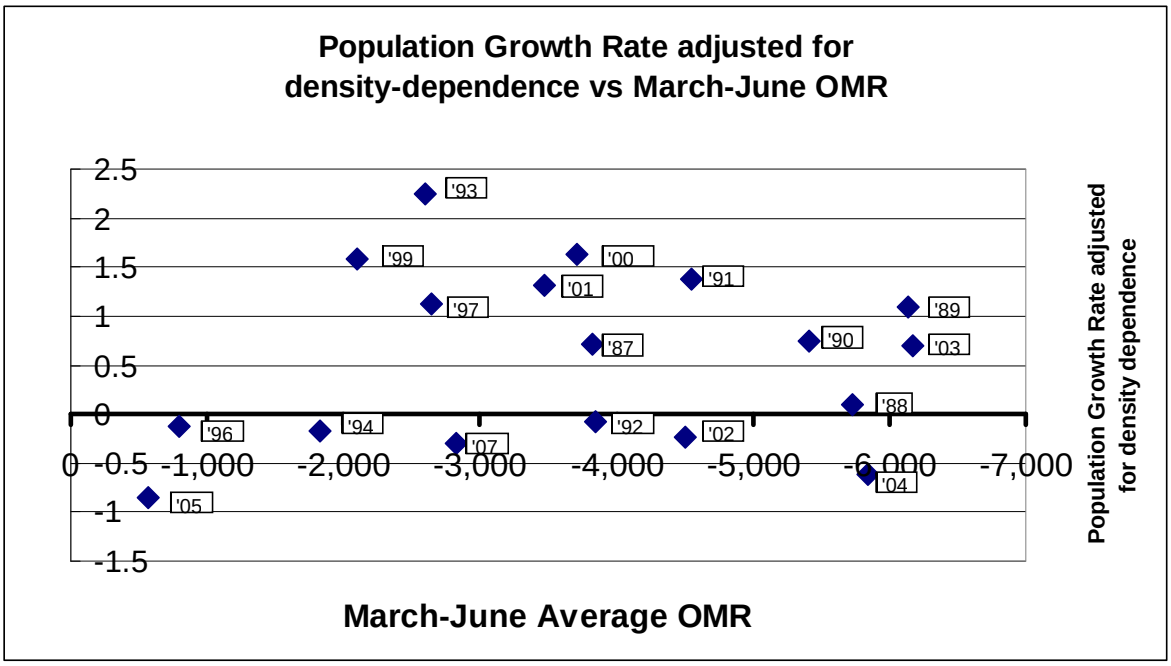
results are shown below as a visual aid. Thus, here too, there is no statistical basis to conclude that the OMR flows cause a negative population level effect within the range of December-March average OMR flows historically observed. For additional technical detail, see Appendix 1 at Point 3.



(3) Juveniles

75. The BiOp includes entrainment estimates for larval-juvenile delta smelt based on the work of Kimmerer (2008), who in turn bases those estimates on a method in which the assumption is made that entrainment is proportional to the southward OMR flow. I tested whether or not average southward OMR flow during the larval/juvenile salvage months of March through June could explain a statistically significant amount of the variation in population growth. I used the Ricker model again as a life-cycle model. March-June average OMR flow for years during the time span 1987 through 2007 in which the average flow was negative (that excluded years 1995, 1998, and 2006) was entered as a candidate explanatory variable and regression analysis was used to test whether or not the candidate variable was statistically significant. A starting year of 1987 was used because that is the starting year used in the BiOp, as data from that year forward "represents current delta smelt population dynamics." *See* BiOp at

236 (AR at 000251). Results show that March-June average OMR does not have a statistically significant impact on smelt population growth rate (the p-value is 0.703, which is above the significance level of 0.05). For additional technical detail, see Appendix 1 at Point 4. Even if entrainment of larval/juvenile smelt is related to spring OMR flow, that entrainment does not have a statistically significant impact on population growth. The result can be seen visually in the graph below which shows that variation in population growth rate (adjusted for density dependence) is not explained by the average March-June OMR flow.



76. March-June OMR does not negatively impact population growth, as can be seen visually in the graph above, where even at the most negative observed average OMR flows, the population growth rate was positive (irrespective of whether a density dependent adjustment is made). For additional technical detail, see Appendix 1 at Point 4. This result implies that there is no scientific justification for proposed RPA Action 3.

C. The Model Used in FWS's Analysis to Compare the Effect of Fall X2 on Population Survival Is Biologically Implausible and Potentially Misleading – It Is Simply Inappropriate for Fish Population Dynamics Modeling

77. FWS used statistical modeling to demonstrate an alleged relationship between Fall X2 and delta smelt abundance. The modeling and analysis are contained in the Effects of the

Proposed Action section of the BiOp, pages 233-238 and 265-274 (AR at 000248-000253 and 000280-000289), and in RPA Action 4 in Attachment B to the BiOp, pages 369-376 (AR at 000384-000391). FWS relied on various studies, particularly the work of Feyrer et al. in a 2007 article, *Multidecadal Trends for Three Declining Fish Species: Habitat Patterns and Mechanisms in the San Francisco Estuary, California, USA* (AR at 018266) and a draft 2008 manuscript, *Modeling the Effects of Water Management Actions on Suitable Habitat and Abundance of a Critically Imperiled Estuarine Fish (Delta Smelt* Hypomesus transpacificus) (AR at 018278); a 2005 article by Bennett, *Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California* (AR at 017004); a 2008 report by Baxter et al., *Pelagic Organism Decline Progress Report: 2007 Synthesis of Results* (AR at 016922); and a 2008 article by Nobriga et al., *Long-Term Trends in Summertime Habitat Suitability for Delta Smelt,* Hypomesus transpacificus (AR at 019940).

(1) FWS Used a Linear Additive Model

78. FWS used a linear additive model to demonstrate an alleged relationship between Fall X2 and delta smelt abundance. The model finds that juvenile abundance, as measured by the TNS, is equal to the sum of a constant number plus the previous year's FMWT index (times a constant number), less X2 (times a constant number). *See* BiOp at 268 (AR at 000283) (Figure E-22). Essentially, this calculation finds that A = B + C - D.

79. FWS followed the linear additive model developed by Feyrer et al. (2007), which claims that Fall X2 has a population level effect. This model runs counter to well-accepted, basic modeling principles for this type of calculation. When analyzing the effect of Fall X2, FWS also cites to a 2005 article by Bennett. *See* BiOp at 236 (AR at 000251). However, Bennett applies a well-established stock-recruit model, namely, the Beverton-Holt model, and an alternative linear multiplicative model. *See* Bennett (2005) at 28-29.

80. The linear additive model produces the result that zero adults in one year could still yield some young in the following year, a result that is biologically implausible. Using the simple translation A (juveniles measured in TNS) = B (constant) + C (adults measured in FMWT) – D (Fall X2), one can see that, if C were set at zero (no adult spawners), B – D could still

produce a positive number for A (juveniles). This model thus has the biologically impossible property of generating juveniles from zero adults.

81. A linear additive model also treats the environmental factor X2 as an additive factor, which has the implausible property of reducing the absolute numbers of juveniles by the same quantity for a given value of X2 irrespective of the total population. For example, if X2 is set at a certain value such that when X2 is added, 1,000 juveniles are lost, that model would produce the result that 1,000 juveniles are always lost irrespective of the total number of juveniles present or the total number of juveniles that actually respond to X2.

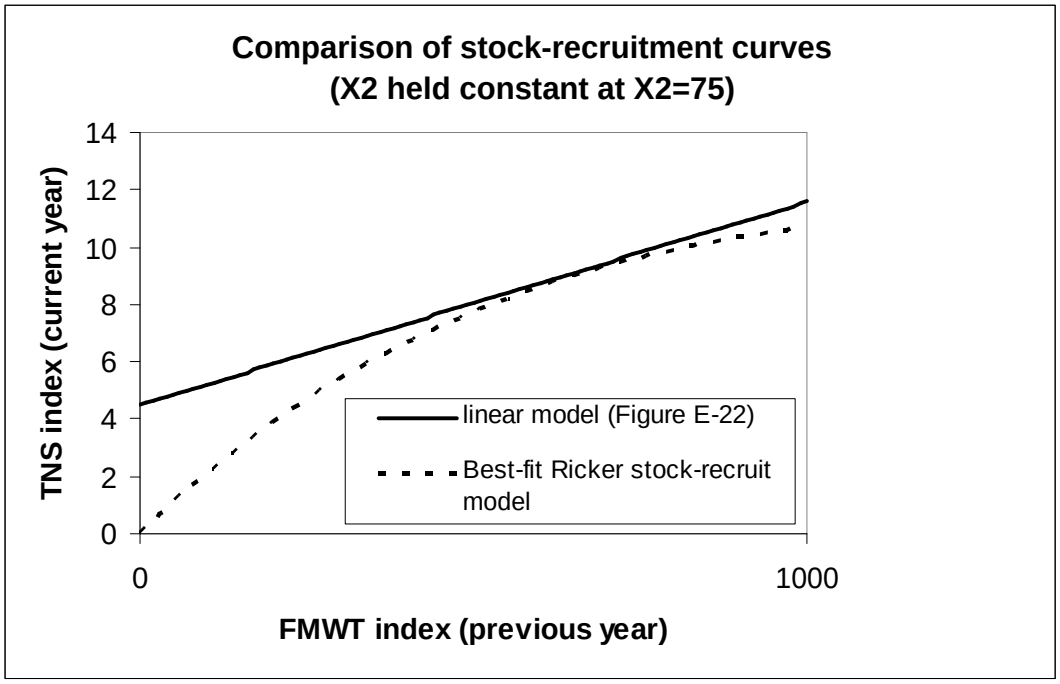
82. For reasons such as these, a linear additive model is inappropriate for stock-recruitment modeling, because the results are biologically impossible.

(2) FWS Should Have Used a Multiplicative Stock-Recruit Model

83. FWS inappropriately used a linear additive model to conduct the analysis that FWS performed with respect to the effect of Fall X2 on population survival. It is well established by those scientists qualified to conduct the type of analysis undertaken by FWS that a multiplicative stock-recruitment should be used. A multiplicative stock-recruit model better reflects actual biological realities when modeling fish populations because it describes survival of a year-class of fish. An example is the Leslie Matrix population model (equation 7.2 in Quinn & Deriso (1999) at 269). Survival processes are inherently multiplicative because the fraction of individuals that survive to a given age is given by the product of daily survivals through each day since the day of birth (*see, e.g.*, cumulative survival in Quinn & Deriso (1999) at 292). A commonly used, well known multiplicative stock-recruit model is the Ricker model. A qualified scientist in this field would be familiar with this model and would have no difficulty using it to perform the analysis that FWS did.

84. Any reliable, scientifically accepted stock-recruit model, such as the Ricker model or the Beverton-Holt model, is not a linear additive model. Such multiplicative stock-recruit models produce the biologically appropriate result that zero adults yields zero young. Thus, regardless of the presence of other factors, if there are zero adult spawners, there will be zero juveniles the following year. A graphical depiction of the difference between a multiplicative

model, such as the Ricker model, and a linear additive model is helpful to illustrate how a multiplicative model better reflects biological reality.



85. A multiplicative model, as opposed to an additive model, yields the sensible result that varying an environmental factor such as X2 will elicit a proportional response in population abundance. This is appropriate for a factor that affects survival because survival is, by definition, a fraction (what proportion of the population survives). In contrast, the linear additive model produces an absolute response irrespective of the size of the population. Multiplicative models are appropriate when describing the survival of a given cohort of fish. Additive terms may be appropriate components in certain types of cohort models when tracking the absolute abundance of a cohort over time—i.e., in situations that involve calculating the total raw population numbers over time, an exercise that has not been done for the delta smelt. *See* Quinn & Deriso (1999) at 323.

86. The BiOp itself questions the use of a linear additive model to evaluate the effect of Fall X2, stating that "some type of transformation of the data would help to define a better fitting model," but declines to correct the situation (such as through the use of a multiplicative model). BiOp at 236 (AR at 000251).

87. The Peer Review also criticized the linear additive model, finding that "[t]he [Effects Analysis] points out that the residuals from this analysis are not normally distributed and that some transformation might be required. We suspect that a few of the data points may have high influence on the outcome. These results together suggest that the model may be inappropriate for the data being used." *Independent Peer Review of USFWS's Draft Effects Analysis for the Operations Criteria and Plan's Biological Opinion, 2008* at 7 (AR at 008819).

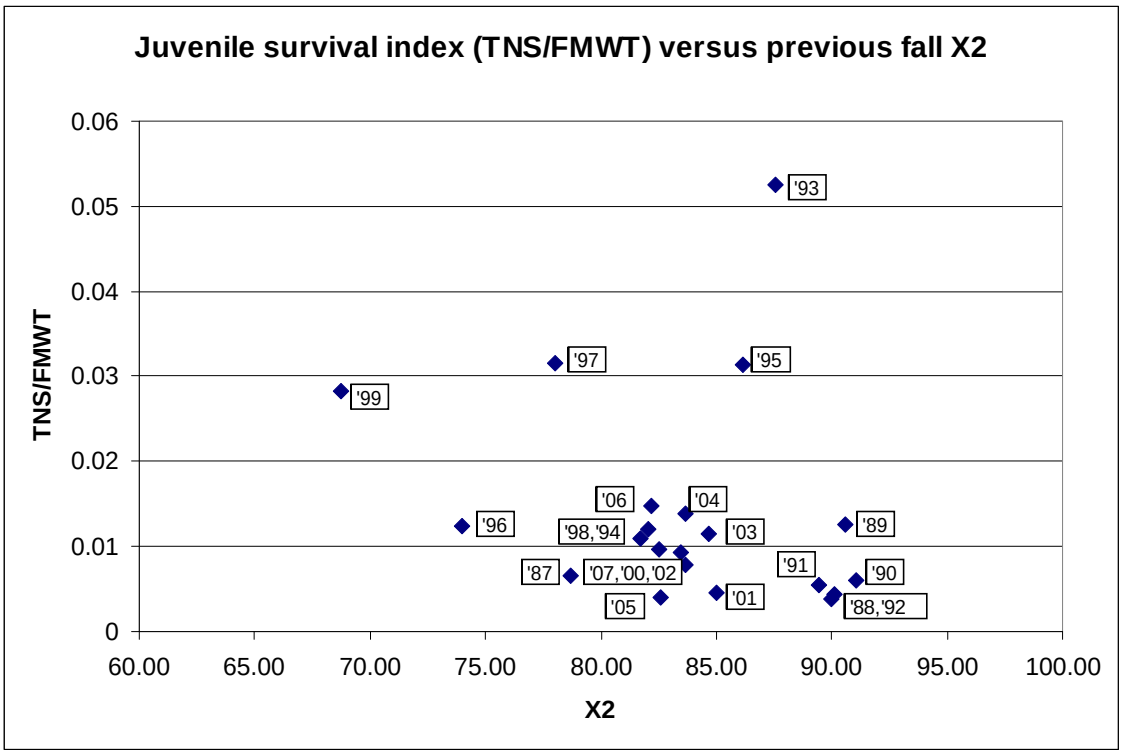
88. During my review of FWS's analysis, I plotted a stock-recruit curve of the relationship between FMWT (previous year) and TNS (current year) using the standard Ricker stock-recruitment model that was obtained by fitting the model to data. See details in Appendix 1 at Point 5. A visual comparison of the linear additive model that FWS used in the BiOp against the Ricker model is shown above. As shown on the comparison, when FMWT is set at zero in the linear model that FWS used, TNS is above zero. In contrast, when FMWT is set at zero in the standard Ricker model, TNS is also zero.

89. In order to evaluate whether there is a relationship between Fall X2 and abundance, I used the publicly available FMWT and TNS data and publicly available Fall X2 data in a standard Ricker stock-recruit model.[5] After employing the Ricker stock-recruit model, I was able to determine that there is no statistically significant relationship between Fall X2, stock abundance, and recruit abundance. The p-value for Fall X2 is 0.059, which is greater than the benchmark significance level of 0.05. See Appendix 1 at Point 5 for additional technical detail. The contrary conclusion that FWS reached is due to its improper use of a biologically implausible linear additive model.

90. I determined that the density dependent term in the Ricker model was not statistically significant. As a result, I used a reduced survival model that omitted the density

[5] FMWT data is available at: http://www.delta.dfg.ca.gov/data/mwt/charts.asp. The BiOp cites to http://www.delta.dfg.ca.gov as a source for FMWT data at page 143 (AR at 000158). TNS data is available at: http://www.delta.dfg.ca.gov/data/projects/?ProjectID=TOWNET. The BiOp cites to this website as a source for TNS data at page 300 (AR at 000315). Fall X2 data is available at: http://www.iep.ca.gov/dayflow/output/index. The BiOp relied on CALSIM modeling to calculate X2 values, and cites to http://www.iep.ca.gov/dayflow for "historical hydrologic data provided in the DAYFLOW database" which was used in the CALSIM modeling. *See* BiOp at 204, 235 (AR at 000219, 000250).

dependent term. The result shows that Fall X2 term is not statistically significant, since the p-value of 0.094 is greater than the 0.05 significance level. The graph below is included as a visual aid to show that there is no relationship between an index of juvenile survival ("TNS/FMWT_1") and Fall X2. If there had been a strong negative effect of Fall X2 on juvenile survival, the graph would have been expected to show a pronounced negative slope. Instead, the graph shows no trend in juvenile survival as X2 increases. For additional technical detail, *see* Appendix 1 at Point 5.



(3) Use of a Scientifically Appropriate Multiplicative Model Shows That Fall X2 Has No Statistically Significant Effect on the Population Growth Rate

91. In my review of the BiOp, I determined that FWS did not evaluate the effect of Fall X2 on the population growth rate. Use of the population growth rate would enable FWS to evaluate effects on the full life-cycle of the delta smelt.

92. Instead of carrying forward the linear additive model, as did FWS, the proper scientific method is to model the relationship between Fall X2 and the population growth rate

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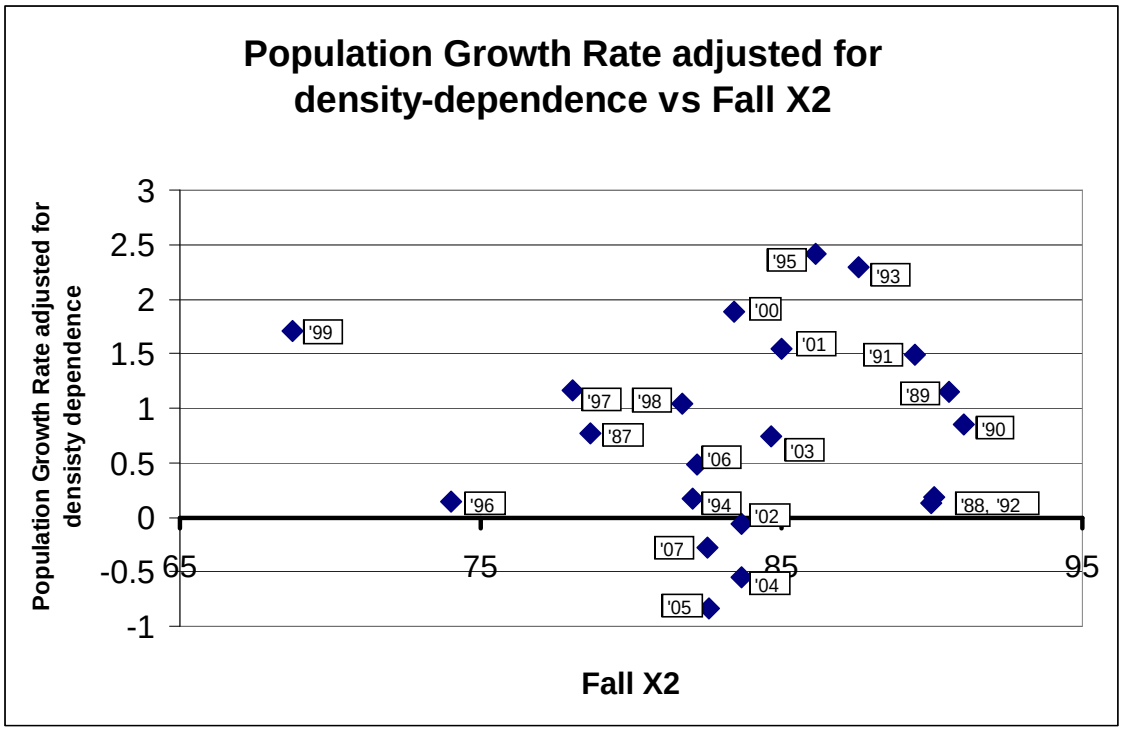
using a multiplicative model. As explained above, a multiplicative model is the scientific standard for fish population dynamics.

93. I used a Ricker model, which is a multiplicative model, to calculate the population growth rate and to evaluate the relationship between Fall X2 and the population growth rate with the regression method described in Appendix 1 at Point 6. I adjusted for density dependence in the modeling. In this application, I determined that the density dependent term in the Ricker model was statistically significant. Thus, the population growth rate had to be adjusted to account for these effects so that the potential effect of Fall X2 could be isolated. For additional technical detail, see Appendix 1 at Point 6. This relationship, adjusted for density dependence, is depicted below.



94. My application of a multiplicative Ricker life-cycle model demonstrates that Fall X2 does not have a statistically significant effect on the population growth rate. As Fall X2 increases, the population growth rate varies randomly. Taken together with the modeling I performed above (comparing Fall X2 to abundance, see ¶ 89) and statistical analysis of the regression estimates, this means that Fall X2 does not have a statistically significant effect on population abundance in a given water year (adults to juveniles), or on the full life-cycle of the

delta smelt (adults to adults). Since FWS's imposition of Fall X2 restrictions in RPA Action 4 is based upon its erroneous use of the wrong model—which, in turn, has led to the incorrect result that Fall X2 has population effects on the delta smelt—it is scientifically unjustified.

D. FWS's Incidental Take Analysis Is Improperly Influenced by Unrepresentative Data Points That Even FWS Rejected for Other Purposes

(1) FWS's Adult Incidental Take Analysis Is Improperly Influenced by an Unrepresentative Data Point

95. FWS's adult incidental take analysis can be found in Attachment C to the BiOp, pages 382-396 (AR at 000397-000411). In developing the incidental take limit for adult entrainment, FWS relied on a series of statistical analyses and calculations in the BiOp and in Kimmerer (2008).

96. The incidental take limit is set at 7.25 times the prior year's FMWT index of adult abundance. BiOp at 386 (AR at 000401). The 7.25 figure represents the average salvage rate from only three years—2006, 2007, and 2008. *See* BiOp at 385-86 (AR at 000400-000401). The BiOp uses the average salvage rate for these three years as a predictor of take levels during each year that the RPAs will be in effect. Although salvage data is analyzed dating back to 1993, the BiOp claims that "these years [2006 through 2008] within the historic dataset best approximate expected salvage under the RPA Component 1," which restricts OMR flows. *Id.*

97. The BiOp lists the annual salvage numbers and salvage rates for the years 1993-2008, and shows that the salvage in 1994 and 2007 were extremely low compared to the other years and to 2006 and 2008 in particular. *See* BiOp at 386 (AR at 000401) (Table C-1). The cumulative salvage index is just 0.88 for 2007, compared to 8.3 for 2006 and 12.6 for 2008. *Id.*

98. In my review, I searched for additional information regarding the conditions that might have contributed to these salvage levels. In another section of the BiOp, I discovered that FWS had considered the salvage level in 2007 as ***unusable*** for purposes of analyzing salvage and OMR flows due to that year's low average water turbidity. *See* BiOp at 348 (AR at 000363) (Figure B-13, Note). The low turbidity explains why salvage in 2007 was extremely low, as turbidity is a strong indicator of presence or absence of delta smelt near the project facilities.

Lower turbidity means fewer fish will be present and, accordingly, fewer fish are capable of being entrained. Thus, FWS recognized that the unusual conditions in 2007 made it an unrepresentative year that would skew its analysis. For FWS to then go ahead and use that salvage level in the incidental take equation is scientifically unjustified.

99. Without the year 2007 factored into the equation, the take coefficient increases from 7.25 to 10.45, which lies within the range of historical estimates based on the figure shown in ¶ 62 above for flows less negative than -7000 cfs. This figure represents the average of the salvage indices in 2006 and 2008, and would significantly increase the permissible take level. FWS's calculation should be corrected to remove the outlier year of 2007.

(2) FWS's Larval/Juvenile Incidental Take Analysis Is Improperly Influenced by an Unrepresentative Data Point

100. FWS's larval/juvenile incidental take analysis can be found in Attachment C to the BiOp, pages 382-396 (AR at 000397-000411). To calculate the incidental take limit for larval/juvenile entrainment, FWS largely followed the same methodology that it used for adults. BiOp at 389 (AR at 000404).

101. The incidental take limit is set at 1.5 times the Concern Level for larvae and juveniles. The Concern Level is equivalent to the average monthly juvenile salvage index from 2005-2008 times the current water year FMWT of adult abundance. BiOp at 390 (AR at 000405). Combining these two formulae, the incidental take limit can be calculated by multiplying 1.5 times the average monthly juvenile salvage index times the FMWT. Only four years are considered – 2005, 2006, 2007, and 2008.

102. The BiOp lists the annual salvage numbers and salvage rates for the years 1995-2008, and shows that the salvage in 2006 was extremely low compared to all other years, with the exception of 1995 and 1998 (see discussion below). *See* BiOp at 392 (AR at 000407) (Table C-4). The juvenile salvage index is just 0.4, compared to 23.4 for 2005, 65.1 for 2007, and 60.9 for 2008. *Id.*

103. In my review of the BiOp, I searched for additional information that might explain the conditions that were present in these years and how they contributed to salvage levels. I was

provided with daily OMR flow data through a FOIA request to FWS. I discovered that in 2006, average OMR flow was strongly positive for the months April through June, the first three (of four) months during which the monthly juvenile salvage index is calculated. OMR flow was negative in July 2006, but typically, very few fish are salvaged in July. *See, e.g.*, BiOp at 391 (AR at 000406) (Figure C-3) (showing that cumulative salvage reaches a plateau in July).

104. When analyzing the effects of OMR flows on salvage in the Effects Analysis section of the BiOp, FWS explained that "net OMR flow generally works very well as a binary switch: negative OMR flow is associated with some degree of entrainment, while positive OMR flow is usually associated with no, or very low, entrainment." BiOp at 163 (AR at 000178). The juvenile salvage index is reported in the BiOp for the years 1995-2008. BiOp at 392 (AR at 000407). During that time, there were three years when salvage was nearly zero – 1995, 1998, and 2006. These are the only three years when OMR flow was positive. *See* BiOp at 254 (AR at 000269) (Figure E-8). Thus, FWS's statement that positive OMR flow yields zero or very low salvage is supported by historical measurements of juvenile salvage and OMR flow. It also undermines FWS's decision to include one of those years – 2006 – in the incidental take equation.

105. Without the year 2006 factored into the equation, the average juvenile salvage index increases, which necessarily increases the Concern Level (monthly juvenile salvage index times FMWT) and the incidental take level (1.5 times Concern Level). The incidental take level increases by approximately 32-33 percent in May, June, and July, and decreases by approximately 14 percent in April (when salvage is low). Overall, in the months with the highest salvage, removal of the unrepresentative year 2006 significantly increases the take level. FWS's calculation should be corrected to remove the year 2006, which had positive OMR flow.

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I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on November 13, 2009 at St. Thomas, U.S. Virgin Islands.

RICHARD B. DERISO, Ph.D.

Appendix

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UNITED STATES DISTRICT COURT

EASTERN DISTRICT OF CALIFORNIA

THE DELTA SMELT CASES, SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. SALAZAR, *et al.* (Case No. 1:09-cv-407) STATE WATER CONTRACTORS v. SALAZAR, *et al.* (Case No. 1:09-cv-422) COALITION FOR A SUSTAINABLE DELTA, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-480) METROPOLITAN WATER DISTRICT v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al*. (Case No. 1:09-cv-631) STEWART & JASPER ORCHARDS, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-892)	1:09-cv-407 OWW GSA 1:09-cv-422 OWW GSA 1:09-cv-631 OWW GSA 1:09-cv-892 OWW GSA PARTIALLY CONSOLIDATED WITH: 1:09-cv-480 OWW GSA **DECLARATION OF DR. RICHARD B. DERISO** Date: March 23, 2010 Time: 8:30 a.m. Ctrm: 3 Judge: Hon. Oliver W. Wanger

I, RICHARD B. DERISO, declare:

1. The facts and statements set forth in this declaration are true of my own knowledge and if called as a witness, I can testify competently thereto. Any opinions expressed in this declaration are based upon my knowledge, experience, training and education, as set forth in section I.

2. My declaration is set forth in the following manner:

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I. INTRODUCTION

3. In July of this year, I prepared a preliminary declaration that set forth a general explanation of the statistical analysis contained in the 2008 Delta Smelt Biological Opinion ("BiOp") prepared by the United States Fish and Wildlife Service ("FWS"). In that declaration, I focused on three areas of analysis performed by FWS—(1) the relationship between Old and Middle River ("OMR") flows and salvage, (2) the effect of Fall X2 on population survival, and (3) the establishment of incidental take levels. In each of these areas, FWS employed statistics, data analysis, and/or statistical modeling—tools that require technical training to understand. The equations, the statistical, mathematical and fishery population dynamic principles, and the modeling exercises involved in the BiOp are highly complicated. Someone without the proper background and training would be unable to thoroughly review what FWS did in a meaningful way.

4. It is my understanding that the Court has authorized the submittal of this declaration so that I may address and explain in detail the issues I identified in my prior declaration. Since my prior declaration, I have been able to complete my review of the BiOp, as well as the relevant publications relied on by FWS and cited in the BiOp. This declaration sets

forth my comprehensive explanation of the statistical modeling and analysis that FWS performed, including its clear, fundamental errors, focusing again on OMR flows, Fall X2, and the incidental take levels. Below, and in the accompanying appendix, I explain what FWS purported to do, and the mistakes they made in reaching their conclusions. I have also provided the information and equations that I used in conducting my review in an appendix so that my statements and explanations can be critically reviewed by others.

II. BACKGROUND AND EXPERIENCE

5. I am the Chief Scientist of the Tuna-Billfish Program at the Inter-American Tropical Tuna Commission ("IATTC"), and I have held this position since 1989. *See* Summary Professional Vitae, attached hereto as Exhibit A. I supervise a scientific staff of approximately 20 scientists and our primary responsibilities are: (1) to collect statistics on the fisheries that operate in the eastern Pacific Ocean, such as tuna and tuna-like species, and (2) to conduct stock assessments annually on the principal tropical tuna species as well as periodically other species such as turtles, sharks, and billfish species. My work involves advising the Commission on the current status of the populations and making conservation recommendations that can permit stocks to be maintained at a level of abundance that will support maximum sustainable yields.

6. IATTC has a long history of successful management of the tuna stocks in the eastern Pacific Ocean. The largest fishery historically has been yellowfin tuna. Yellowfin tuna is currently at a level of abundance above that which would support maximum sustainable yield.

7. I have a Ph.D. in Biomathematics (Quantitative Ecology) from the University of Washington, a Master's of Science in Mathematics from the University of Florida, and a Bachelor's of Science in Industrial Engineering from Auburn University. I have been teaching courses in fish population dynamics, quantitative ecology, and related areas for over twenty years. I was an Associate Adjunct Professor at the Scripps Institution of Oceanography, University of California, San Diego, from 1990 to 2006 and an Affiliate Associate Professor of Fisheries at the University of Washington from 1987 to 2006. Among the graduate courses I have taught are "Theoretical Models of Exploited Animal Populations" at the University of Washington; "Decision Analysis for Exploited Populations" at the University of Washington; and

"Quantitative Theory of Populations and Communities" at Scripps Institution of Oceanography. I have additional professional experience through a current membership on the Scientific and Statistical Committee of the Western Pacific Regional Fisheries Management Council and a past membership on the Ocean Studies Board which governs the U.S. National Research Council, where I served as co-chairman of the Committee on Fish Stock Assessment Methods. I was also formerly a Population Dynamicist for the International Pacific Halibut Commission. I have been a consultant to several agencies and institutions, both public and private.

8. I have authored or co-authored over 50 peer reviewed publications and technical reports, including Deriso, R., Maunder, M., and Pearson, W, *Incorporating covariates into fisheries stock assessment models with application to Pacific herring*, Ecol. App. 18(5): 1270-1286 (2008); Deriso, R., Maunder, M., and Skalski, J., *Variance estimation in integrated assessment models and its importance for hypothesis testing*, Can. J. Fish. Aquat. Sci. 64: 187-197 (2007); and Quinn, T. and Deriso, R., *Quantitative Fish Dynamics*, Oxford University Press (1999). *See* List of Publications, attached hereto as Exhibit B.

9. I have been retained to evaluate the effects of entrainment on fish populations in many circumstances throughout the United States. I have consulted on the environmental review of once-through cooling systems of the Indian Point nuclear power plants on the Hudson and Delaware Rivers, focusing on impingement and entrainment of fish, with a particular emphasis on their impacts to population. For this analysis, I was retained by ESSA Technologies Ltd. through a contract with the New York State Department of Environmental Conservation. This analysis included modeling, and reviewing models of, the impacts of entrainment and impingement on fish populations. I am a member of the Estuary Enhancement Program Advisory Committee that reviews the mitigation measures for losses of fish through impingement and entrainment at the Salem Nuclear Power Plant on the Delaware River in New Jersey. I have evaluated both the mortality and related impacts of hydroelectric dam operations on Chinook salmon populations on the Columbia and Snake Rivers.

10. I am familiar with, understand, and am able to explain to the Court the concepts and techniques used in the 2008 Delta Smelt Biological Opinion to evaluate the impacts of the

Central Valley Project and the State Water Project operations on the delta smelt population. My testimony and opinions are offered in the context of explaining the standard practices and statistical methods that are used in fish population dynamics to evaluate impacts to fish populations, and the practices and statistical methods employed by the FWS in the BiOp.

III. GENERALLY ACCEPTED PRINCIPLES OF FISH POPULATION DYNAMICS THAT APPLY TO AN ANALYSIS OF IMPACTS TO FISH SPECIES

11. In the BiOp, FWS sought to evaluate the effects of the Central Valley Project and State Water Project on the threatened delta smelt. When looking at potential impacts of a project to fish species, the standard of practice is for qualified professionals to employ certain well-established principles of fish population dynamics.

A. Principle 1: Quantitative Analysis Should Be Conducted

12. The fundamental approach to assessing fish population dynamics is through quantitative statistical analysis (mathematical models) of population dynamics. "Quantitative analysis" involves the use of actual measured data and the testing of relationships between that data. The nature and degree of project impacts on a species must be determined using quantitative methods where quantitative data is available. Similarly, measures designed to benefit the species and avoid harm must be based on a quantitative approach. Only in this way can impacts and benefits be measured for proper evaluation of their effect on the species.

13. By contrast, a qualitative approach may be appropriate where no quantitative data or measurements are available. Qualitative analysis consists of a more subjective evaluation of the degrees of importance of particular factors and circumstances for which quantitative data and measurements are not appropriate or do not exist.

B. Principle 2: Impacts to the Total Population Should Be Evaluated

14. Population dynamics also involve a qualified scientist conducting an evaluation of project impacts to a threatened fish by focusing on impacts to the total population. Measuring effects on a single fish, or a limited group of fish, does not lead to reliable conclusions about population level effects. Such population level conclusions are essential when evaluating a project's impacts on the species as a whole and its ability to survive and recover.

15. Population level effects are properly evaluated using rates and proportions. This means that a given impact or variable cannot be taken as significant on its own without accounting for the *relative* impact on the total population. The population growth rate is an appropriate and reliable measure of population increases and decreases from year to year.

C. Principle 3: Models Should Be Reliable and Biologically Plausible

16. The standard of practice for a fish population dynamicist requires that any statistical models that are utilized must be reliable and biologically plausible. Such statistical models are based on mathematical formulas that assign numeric values to biotic and abiotic variables to explain the relationships among them. To be biologically plausible means that the mathematical formulas used must reflect the reality that the "variables" are reflective of the biology of the living organisms that are being assessed. For example, living organisms have a limited life span and limited reproductive capabilities that must be taken into account in any model used to evaluate their behavior and vulnerabilities. Thus, the models that are properly used are designed to attribute a quantitative value to those influential biological factors so that the model enables quantitative measurement of their interrelationships. Such models are designed to reflect biological realities and to evaluate the relationship between living stock and recruits.

D. Principle 4: Data Should Be Used Consistently

17. In performing a quantitative fish population analysis, generally accepted scientific standards require that the study be internally consistent in its use of data. Data that is rejected in one aspect of the analysis should not be relied upon elsewhere in the same study.

18. With these general principles in mind, I turn to the subject of this action, the 2008 Delta Smelt Biological Opinion for the Operations Criteria and Plan for the State Water Project and the Central Valley Project.

IV. THE BIOP'S EVALUATION OF PROJECT EFFECTS AND THE BIOP'S RPAS ARE BASED ON A "QUANTITATIVE" ANALYSIS

19. The core analyses and conclusions in the BiOp are contained in the sections entitled "Effects of the Proposed Action" (BiOp at 202-239 [Administrative Record ("AR") at 000217-000254]), "Reasonable and Prudent Alternative" ("RPA") (BiOp at 279-285, 324-81 [AR

at 000294-000300, 000339-000396]), and "Incidental Take Statement" ("ITS") (BiOp at 285-295 [AR at 000300-000310]). These sections define the effects of the water projects on the delta smelt and the restrictions which FWS imposed to avoid jeopardy.

20. In the section of the BiOp entitled "Effects Analysis Methods," FWS explains that the effects of the project pumps on entrainment (OMR flows and salvage, and incidental take levels) and the fall habitat suitability and its effect on population (Fall X2) "are quantitatively analyzed."

> The effects analyses range from qualitative descriptions and conceptual models of project effects to quantitative analyses. The effects of Banks and Jones pumping on adult delta smelt entrainment, larval-juvenile delta smelt entrainment, and fall habitat suitability and its predicted effect on the summer townet survey abundance index are quantitatively analyzed. The remainder of proposed action elements and effects are not analyzed quantitatively because data are not available to do so or it is the opinion of the FWS that they have minor effects on delta smelt.

BiOp at 208-209 (AR at 000223-000224). This representation is consistent with my review of the BiOp—FWS conducted a quantitative statistical analysis in order to (1) evaluate project effects on the smelt population and (2) develop RPAs designed to mitigate and avoid any such effects to the extent necessary to avoid jeopardy to the species and adverse modification of its critical habitat. As I would expect of most any scientific exercise, FWS relied on and used data when it was available, unless FWS concluded that the issue was too "minor."

21. Because the BiOp concludes that the projects jeopardize the species and adversely modify its critical habitat, it includes RPAs that restrict project operations in an attempt to avoid jeopardy and adverse modification. The RPAs address categories of effects to which FWS applied quantitative analyses: adult entrainment and larval/juvenile entrainment as related to OMR flows, and fall habitat. These are outlined in more detail below.

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22. **Actions 1 and 2 (Winter OMR Flows)**.[1] Actions 1 and 2 are designed to avoid jeopardy to adults from entrainment. These Actions restrict Old and Middle River ("OMR") flows to reduce adult salvage in the winter. Action 1 is triggered first and lasts for 14 days, followed immediately by Action 2, which is triggered if certain criteria are present and lasts until spawning begins or a certain water temperature is reached. Both of these Actions prescribe a similar range of OMR flows, but at different times of the year. The quantitative analysis presented in Attachment B to support the prescribed OMR flow levels in Actions 1 and 2 is set forth in the BiOp at 345-349 and is represented in two graphs labeled Figure B-13 and Figure B-14, which appear to share the same data. *See* BiOp at 348, 350 (AR at 000363, 000365). Figure B-13 depicts the BiOp's analysis of the relationship between winter OMR flows and adult salvage, concluding that as flows become more negative, salvage increases. Based on this relationship, Actions 1 and 2 set less negative flow levels to reduce salvage.

23. **Action 3 (Spring OMR Flows)**. Action 3 is designed to avoid jeopardy to larvae and juveniles from entrainment. This Action restricts OMR flows to reduce larval/juvenile salvage in the spring. FWS did not apply statistical modeling to evaluate whether or not reductions in OMR flows or X2 would reduce impacts to juveniles, because there is no actual data on larval and juvenile salvage for fish smaller than 20 millimeters. Instead, FWS relied on the assumption that larval and juvenile movement can be predicted using a particle tracking model. A particle tracking model is a theoretical simulation of the flow of neutrally buoyant particles through a water system, where particles are used as surrogates for actual fish. Similar to Actions 1 and 2, Action 3 sets less negative flow levels to reduce salvage.

24. **Action 4 (Fall X2)**. Action 4 is designed to protect fall habitat for adults. This Action prescribes Delta outflows to push X2 more seaward during the fall. The BiOp relies primarily on the quantitative analysis represented by the summary statistics for the stock-recruit

[1] The RPAs are divided into four "Components," which are supported by supplemental information in Attachment B to the BiOp. Attachment B breaks down the RPA Components into five "Actions," such that Component 1 is represented by Actions 1 and 2, Component 2 is supported by Action 3, Component 3 is supported by Action 4, and Component 4 is supported by Action 5. Because most of the technical analysis is contained in Attachment B, and for ease of reference, I will refer to the RPAs in terms of the Actions rather than the Components.

model set forth in Figure E-22 to establish that the location of Fall X2 has a significant effect on delta smelt abundance. *See* BiOp at 268 (AR at 000283). Based on this purported relationship, Action 4 sets Delta outflow levels to control the location of X2.

25. **Incidental Take Statement**. The BiOp also includes an Incidental Take Statement, which prescribes the acceptable level of take of larval/juvenile and adult delta smelt using quantitative methods. For each of larvae/juveniles and adults, FWS took the average salvage rate from certain prior years which it deemed to be representative of future conditions under the RPAs. The average salvage rate from the prior representative years was set as the maximum take level under the RPAs. *See* BiOp at 385-390 (AR at 000400-000405).

26. To summarize, FWS used quantitative methods to evaluate the effects of water project operations (OMR flows) on the species, on its fall habitat (as represented by Fall X2), and to establish incidental take levels. I will next explain the clear, fundamental errors I have identified in that quantitative analysis.

V. THE QUANTITATIVE ANALYSIS BY FWS DOES NOT FOLLOW STANDARD FISH POPULATION ASSESSMENT METHODS

A. Actions 1 & 2 (Winter OMR Flows): Use of Raw Salvage Numbers Instead of the Salvage Rate

27. Actions 1 and 2 prescribe OMR flow levels based on the BiOp's calculation of the relationship between OMR flows and adult salvage. This relationship is depicted in Figure B-13 and compares OMR flow levels to raw salvage numbers. The salvage numbers used are the total number of fish counted at the salvage facilities.

28. Raw salvage numbers do not represent the proportion of the total population that is lost to salvage, which is the salvage rate. For example, a raw salvage total of 100 adults has vastly different significance depending on whether the total population is 200 (salvage rate of 50 percent) or 10,000 (salvage rate of 1 percent). Thus, Figure B-13 does not show what effect OMR flows have on the total delta smelt population.

29. Use of raw salvage numbers, rather than the salvage rate, could be appropriate if the total delta smelt population was known and a model that incorporates every life stage of the

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species (a life-cycle model)[2] was being used. Salvage of delta smelt is a source of loss of individuals—it is analogous to using catch as a mortality loss to the population. If the total delta smelt population was known, then the salvage numbers themselves could be incorporated directly into a life-cycle model and would make it possible to determine the population effects of salvage. A simple version of such a model is explained in Hilborn, R. & Walters, C., *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*, Chapman & Hall (1992) at 298:

> The changes in a population's biomass from one time to the next can be simply written as
>
> next biomass = last biomass + recruitment + growth – catch – natural mortality.

Salvage would take the role of catch in a similar life-cycle model for delta smelt.

30. Here, however, the total population of delta smelt is unknown, although there have been recent attempts to provide such estimates. Because actual abundance is not known, raw salvage numbers cannot be used to show population level effects.

31. In the absence of actual adult abundance numbers, adult abundance is estimated by the Fall Midwater Trawl Survey ("FMWT"), which collects samples around the Delta. An index of the FMWT is used to track the relative increase or decrease in adult abundance from year to year. The survey counts the number of smelt captured in a net of known dimensions and multiplies it by the volume of water actually sampled. That number is then applied to the entire estimated volume of water where the smelt is believed to reside. From this data, an index is derived.

32. The FMWT index is scientifically reasonable and widely relied upon by scientists studying the delta smelt, though not without its technical flaws. It is a numerical scale used to compare variables derived from a series of observed facts with one another or with some reference number to reveal relative changes as a function of time. Because actual abundance is not known, raw salvage numbers cannot be used to show population level effects.

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[2] A life-cycle model is a well-accepted and reliable method of evaluating population dynamics from generation to generation (adults to adults), rather than focusing solely on one age group or the change from adults to juveniles.

33. For adult delta smelt, the scientifically accepted and reliable method is to use the cumulative salvage index to evaluate whether a relationship exists between OMR flows and adult salvage. The cumulative salvage index is equal to the raw number salvaged divided by the prior year FMWT index. *See* BiOp at 338 (AR at 000353). In this way, the cumulative salvage index represents an index of the proportion of abundance that is lost to salvage each year. In the absence of abundance figures, the prior year FMWT index stands as a usable denominator for a ratio that would reveal any population level effects from entrainment.

B. Actions 1, 2 & 3 (Winter and Spring OMR Flows): Failure to Evaluate the Smelt's Population Growth Over Time

34. The BiOp's failure to evaluate population level effects using the correct variable (salvage rate) is consistent with its more general failure to use the well-accepted, reliable statistical models typically used to evaluate population level effects. The BiOp did not employ life-cycle modeling**,** which, among other things, is used to estimate a population's growth.

35. Life-cycle modeling is a well-accepted and reliable method of evaluating population dynamics from generation to generation (adults to adults). It typically consists of the simple models known as biomass dynamic models and stock production models, or the more complex models such as age-structured models. *See* Quinn & Deriso (1999) at ch. 2, 6-8; Hilborn & Walters (1992) at 297.

36. In fisheries science, often the total number of fish in a population is unknown. It is standard practice that, given the data available, population level effects can be determined using surrogate methods such as the population growth rate and the salvage rate.

37. Similar to Actions 1 and 2, the BiOp omits any analysis of the effect of spring OMR flows (Action 3) on the delta smelt population growth rate. A standard life-cycle model could be applied to determine whether spring OMR flows, which would potentially affect larvae and juveniles, are affecting the change in total population from year to year. This kind of quantitative analysis would make it possible to reliably calculate population level effects for delta smelt.

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C. Action 4 (Fall X2): Use of a Linear Additive Model Instead of a Multiplicative Model

38. FWS's quantitative Fall X2 analysis for Action 4 of the BiOp is based on a stock-recruitment model. A stock-recruitment model is a model used to evaluate population level effects that quantitatively characterizes the relationship between the parental "stock" and the progeny it produces ("recruits"). In the BiOp, the parental stock is measured through the FMWT and the progeny is measured at the juvenile life stage through the Summer Townet Survey ("TNS").

39. There are many different stock-recruitment models. In selecting a model, one necessary criterion is that the model must be biologically plausible. This means that the mathematical formulas reflect biological reality and limitations, as described above.

40. FWS employed a linear additive stock-recruitment model when evaluating Action 4. A linear additive model adds several factors together to achieve a sum, without use of logarithms. A simple example is A + B = C. This type of model is not appropriate for stock and recruitment relationships, for two main reasons.

41. First, adding and subtracting factors can generate a positive sum, even if one of the factors is zero. This seems mathematically accurate, but it does not work in a situation where the factors are living organisms with certain non-mathematical properties. For instance, in an equation where various factors are added to adult abundance to determine the effect on their juvenile offspring, one can achieve a positive sum (number of juveniles) even if the factor representing the number of adults is zero. In terms of biological reality, zero adults cannot produce offspring. Thus, simply adding the factors does not reflect the manner in which populations grow.

42. Second, a linear additive model treats factors as having a fixed effect on the population, rather than a proportional effect. That is, by adding a factor, it will always increase or decrease the sum by the same absolute amount. While mathematically accurate, this does not work when the factors being added are habitat components that have a changing proportional effect on the sum (population abundance), not a fixed effect. When the total population is

smaller, a smaller number of individuals exist that can potentially be affected by a given factor. This is accounted for by using proportions and rates.

43. In contrast, multiplicative stock-recruitment models produce biologically accurate results and they are appropriate for fish population dynamics. Simply put, a multiplicative model reads as A x B = C. Two multiplicative models available to FWS are the Beverton-Holt and Ricker models. These models are typically used because they are well-accepted by the scientific peer community and are reliable.[3]

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[3] *See, e.g.*, Jorgensen, S. & Fath, B. (eds.), *Encyclopedia of Ecology*, Academic Press (2008); Knowler, D., Estimation of a Stock-Recruitment Relationship for Black Sea Anchovy (Engraulis encrasicolus) Under the Influence of Nutrient Enrichment and the Invasive Comb-Jelly, Mnemiopsis leidyi, 84:3 Fisheries Research 275-281 (May 2007); Owen-Smith, N., Introduction to Modeling Wildlife and Resource Conservation, Blackwell Publ'g (2007); Brauer, F. & Castillo-Chavez, C., Mathematical Models in Biology and Epidemiology, Springer-Verlag New York, Inc. (2006); Kritzer, J. & Sale, P. (eds.), Marine Metapopulations, Elsevier Academic Press (2006); Mangel, M., The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology, Cambridge Univ. Press (2006); Ferrier, R., et al. (eds.), Evolutionary Conservation Biology, Cambridge Studies in Adaptive Dynamics, Cambridge Univ. Press (2004); Hoff, M., Biotic and Abiotic Factors Related to Rainbow Smelt Recruitment in the Wisconsin Waters of Lake Superior, 1978-1997, 30 Journal of Great Lakes Research, Supp. 1 Exploring Superior, 414-422 (2004); Walters, C. & Martell, S., Fisheries Ecology and Management, Princeton Univ. Press (2004); Hart, P. & Reynolds, R. (eds.), Handbook of Fish Biology and Fisheries, 1 Fish Biology, Blackwell Publ'g (2002); Haddon, M., Modeling and Quantitative Methods in Fisheries, Chapman & Hall (2001); Jennings, S., et al., Marine Fisheries Ecology, Blackwell Publ'g (2001); Lorda, E. et al., Application of a Population Dynamics Model to the Probabilistic Assessment of Cooling Water Intake Effects of Millstone Nuclear Power Station (Waterford, CT) on a Nearby Winter Flounder Spawning Stock, 3 Envtl. Science & Policy, Supp. 1, 471-482 (Sept. 2000); McCallum, H., Population Parameters: Estimation for Ecological Models, Blackwell Publ'g (2000); Guenette, S. & Pitcher, T., An Age-Structured Model Showing the Benefits of Marine Reserves in Controlling Overexploitation, 39:3 Fisheries Research 295-303 (Jan. 1999); Quinn & Deriso (1999); Ricklefs, R. & Miller, G., Ecology, 4th ed., W.H. Freeman (1999); Hilborn & Walters (1992); Rothschild, B., Dynamics of Marine Fish Populations, Harvard Univ. Press (1986); Walters, C., Adaptive Management of Renewable Resources, MacMillan Publ'g Co. (1986); Mangel, M., Decision and Control in Uncertain Resource Systems, Academic Press (1985); Pauly, D., Fish Population Dynamics in Tropical Waters: A Manual for Use With Programmable Calculators, 8 ICLARM Studies & Reviews (1984); Fournier, D. & Archibald, C., A General Theory for Analyzing Catch at Age Data, 39 Canadian Journal of Fisheries & Aquatic Sciences 1195-1207 (1982); Pitcher, T. & Hart, P., Fisheries Ecology, Kluwer Academic Publ'g (1982); Walters, C. & Ludwig, D., Effects of Measurement Errors on the Assessment of Stock-Recruitment Relationships, 38 Canadian Journal of Fisheries & Aquatic Sciences 704-710 (1981); Clark, C., Mathematical Bioeconomics: The Optimal Management of Renewable Resources, Wiley (1976); Ricker, W., Handbook of Computation for Biological Statistics of Fish Populations, Bulletin 119 of the Canada Fisheries Res. Bd. (1958), issued again as Ricker, W., Computation and Interpretation of Biological Statistics of Fish Populations, Bulletin 191 of the Canada Fisheries Res. Bd. (1975); Weatherley, A., Growth and Ecology of Fish Populations, Academic Press (1972); Beverton, R. & Holt, S., On the Dynamics of Exploited Fish Populations, 14 Fishery Investigations Series II, Ministry of Agriculture, Fisheries & Food (1957).

44. For measuring population level effects, multiplicative or rate-based models such as Ricker and Beverton-Holt should be used to achieve scientifically accepted, reliable results. Additive models should not, because they generate inaccurate and unreliable results. These are the two most widely-used models in actual practice because they were designed to be biologically accurate and reflect the relationship between stock and recruits. A feature of a multiplicative model is that when there are zero adults on one side of the equation, there are zero young on the other side; i.e., zero adults yields zero offspring. This follows because any number multiplied by zero will always equal zero. As stated in Ricker (1975) at 281, the model is designed "so that when there is no adult stock there is no reproduction . . . ." The same result can be expected using other types of multiplicative models.

D. ITS: Use of Rejected Data Points Instead of Representative Data Points

45. The BiOp sets the adult incidental take limit based on the average salvage rate from the years 2006, 2007, and 2008, which FWS determined to be representative of future conditions under the RPAs. BiOp at 385-86 (AR at 000400-000401). According to the list of salvage levels contained in the ITS, salvage in 2007 was extremely low compared to other years and to 2006 and 2008 in particular. *See* BiOp at 386 (AR at 000401) (Table C-1). In another section of the BiOp, FWS itself had considered the salvage level in 2007 as unusable for purposes of analyzing salvage and OMR flows due to that year's low average water turbidity, a presence/absence indicator. *See* BiOp at 348 (AR at 000363) (Figure B-13, Note). Thus, FWS recognized that the unusual conditions in 2007 made it an unrepresentative year that would skew its analysis of salvage impacts. Use of an unrepresentative data point that was rejected elsewhere in the same study runs counter to basic principles of quantitative fish assessment. FWS does not attempt to justify why the data point would be used in one instance and not another, so one possible explanation is that it is simply a material error in the analysis.

46. To calculate the incidental take limit for larvae and juveniles, FWS largely followed the same methodology that it used for adults. BiOp at 389 (AR at 000404). The take limit is set based on the average monthly juvenile salvage index from four years – 2005, 2006,

2007, and 2008. According to data listed in the BiOp, the salvage in 2006 was extremely low compared to other years. *See* BiOp at 392 (AR at 000407) (Table C-4). I examined this year carefully and discovered through my review of OMR flow data obtained from a Freedom of Information Act ("FOIA") request to FWS[4], that in 2006, average OMR flow was strongly positive in April through June. When analyzing the effects of OMR flows on salvage in the Effects Analysis section of the BiOp, FWS explained that positive OMR flow yields zero or very low salvage. BiOp at 163 (AR at 000178). Thus, FWS's use of 2006 as a "representative" year for larval/juvenile salvage is internally inconsistent with its explanation elsewhere that positive OMR flow (which is what occurred in spring 2006) yields little or no salvage. The year 2006 was therefore not representative and should have been omitted, as it was elsewhere by FWS for other purposes.

VI. THE BIOP'S APPLICATION OF STATISTICAL MODELS AND INPUT VARIABLES IS INCONSISTENT WITH STANDARD PRINCIPLES OF FISHERIES POPULATION DYNAMICS

47. To decipher the models and methods that FWS used, I reviewed and interpreted the limited graphs and tables provided in the BiOp, along with similar information and studies in the administrative record.

48. I compared FWS's models against the standard models employed by the scientific community, and particularly those models that are commonly used in fish population modeling. My review and comparison revealed that the BiOp does not use the well-accepted models in more

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[4] My review of the BiOp and the administrative record revealed that FWS had not provided all of the underlying data that FWS relied on in performing its work on the BiOp. In my experience, a full scientific analysis is not possible without making the underlying data available so that the work may be checked and evaluated by others. This omission hinders the ability to conduct a standard peer review of the FWS analysis without estimating data point values from the graphs or searching for data in other sections. FWS's failure to include the data underlying its basic analyses and determinations is an inexplicable defect given the conclusions FWS reaches. After I identified the missing categories of data, the Metropolitan Water District of Southern California requested that data through a FOIA request. On October 29, 2009, more than ten weeks after the request was made, FWS provided a disc containing portions of the data underlying the BiOp. Included on that disc were daily OMR flow data. I used those data to calculate several average OMR flows, including monthly average flows, as noted in this declaration.

than one place, but rather relies on models that are not biologically sound and lead to erroneous results.

49. I evaluated the same data presented in the BiOp and input it into the standard models to determine whether the end result would be different. The results are fundamentally different from the results reached in the BiOp.

50. Based on the material I reviewed, the fundamental errors I have identified call into question the jeopardy and adverse modification conclusions in the BiOp and reveal that FWS had no reliable scientific basis for imposing the RPAs adopted.

A. FWS's Analysis of the Relationship Between Old and Middle River Flows and Adult Salvage Is Flawed

51. The BiOp's analysis of the effects of the projects on adult delta smelt and its conclusion that winter flow restrictions are necessary are based on a statistical model of the alleged relationship between OMR flows and adult salvage. The modeling and analysis are contained in the Effects of the Proposed Action section of the BiOp, pages 202-279 (AR at 000217-000294), and RPA Actions 1 and 2 in Attachment B to the BiOp, pages 329-356 (AR at 000344-000371). Actions 1 and 2 rely on Figure B-13 on page 348 (AR at 000363) and on various studies, including Kimmerer, W., *Losses of Sacramento River Chinook Salmon and Delta Smelt to Entrainment in Water Diversions in the Sacramento-San Joaquin Delta* (AR at 018854), and the work of Pete Smith, which is cited by Kimmerer.

(1) Improper Use of Total Adult Salvage Numbers Instead of Cumulative Salvage Index

52. FWS uses total adult salvage numbers to demonstrate an alleged relationship between OMR flows and adult salvage. *See* BiOp at 163-65; 347-50 (AR at 000178-000180; 000362-000365). The alleged relationship is derived from the graph in Figure B-13 which compares the number of adults salvaged each year to the corresponding OMR flow rate for that year. BiOp at 164, 348 (AR at 000179; 000363).

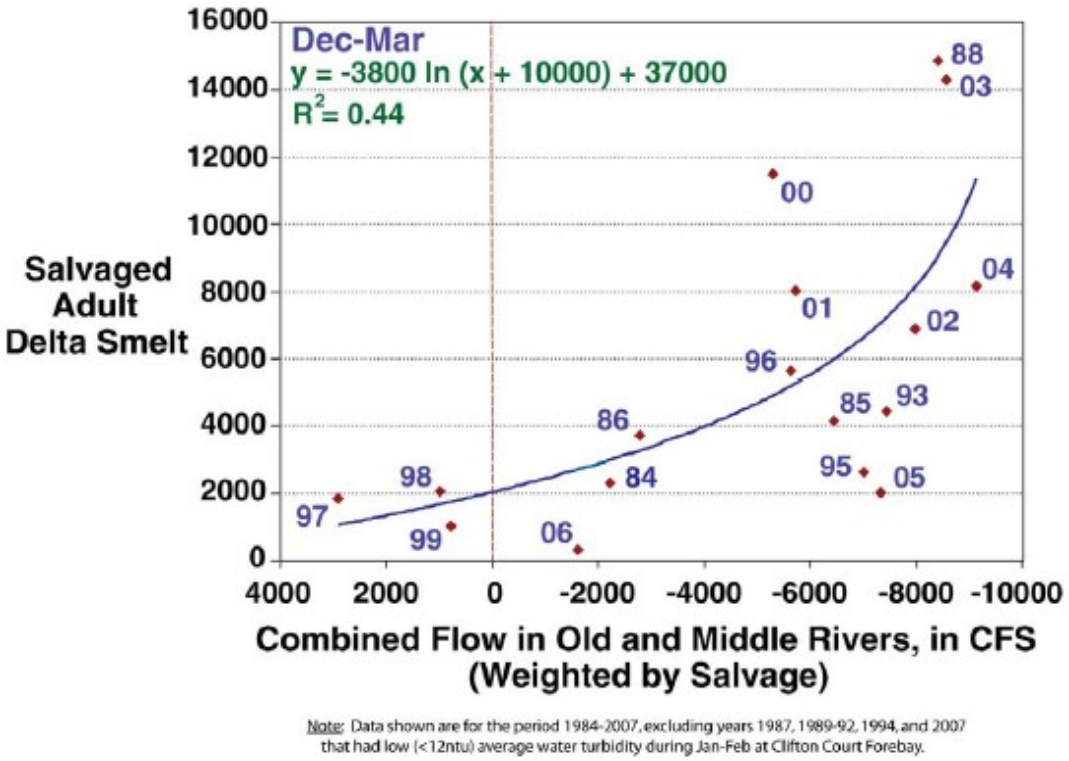

Figure B-13. OMR-Salvage relationship for adult delta smelt. (source, P. Smith). Data from this figure were the raw data used in the piecewise polynomial regression analysis.

53. FWS relied on this graph to conclude that OMR flows correlate to total salvage numbers—suggesting that as negative OMR flows increase, more adults are salvaged.

54. This conclusion by FWS is scientifically flawed because raw salvage numbers do not have a directly proportional effect on population and do not take into account the overall size of the population as determined by representative survey data. Nonetheless, FWS relied on Figure B-13 and Figure B-14 (which appear to share the same data) to set OMR flow levels in RPA Actions 1 and 2. In other words, FWS set OMR flow levels in Actions 1 and 2 without determining population level effects.

55. The scientifically appropriate approach would have been for FWS to use the cumulative salvage index to evaluate whether a relationship exists between OMR flows and adult salvage. FWS had already developed that index for other purposes. *See* BiOp at 386 (AR at 000401) (using the cumulative salvage index in another context, to calculate the incidental take). The cumulative salvage index represents an index of the salvage rate, taking into account data on the size of the population. This has long been recognized as appropriate for analysis of delta

smelt by those scientists actively studying the smelt. *See, e.g.*, Bennett, W., *Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California*, San Francisco Estuary & Watershed Science, Cal. Bay-Delta Auth. Science Program & John Muir Inst. of the Env't (2005) at 37 ("As first step [sic], assessing the potential impacts of the water project operations on delta smelt requires estimating the proportion lost relative to population abundance."). The cumulative salvage index is proportional to the fraction of adult fish that are lost due to water diversion.

56. The concept of dividing fish loss by abundance is well-accepted and reliable and is applied in other, similar applications, such as part of the procedure for estimating the impact of entrainment and impingement of fishes by water withdrawals of once-through cooling systems for nuclear power plants on the Hudson River.

> This approach is based on conditional mortality rates, or the fraction of an initial population that would be killed by some agent during the year if no other sources of mortality operated. Conditional entrainment mortality rates are used as estimates of the direct impact of power plants on individual year classes . . . . (2) Conditional mortality rates can be entered directly into life-cycle models for assessing potential long-term impacts on fish populations.

Barnthouse, L., et al. (eds.), *Science, Law, and Hudson River Power Plants: a Case Study in Environmental Impact Assessment*, Am. Fisheries Soc'y Monograph 4, Am. Fisheries Soc'y (1988) at 122.

57. Another example is biological reference points ("BRP") which can be used as targets for optimal fishing: "A BRP can be expressed as a fishing mortality rate (F) and/or as a level of stock biomass (B)." Comm. on Fish Stock Assessment Methods, Nat'l Research Council, *Improving Fish Stock Assessment Methods*, Nat'l Academy Press (1998) at 45. The fishing mortality rate (F) depends mathematically on the ratio of catch divided by biomass and it is similar to a cumulative salvage index in that both represent a ratio of losses to abundance.

58. Since total population data does not exist, the cumulative salvage index uses a survey index which gives a relative increase or decrease in annual survey numbers to monitor population levels. Use of the cumulative salvage index to evaluate the effects of OMR flows is

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scientifically accepted, reliable, and superior to using the raw salvage numbers themselves (as used in Figure B-13), for the following reasons:

59. The total number of adults salvaged does not indicate population level effects. *See* BiOp at 338 (AR at 000353) ("the total number salvaged at the facilities does not necessarily indicate a negative impact upon the overall delta smelt population"). Stated differently, to make sense of total adult salvage numbers, total adult abundance must be taken into account. For example, a salvage of 100 adults has vastly different significance depending on whether the total population is 200 or 50,000.

60. In contrast, the cumulative salvage index is an index of the *proportion* of adults salvaged from the total population, using the FMWT to relate salvage to population levels. The cumulative salvage index is equal to the number salvaged divided by the prior year FMWT index. *See* BiOp at 338 (AR at 000353).

61. Use of the cumulative salvage index, rather than total salvage numbers, was recommended by the Peer Review. *See Independent Peer Review of USFWS's Draft Effects Analysis for the Operations Criteria and Plan's Biological Opinion, 2008* at 6 (AR at 008818) ("The Panel suggests that the use of predicted salvage of adult smelt should be normalized for population size. . . . Expressing salvage as a normalized index may help remove some of the confounding of the temporal trends during the baseline period.").

(2) Use of the Cumulative Salvage Index Shows That There Is No Statistically Significant Relationship Between OMR Flows and Adult Salvage for Flows Less Negative Than -6100 Cubic Feet per Second at the Very Least

62. To assess FWS's methods, I plotted a graph of the relationship between the cumulative salvage index (salvage rate) and the OMR flows for each year that was analyzed in the BiOp. In developing this graph, I used the cumulative salvage index data provided in the BiOp. *See, e.g.,* BiOp at 386 (AR at 000401). Because Figure B-13 uses salvage weighted OMR flows, which are not listed anywhere in the BiOp, I visually estimated a magnified version of the OMR flow curve in Figure B-13 and interpolated the data points for each year.

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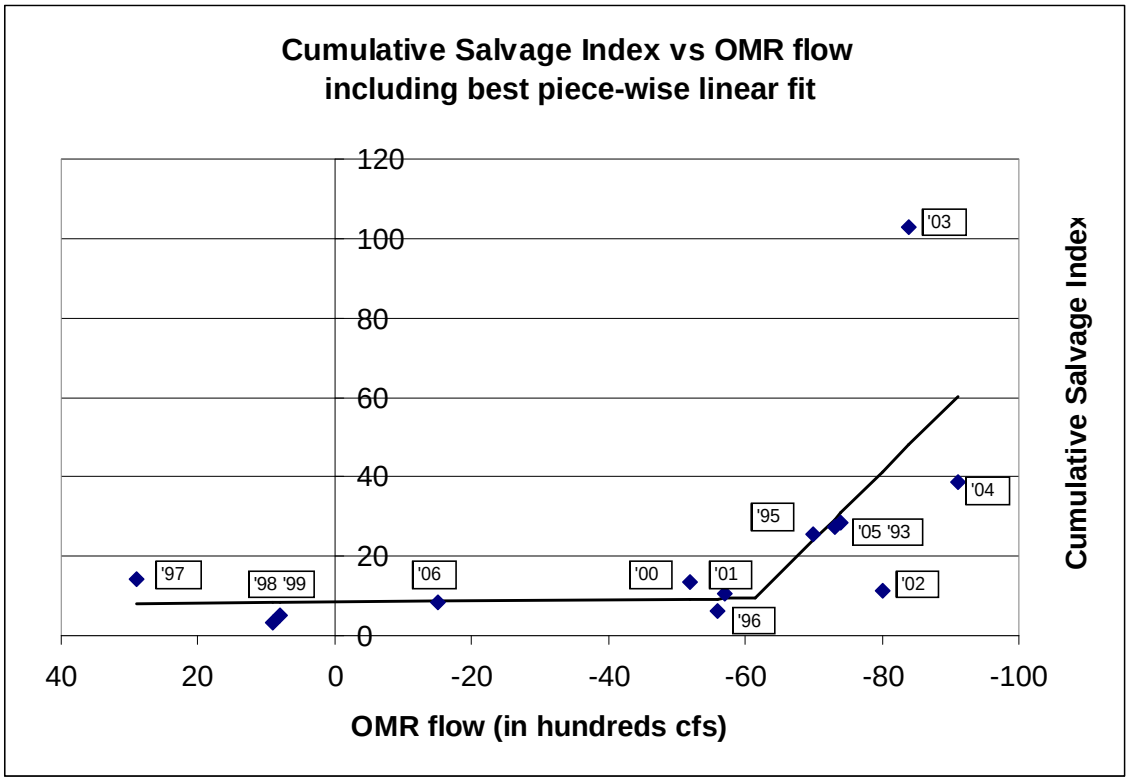

The Cumulative Salvage Index (Table B-2 & C-1) and corresponding Dec-Mar salvage weighted OMR (Figure B-13); note the salvage weighted OMR flows were visually estimated from Figure B-13. Years span 1993-2006 but exclude 1994 because that was also excluded in Figure B-13. A piece-wise linear model (the line on the figure) is also shown whose coefficients were obtained by the statistical procedure of maximum likelihood estimation.

63. The graph of salvage rate versus OMR flow shows that salvage rate remains flat as OMR flows increase until OMR flows reach -6100 to -7000 cubic feet per second ("cfs"). At -7000 cfs, salvage rate begins to increase as negative OMR flows increase. The graph demonstrates that OMR flows do not correlate to the salvage rate at flows less negative than -6100 cfs at the very least. I have determined that, based on the data available and using the appropriate reliable analytic method, there is no scientific basis for FWS's imposition of OMR flow restrictions at flows less negative than -6100 cfs (and potentially -7000 cfs). For additional technical detail, see Appendix 1 at Point 1.

64. As shown in the x-axis label on Figure B-13 (see ¶ 52 above), FWS used "Combined Flow in Old and Middle Rivers, in CFS (Weighted by Salvage)" to evaluate the relationship between OMR flows and salvage. "Weighted by Salvage" is not defined in the

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BiOp; however, a logical definition is that the salvage weighted average OMR flow is an average over several time periods, such as weeks, and the influence that a given week's OMR flow has on the overall average is set proportional to the salvage in that week.

65. FWS's October 29, 2009 FOIA response included daily OMR flow data (as opposed to the weighted average flows used in Figure B-13). I constructed December through March average OMR estimates based on the daily OMR flows provided by FWS. I modeled the relationship between the straight average OMR flows and the cumulative salvage index and confirmed that the results are consistent with those reached using the Figure B-13 weighted average flows. Using the straight average, the flows were not significant until a much more negative flow level (approximately -7943 cfs). The results are shown in Appendix 1 at Point 1.

B. The BiOp Fails to Evaluate Population Level Effects Using the Population Growth Rate – Interpreting the Data in This Way Shows That Salvage and OMR Flows Do Not Have a Statistically Significant Effect on the Population Growth Rate

66. Given the data in FWS's possession, and given its goal of evaluating the projects' effect on the total population, the appropriate analysis is to use that data to evaluate the effect on the population from year to year. This includes interpretation of the data to determine the effect of salvage (or more generally, population removals) on the population growth rate by application of a life-cycle model, as is standard practice in fisheries stock assessment. This approach is confirmed by the authors of widely read and accepted texts, which discuss the reliable methods of undertaking these analyses. *See, e.g.*, Quinn & Deriso (1999) at ch. 2; Hilborn & Walters (1992) at ch. 8. The population growth rate represents the relative increase or decrease in adults from one year to the next, which is a full life-cycle approach. Owen-Smith (2007) at 28. This approach is critical for evaluating the species' potential for recovery in that it measures the population's ability to rebound from year to year. *See, e.g.*, Bennett (2005) at 41 ("Population modeling may be the best way to evaluate the potential impacts of water export operations relative to other sources of mortality.").

67. Interpreting the data to evaluate the effect of salvage on the population growth rate is necessary because the survival of the species at one life stage cannot necessarily be the basis

for population level conclusions. To evaluate the effects of salvage, one must look beyond a single phase of life (i.e., FMWT only) or even adults to juveniles (i.e., FMWT to TNS). A complete analysis requires an evaluation of trends from one year's FMWT to the next year's FMWT because mortality in one life stage may be offset by mortality in another life stage or it may be affected by density dependence (described below in ¶ 68). As noted by Bennett (2005) at 44, when discussing simulation results of a hypothetical population model for delta smelt, "These results show how export mortality could be easily offset or masked by very small changes in mortality at other life stages." A generation-to-generation analysis eliminates or reduces the risk that population level conclusions will be drawn based on mortality effects in one life stage or the apparent change in mortality effects due to offsets in another life stage.

68. Delta smelt appear to exhibit reduced population growth when population abundance is high due to density dependence. Density dependence can occur through many mechanisms, as described by Ricker (1975) at 280: "Although cannibalism of young by adults is possible in many species, it is likely that the effect of parental stock density upon recruitment is usually exerted *via* the density of the eggs or larvae they produce, survival of the latter being affected by density-dependent competition for food or space, compensatory predation, etc." Thus, density dependent effects must be taken into account when evaluating the population growth rate. Density dependence terms are present in all major stock production, biomass dynamic, and stock-recruitment models, including the Ricker model. *See* Quinn & Deriso (1999) at chs. 2, 3.

69. Standard practice dictates that population level conclusions should not be based solely on raw salvage numbers. Rather, a fish population dynamicist should evaluate population level effects using the cumulative salvage index (salvage rate), and also evaluate the effect of the cumulative salvage index on the population growth rate, just as is typically done with harvest rates. As noted by Bennett (2005) at 37, "In several respects, losses to the water export facilities are analogous to harvest in a fishery, with the main exception that 'harvest' in this case includes all life stages (except eggs)." Harvest rates are routinely evaluated for their population level effects, and their consequence to population growth levels over time, in fisheries stock

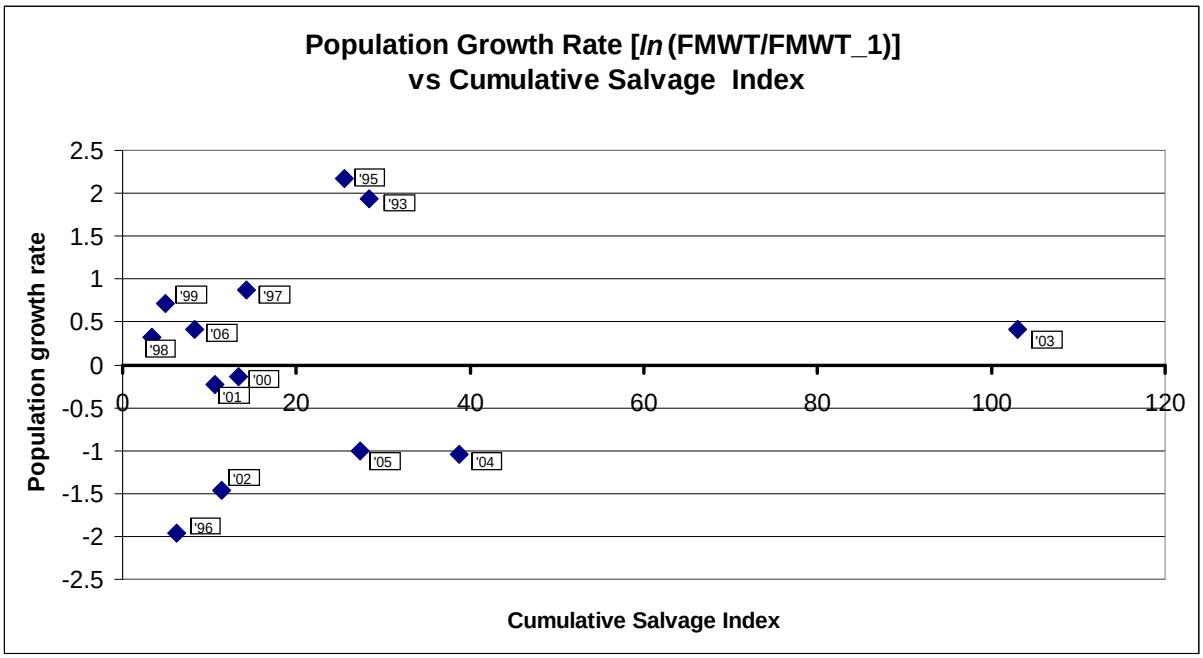
evaluations. *See, e.g.*, Quinn & Deriso (1999) at ch. 2; Hilborn & Walters (1992) at ch. 8. Only by looking at population level effects can it be determined whether salvage is impacting the delta smelt population and its ability to recover in a statistically significant way.

70. Through my review of the modeling and analysis in the BiOp, I determined that FWS did not apply a life-cycle approach in the BiOp. FWS did not attempt to evaluate the effect of the projects on the population growth rate. The BiOp completely omits any analysis or conclusions about project effects on the overall life cycle of the delta smelt and its ability to recover from year to year. However, the data to perform such an analysis is all available, and evaluating population growth rate effects is an elementary exercise. When I looked at the data for such effects, I readily recognized that there is no statistically significant relationship between salvage and the population growth rate.

(1) Adults – Salvage

71. Applying standard principles to calculate population level effects, and using the correct variable to determine those effects (the salvage rate), I modeled the relationship between the cumulative salvage index and the population growth rate. The life-cycle model used for this analysis is a standard Ricker stock-recruitment model in which consecutive year FMWT estimates take the role of stock and recruitment, respectively. I used the cumulative salvage index data taken from the BiOp itself. *See* BiOp at 386 (AR at 000401).

72. The output of this standard model shows that there is no statistically significant relationship between salvage and the population growth rate. This demonstration is based upon using 0.05 as the significance level—the standard benchmark in applied statistics for determining a significance level. *See, e.g.*, Sigler, S., *Fisher and the 5% Level*, 21:4 Chance, Springer New York (Dec. 2008). Statistical significance is found when the p-value is less than 0.05. The p-value is the probability that the result obtained in a statistical test is due to chance rather than a true relationship between variables. In the analysis that I performed, the p-value was 0.76, which is greater than the benchmark and thus not statistically significant. *See* Appendix 1 at Point 2 for additional technical detail. The population growth rate and cumulative salvage index are depicted in the graph below as a visual aid.

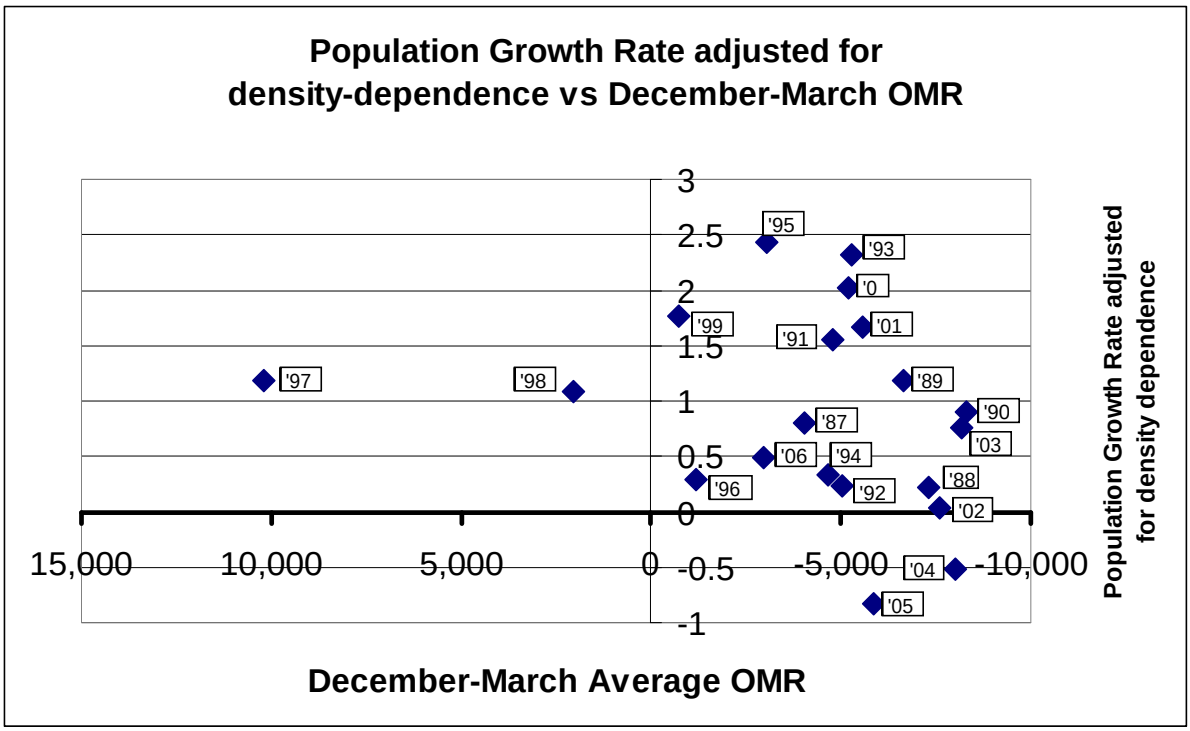


73. If the cumulative salvage index had a strong negative effect on population growth, the above graph would have been expected to show a pronounced negative slope. Instead, the graph shows no trend in population growth rate as the salvage rate increases. If the population has a growth rate of zero, then the population is neither increasing nor declining. A positive growth rate means the population is increasing on an annual basis, and a negative growth rate means the population is declining on an annual basis. Here, the population growth rate did not trend in a negative direction as the cumulative salvage index increased, so there is no statistical basis to conclude that cumulative salvage has a negative population level effect within the range of cumulative salvage index levels historically observed.

(2) Adults – OMR Flows

74. I conducted a second analysis to evaluate the relationship between December-March average OMR flows and the population growth rate. I calculated the average flows using the daily OMR flow data from the October 29, 2009 FOIA request. Using a standard Ricker stock-recruitment model and the standard 0.05 significance level, I found that the relationship between March-December OMR flows and the population growth rate is not statistically significant. The p-value is 0.321, which is above the significance level of 0.05. The modeling

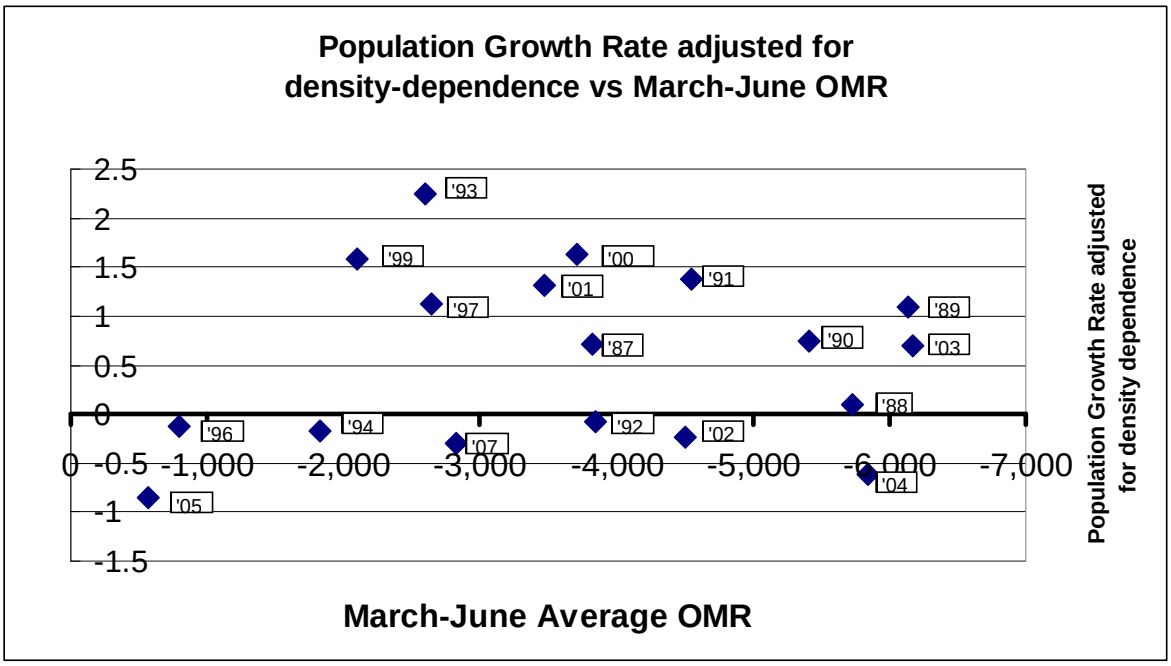
results are shown below as a visual aid. Thus, here too, there is no statistical basis to conclude that the OMR flows cause a negative population level effect within the range of December-March average OMR flows historically observed. For additional technical detail, see Appendix 1 at Point 3.



(3) Juveniles

75. The BiOp includes entrainment estimates for larval-juvenile delta smelt based on the work of Kimmerer (2008), who in turn bases those estimates on a method in which the assumption is made that entrainment is proportional to the southward OMR flow. I tested whether or not average southward OMR flow during the larval/juvenile salvage months of March through June could explain a statistically significant amount of the variation in population growth. I used the Ricker model again as a life-cycle model. March-June average OMR flow for years during the time span 1987 through 2007 in which the average flow was negative (that excluded years 1995, 1998, and 2006) was entered as a candidate explanatory variable and regression analysis was used to test whether or not the candidate variable was statistically significant. A starting year of 1987 was used because that is the starting year used in the BiOp, as data from that year forward "represents current delta smelt population dynamics." *See* BiOp at

236 (AR at 000251). Results show that March-June average OMR does not have a statistically significant impact on smelt population growth rate (the p-value is 0.703, which is above the significance level of 0.05). For additional technical detail, see Appendix 1 at Point 4. Even if entrainment of larval/juvenile smelt is related to spring OMR flow, that entrainment does not have a statistically significant impact on population growth. The result can be seen visually in the graph below which shows that variation in population growth rate (adjusted for density dependence) is not explained by the average March-June OMR flow.



76. March-June OMR does not negatively impact population growth, as can be seen visually in the graph above, where even at the most negative observed average OMR flows, the population growth rate was positive (irrespective of whether a density dependent adjustment is made). For additional technical detail, see Appendix 1 at Point 4. This result implies that there is no scientific justification for proposed RPA Action 3.

C. The Model Used in FWS's Analysis to Compare the Effect of Fall X2 on Population Survival Is Biologically Implausible and Potentially Misleading – It Is Simply Inappropriate for Fish Population Dynamics Modeling

77. FWS used statistical modeling to demonstrate an alleged relationship between Fall X2 and delta smelt abundance. The modeling and analysis are contained in the Effects of the

Proposed Action section of the BiOp, pages 233-238 and 265-274 (AR at 000248-000253 and 000280-000289), and in RPA Action 4 in Attachment B to the BiOp, pages 369-376 (AR at 000384-000391). FWS relied on various studies, particularly the work of Feyrer et al. in a 2007 article, *Multidecadal Trends for Three Declining Fish Species: Habitat Patterns and Mechanisms in the San Francisco Estuary, California, USA* (AR at 018266) and a draft 2008 manuscript, *Modeling the Effects of Water Management Actions on Suitable Habitat and Abundance of a Critically Imperiled Estuarine Fish (Delta Smelt* Hypomesus transpacificus) (AR at 018278); a 2005 article by Bennett, *Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California* (AR at 017004); a 2008 report by Baxter et al., *Pelagic Organism Decline Progress Report: 2007 Synthesis of Results* (AR at 016922); and a 2008 article by Nobriga et al., *Long-Term Trends in Summertime Habitat Suitability for Delta Smelt,* Hypomesus transpacificus (AR at 019940).

(1) FWS Used a Linear Additive Model

78. FWS used a linear additive model to demonstrate an alleged relationship between Fall X2 and delta smelt abundance. The model finds that juvenile abundance, as measured by the TNS, is equal to the sum of a constant number plus the previous year's FMWT index (times a constant number), less X2 (times a constant number). *See* BiOp at 268 (AR at 000283) (Figure E-22). Essentially, this calculation finds that A = B + C - D.

79. FWS followed the linear additive model developed by Feyrer et al. (2007), which claims that Fall X2 has a population level effect. This model runs counter to well-accepted, basic modeling principles for this type of calculation. When analyzing the effect of Fall X2, FWS also cites to a 2005 article by Bennett. *See* BiOp at 236 (AR at 000251). However, Bennett applies a well-established stock-recruit model, namely, the Beverton-Holt model, and an alternative linear multiplicative model. *See* Bennett (2005) at 28-29.

80. The linear additive model produces the result that zero adults in one year could still yield some young in the following year, a result that is biologically implausible. Using the simple translation A (juveniles measured in TNS) = B (constant) + C (adults measured in FMWT) – D (Fall X2), one can see that, if C were set at zero (no adult spawners), B – D could still

produce a positive number for A (juveniles). This model thus has the biologically impossible property of generating juveniles from zero adults.

81. A linear additive model also treats the environmental factor X2 as an additive factor, which has the implausible property of reducing the absolute numbers of juveniles by the same quantity for a given value of X2 irrespective of the total population. For example, if X2 is set at a certain value such that when X2 is added, 1,000 juveniles are lost, that model would produce the result that 1,000 juveniles are always lost irrespective of the total number of juveniles present or the total number of juveniles that actually respond to X2.

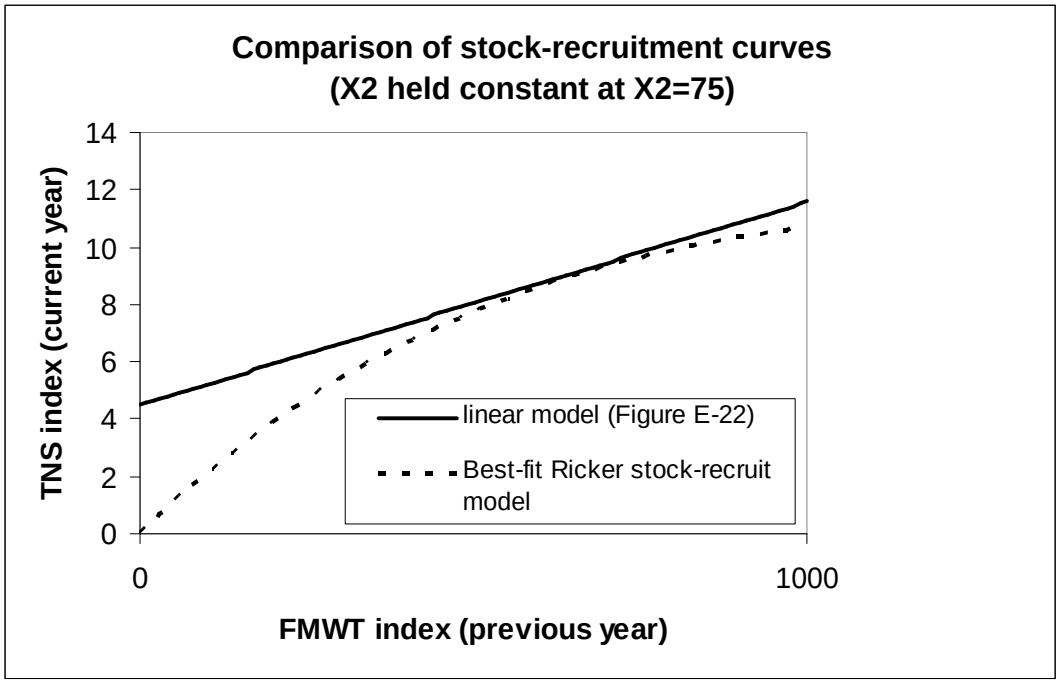
82. For reasons such as these, a linear additive model is inappropriate for stock-recruitment modeling, because the results are biologically impossible.

(2) FWS Should Have Used a Multiplicative Stock-Recruit Model

83. FWS inappropriately used a linear additive model to conduct the analysis that FWS performed with respect to the effect of Fall X2 on population survival. It is well established by those scientists qualified to conduct the type of analysis undertaken by FWS that a multiplicative stock-recruitment should be used. A multiplicative stock-recruit model better reflects actual biological realities when modeling fish populations because it describes survival of a year-class of fish. An example is the Leslie Matrix population model (equation 7.2 in Quinn & Deriso (1999) at 269). Survival processes are inherently multiplicative because the fraction of individuals that survive to a given age is given by the product of daily survivals through each day since the day of birth (*see, e.g.*, cumulative survival in Quinn & Deriso (1999) at 292). A commonly used, well known multiplicative stock-recruit model is the Ricker model. A qualified scientist in this field would be familiar with this model and would have no difficulty using it to perform the analysis that FWS did.

84. Any reliable, scientifically accepted stock-recruit model, such as the Ricker model or the Beverton-Holt model, is not a linear additive model. Such multiplicative stock-recruit models produce the biologically appropriate result that zero adults yields zero young. Thus, regardless of the presence of other factors, if there are zero adult spawners, there will be zero juveniles the following year. A graphical depiction of the difference between a multiplicative

model, such as the Ricker model, and a linear additive model is helpful to illustrate how a multiplicative model better reflects biological reality.



85. A multiplicative model, as opposed to an additive model, yields the sensible result that varying an environmental factor such as X2 will elicit a proportional response in population abundance. This is appropriate for a factor that affects survival because survival is, by definition, a fraction (what proportion of the population survives). In contrast, the linear additive model produces an absolute response irrespective of the size of the population. Multiplicative models are appropriate when describing the survival of a given cohort of fish. Additive terms may be appropriate components in certain types of cohort models when tracking the absolute abundance of a cohort over time—i.e., in situations that involve calculating the total raw population numbers over time, an exercise that has not been done for the delta smelt. *See* Quinn & Deriso (1999) at 323.

86. The BiOp itself questions the use of a linear additive model to evaluate the effect of Fall X2, stating that "some type of transformation of the data would help to define a better fitting model," but declines to correct the situation (such as through the use of a multiplicative model). BiOp at 236 (AR at 000251).

87. The Peer Review also criticized the linear additive model, finding that "[t]he [Effects Analysis] points out that the residuals from this analysis are not normally distributed and that some transformation might be required. We suspect that a few of the data points may have high influence on the outcome. These results together suggest that the model may be inappropriate for the data being used." *Independent Peer Review of USFWS's Draft Effects Analysis for the Operations Criteria and Plan's Biological Opinion, 2008* at 7 (AR at 008819).

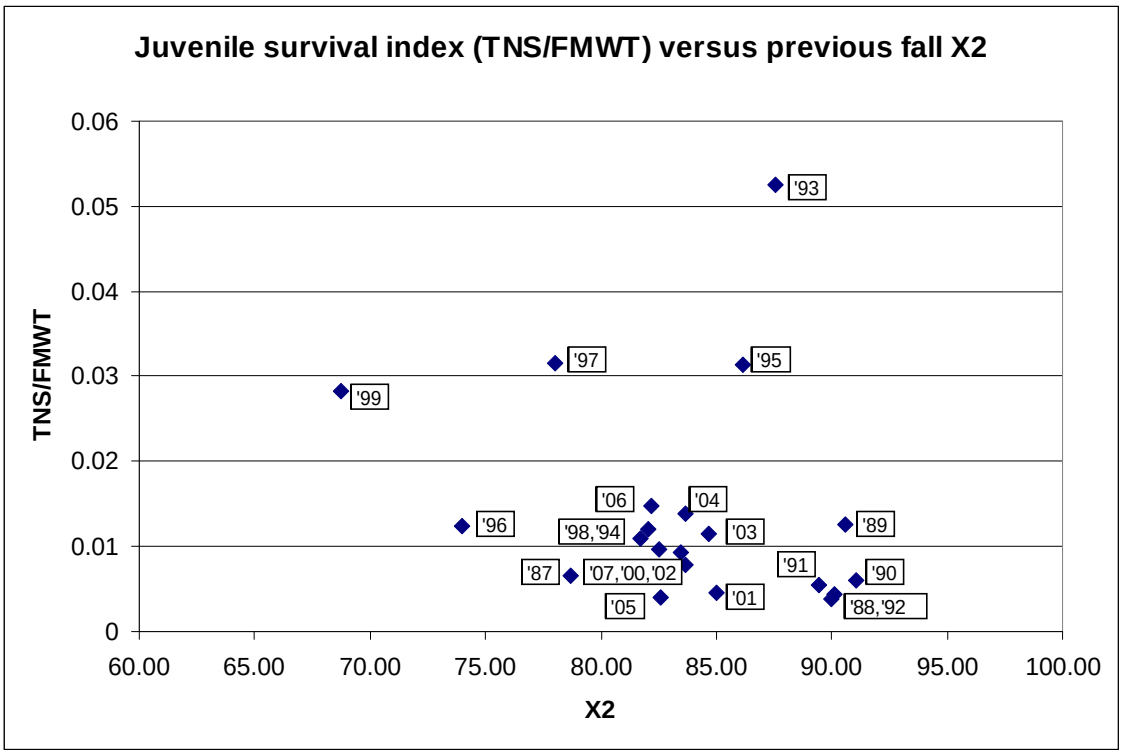
88. During my review of FWS's analysis, I plotted a stock-recruit curve of the relationship between FMWT (previous year) and TNS (current year) using the standard Ricker stock-recruitment model that was obtained by fitting the model to data. See details in Appendix 1 at Point 5. A visual comparison of the linear additive model that FWS used in the BiOp against the Ricker model is shown above. As shown on the comparison, when FMWT is set at zero in the linear model that FWS used, TNS is above zero. In contrast, when FMWT is set at zero in the standard Ricker model, TNS is also zero.

89. In order to evaluate whether there is a relationship between Fall X2 and abundance, I used the publicly available FMWT and TNS data and publicly available Fall X2 data in a standard Ricker stock-recruit model.[5] After employing the Ricker stock-recruit model, I was able to determine that there is no statistically significant relationship between Fall X2, stock abundance, and recruit abundance. The p-value for Fall X2 is 0.059, which is greater than the benchmark significance level of 0.05. See Appendix 1 at Point 5 for additional technical detail. The contrary conclusion that FWS reached is due to its improper use of a biologically implausible linear additive model.

90. I determined that the density dependent term in the Ricker model was not statistically significant. As a result, I used a reduced survival model that omitted the density

[5] FMWT data is available at: http://www.delta.dfg.ca.gov/data/mwt/charts.asp. The BiOp cites to http://www.delta.dfg.ca.gov as a source for FMWT data at page 143 (AR at 000158). TNS data is available at: http://www.delta.dfg.ca.gov/data/projects/?ProjectID=TOWNET. The BiOp cites to this website as a source for TNS data at page 300 (AR at 000315). Fall X2 data is available at: http://www.iep.ca.gov/dayflow/output/index. The BiOp relied on CALSIM modeling to calculate X2 values, and cites to http://www.iep.ca.gov/dayflow for "historical hydrologic data provided in the DAYFLOW database" which was used in the CALSIM modeling. *See* BiOp at 204, 235 (AR at 000219, 000250).

dependent term. The result shows that Fall X2 term is not statistically significant, since the p-value of 0.094 is greater than the 0.05 significance level. The graph below is included as a visual aid to show that there is no relationship between an index of juvenile survival ("TNS/FMWT_1") and Fall X2. If there had been a strong negative effect of Fall X2 on juvenile survival, the graph would have been expected to show a pronounced negative slope. Instead, the graph shows no trend in juvenile survival as X2 increases. For additional technical detail, *see* Appendix 1 at Point 5.



(3) Use of a Scientifically Appropriate Multiplicative Model Shows That Fall X2 Has No Statistically Significant Effect on the Population Growth Rate

91. In my review of the BiOp, I determined that FWS did not evaluate the effect of Fall X2 on the population growth rate. Use of the population growth rate would enable FWS to evaluate effects on the full life-cycle of the delta smelt.

92. Instead of carrying forward the linear additive model, as did FWS, the proper scientific method is to model the relationship between Fall X2 and the population growth rate

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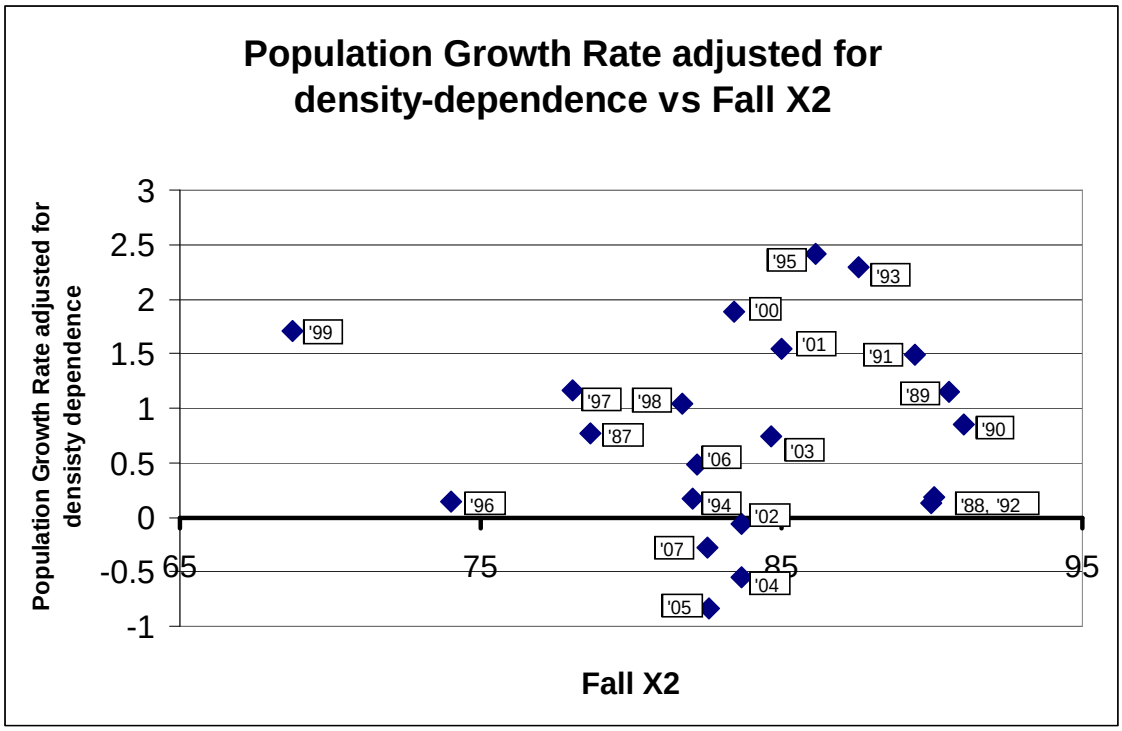
using a multiplicative model. As explained above, a multiplicative model is the scientific standard for fish population dynamics.

93. I used a Ricker model, which is a multiplicative model, to calculate the population growth rate and to evaluate the relationship between Fall X2 and the population growth rate with the regression method described in Appendix 1 at Point 6. I adjusted for density dependence in the modeling. In this application, I determined that the density dependent term in the Ricker model was statistically significant. Thus, the population growth rate had to be adjusted to account for these effects so that the potential effect of Fall X2 could be isolated. For additional technical detail, see Appendix 1 at Point 6. This relationship, adjusted for density dependence, is depicted below.



94. My application of a multiplicative Ricker life-cycle model demonstrates that Fall X2 does not have a statistically significant effect on the population growth rate. As Fall X2 increases, the population growth rate varies randomly. Taken together with the modeling I performed above (comparing Fall X2 to abundance, see ¶ 89) and statistical analysis of the regression estimates, this means that Fall X2 does not have a statistically significant effect on population abundance in a given water year (adults to juveniles), or on the full life-cycle of the

delta smelt (adults to adults). Since FWS's imposition of Fall X2 restrictions in RPA Action 4 is based upon its erroneous use of the wrong model—which, in turn, has led to the incorrect result that Fall X2 has population effects on the delta smelt—it is scientifically unjustified.

D. FWS's Incidental Take Analysis Is Improperly Influenced by Unrepresentative Data Points That Even FWS Rejected for Other Purposes

(1) FWS's Adult Incidental Take Analysis Is Improperly Influenced by an Unrepresentative Data Point

95. FWS's adult incidental take analysis can be found in Attachment C to the BiOp, pages 382-396 (AR at 000397-000411). In developing the incidental take limit for adult entrainment, FWS relied on a series of statistical analyses and calculations in the BiOp and in Kimmerer (2008).

96. The incidental take limit is set at 7.25 times the prior year's FMWT index of adult abundance. BiOp at 386 (AR at 000401). The 7.25 figure represents the average salvage rate from only three years—2006, 2007, and 2008. *See* BiOp at 385-86 (AR at 000400-000401). The BiOp uses the average salvage rate for these three years as a predictor of take levels during each year that the RPAs will be in effect. Although salvage data is analyzed dating back to 1993, the BiOp claims that "these years [2006 through 2008] within the historic dataset best approximate expected salvage under the RPA Component 1," which restricts OMR flows. *Id.*

97. The BiOp lists the annual salvage numbers and salvage rates for the years 1993-2008, and shows that the salvage in 1994 and 2007 were extremely low compared to the other years and to 2006 and 2008 in particular. *See* BiOp at 386 (AR at 000401) (Table C-1). The cumulative salvage index is just 0.88 for 2007, compared to 8.3 for 2006 and 12.6 for 2008. *Id.*

98. In my review, I searched for additional information regarding the conditions that might have contributed to these salvage levels. In another section of the BiOp, I discovered that FWS had considered the salvage level in 2007 as ***unusable*** for purposes of analyzing salvage and OMR flows due to that year's low average water turbidity. *See* BiOp at 348 (AR at 000363) (Figure B-13, Note). The low turbidity explains why salvage in 2007 was extremely low, as turbidity is a strong indicator of presence or absence of delta smelt near the project facilities.

Lower turbidity means fewer fish will be present and, accordingly, fewer fish are capable of being entrained. Thus, FWS recognized that the unusual conditions in 2007 made it an unrepresentative year that would skew its analysis. For FWS to then go ahead and use that salvage level in the incidental take equation is scientifically unjustified.

99. Without the year 2007 factored into the equation, the take coefficient increases from 7.25 to 10.45, which lies within the range of historical estimates based on the figure shown in ¶ 62 above for flows less negative than -7000 cfs. This figure represents the average of the salvage indices in 2006 and 2008, and would significantly increase the permissible take level. FWS's calculation should be corrected to remove the outlier year of 2007.

(2) FWS's Larval/Juvenile Incidental Take Analysis Is Improperly Influenced by an Unrepresentative Data Point

100. FWS's larval/juvenile incidental take analysis can be found in Attachment C to the BiOp, pages 382-396 (AR at 000397-000411). To calculate the incidental take limit for larval/juvenile entrainment, FWS largely followed the same methodology that it used for adults. BiOp at 389 (AR at 000404).

101. The incidental take limit is set at 1.5 times the Concern Level for larvae and juveniles. The Concern Level is equivalent to the average monthly juvenile salvage index from 2005-2008 times the current water year FMWT of adult abundance. BiOp at 390 (AR at 000405). Combining these two formulae, the incidental take limit can be calculated by multiplying 1.5 times the average monthly juvenile salvage index times the FMWT. Only four years are considered – 2005, 2006, 2007, and 2008.

102. The BiOp lists the annual salvage numbers and salvage rates for the years 1995-2008, and shows that the salvage in 2006 was extremely low compared to all other years, with the exception of 1995 and 1998 (see discussion below). *See* BiOp at 392 (AR at 000407) (Table C-4). The juvenile salvage index is just 0.4, compared to 23.4 for 2005, 65.1 for 2007, and 60.9 for 2008. *Id.*

103. In my review of the BiOp, I searched for additional information that might explain the conditions that were present in these years and how they contributed to salvage levels. I was

provided with daily OMR flow data through a FOIA request to FWS. I discovered that in 2006, average OMR flow was strongly positive for the months April through June, the first three (of four) months during which the monthly juvenile salvage index is calculated. OMR flow was negative in July 2006, but typically, very few fish are salvaged in July. *See, e.g.*, BiOp at 391 (AR at 000406) (Figure C-3) (showing that cumulative salvage reaches a plateau in July).

104. When analyzing the effects of OMR flows on salvage in the Effects Analysis section of the BiOp, FWS explained that "net OMR flow generally works very well as a binary switch: negative OMR flow is associated with some degree of entrainment, while positive OMR flow is usually associated with no, or very low, entrainment." BiOp at 163 (AR at 000178). The juvenile salvage index is reported in the BiOp for the years 1995-2008. BiOp at 392 (AR at 000407). During that time, there were three years when salvage was nearly zero – 1995, 1998, and 2006. These are the only three years when OMR flow was positive. *See* BiOp at 254 (AR at 000269) (Figure E-8). Thus, FWS's statement that positive OMR flow yields zero or very low salvage is supported by historical measurements of juvenile salvage and OMR flow. It also undermines FWS's decision to include one of those years – 2006 – in the incidental take equation.

105. Without the year 2006 factored into the equation, the average juvenile salvage index increases, which necessarily increases the Concern Level (monthly juvenile salvage index times FMWT) and the incidental take level (1.5 times Concern Level). The incidental take level increases by approximately 32-33 percent in May, June, and July, and decreases by approximately 14 percent in April (when salvage is low). Overall, in the months with the highest salvage, removal of the unrepresentative year 2006 significantly increases the take level. FWS's calculation should be corrected to remove the year 2006, which had positive OMR flow.

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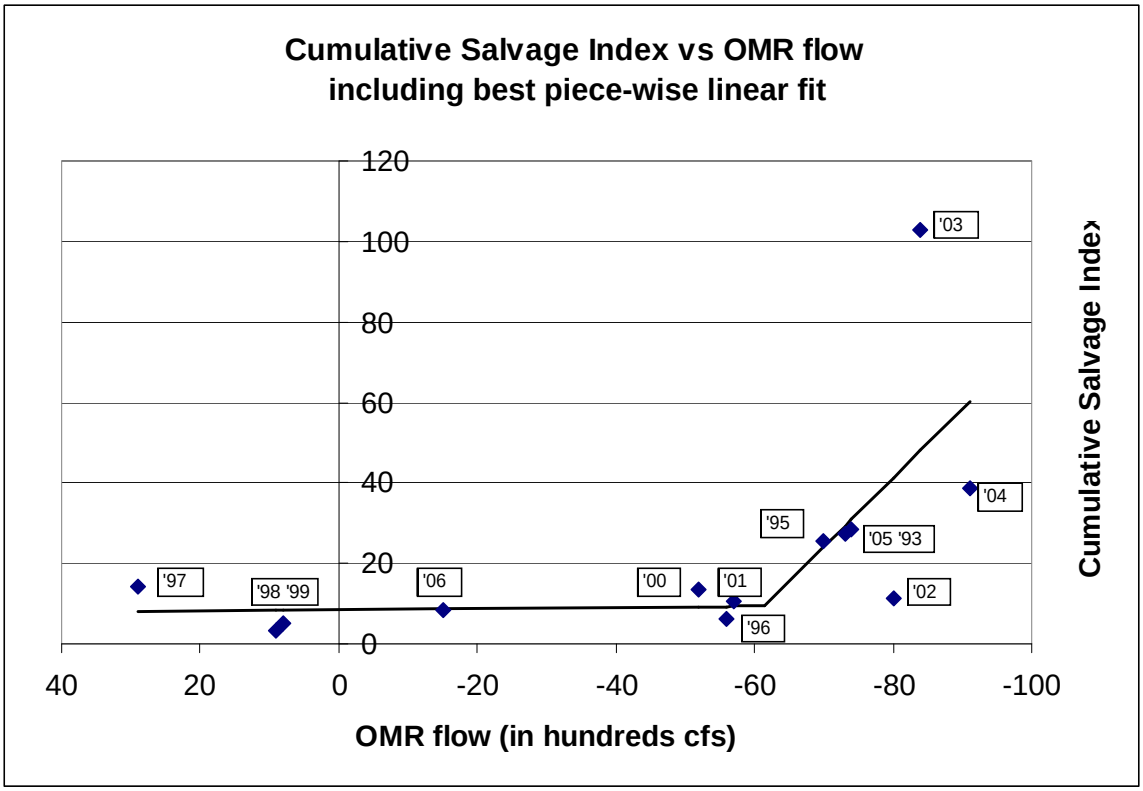
I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on November 13, 2009 at St. Thomas, U.S. Virgin Islands.

RICHARD B. DERISO, Ph.D.

Appendix

Appendix 1: Supporting Technical Details to Analyses Described in "Declaration of Dr. Richard B. Deriso"

Point 1.



The Cumulative Salvage Index (Table B-2 & C-1) and corresponding Dec-Mar salvage weighted OMR (Figure B-13); note the OMR estimates were visually estimated from Figure B-13. Years span 1993-2006 but exclude 1994 because that was also excluded in Figure B-13.

Year	OMR	Cumulative Salvage Rate Index
1993	-74	28.4
1995	-70	25.5
1996	-56	6.27
1997	29	14.3
1998	9	3.39
1999	8	4.94
2000	-52	13.34
2001	-57	10.6
2002	-80	11.4
2003	-84	103
2004	-91	38.8
2005	-73	27.3
2006	-15	8.3

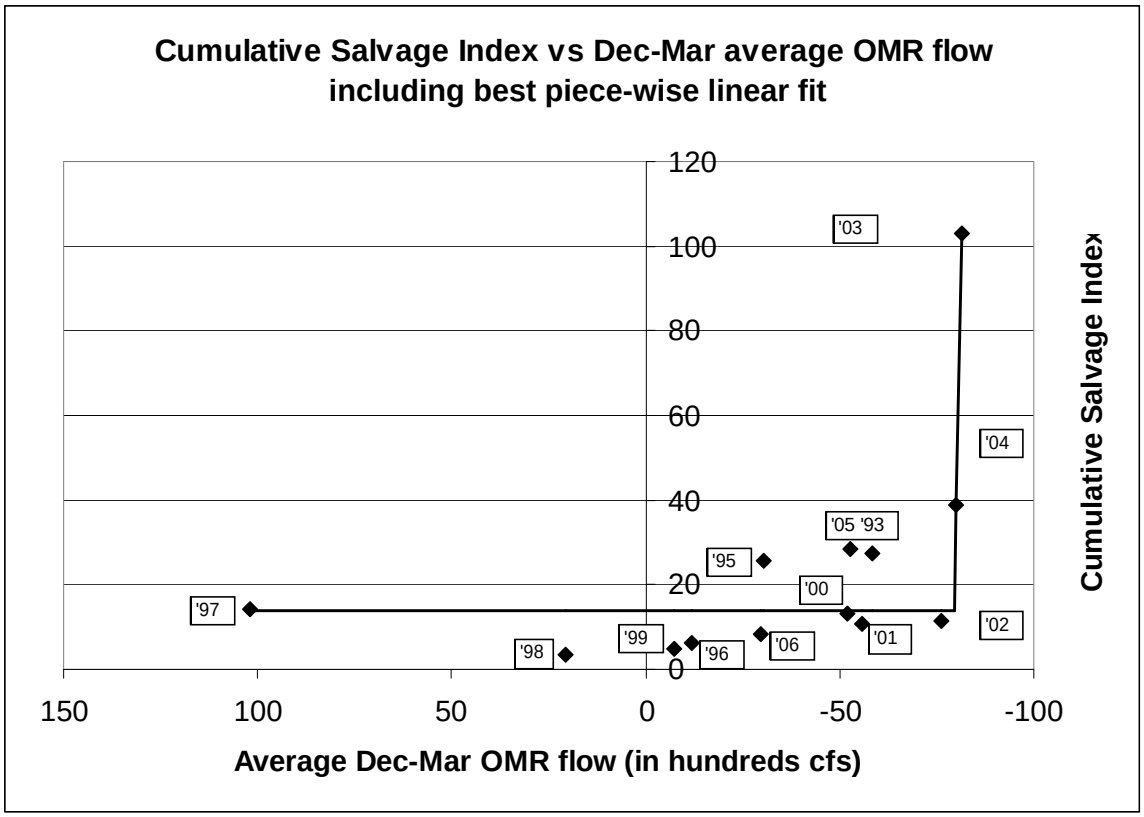
A piece-wise linear model was fit to the data above by minimizing the squared residuals between predicted and observed salvage rates. A logistic switch point was made part of the equation as an approximation to a 0/1 switch governing which piece of the model was appropriate for a given OMR. The best-fit regression equation is given as

$$Y = p[60.25 - 1.72(OMR+91)] + (1-p)[9.38 - .015(OMR+61.386)]$$

where $p = 1$ if $OMR < -61.386$ and $p=0$ otherwise and Y is the predicted salvage rate

Another set of OMR data was examined in relation to the cumulative salvage index. The second set of OMR flow data is the average December-March OMR flow. Daily OMR flow data were provided by FWS to the Metropolitan Water District of Southern California pursuant to a Freedom of Information Act request which were used to calculate several average OMR flows shown in this Appendix. A graph of salvage versus December-March average OMR flow is listed in Figure E-1 of the BiOp.

Year	Average Dec-Mar OMR flow (100's cfs)	Cumulative Salvage Index
1993	-52.798	28.4
1995	-30.315	25.5
1996	-11.817	6.27
1997	101.887	14.3
1998	20.465	3.39
1999	-7.402	4.94
2000	-51.784	13.34
2001	-55.587	10.6
2002	-76.153	11.4
2003	-81.611	103
2004	-80.045	38.8
2005	-58.584	27.3
2006	-29.757	8.3

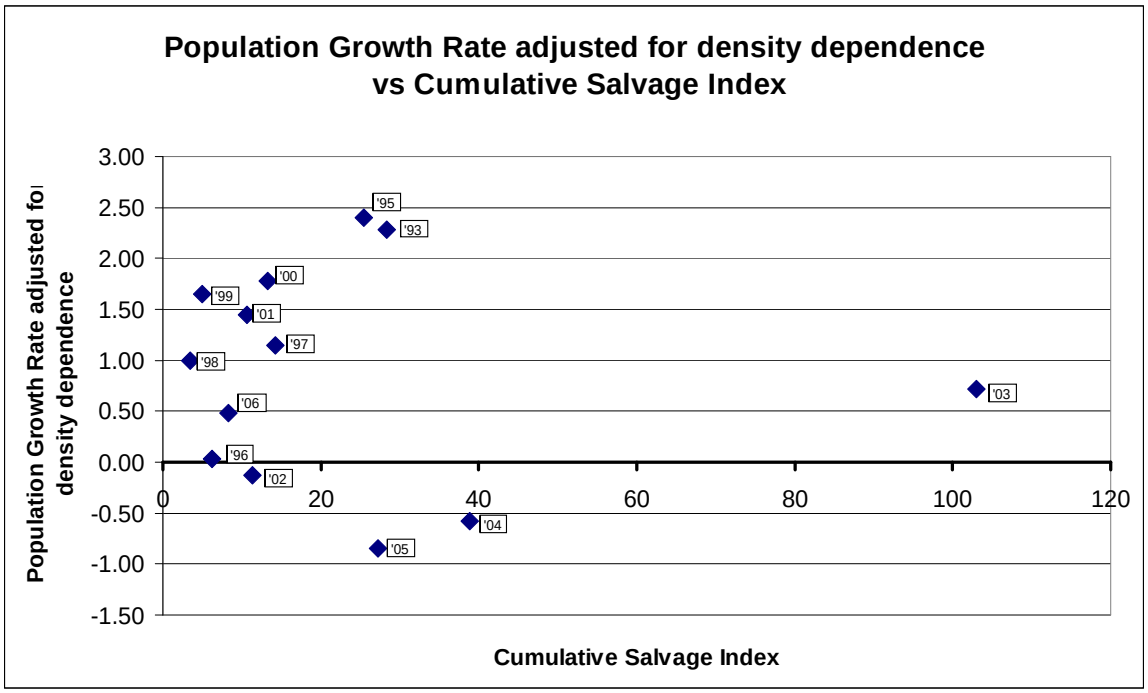


A piece-wise linear model was fit to the data above by minimizing the squared residuals between predicted and observed salvage rates. A logistic switch point was made part of the equation as an approximation to a 0/1 switch governing which piece of the model was appropriate for a given OMR. The slope of the linear piece of the model prior to the switch point was tested for statistical significance. The slope was not significantly different from zero so a piece-wise linear model with zero slope is chosen as the better model as shown in the figure above. The statistical test is based on a likelihood ratio test: The quantity 2*(change in logarithm of likelihood when going from the simple zero-slope model to more complex non-zero slope model) = 1.18, which falls short of the cut-off value of 3.84, which is the 5% significance level for a chi-square test statistic with one degree of freedom (Mood, A et al., *Introduction to the Theory of Statistics*, McGraw-Hill, Inc. (1974)). The switch-point occurs at average Dec-Mar OMR flows of -7,943 cfs. The best-fit regression model is

$$Y = p[102.99 - 40.92(OMR+81.611)] + (1-p)[13.977]$$

where $p = 1$ if $OMR < -79.436$ and $p=0$ otherwise and Y is the predicted cumulative salvage index

Point 2.



Year	Cumulative salvage index	S= FMWT year-1	*ln*(R/S) = ln(FMWT_0/FMWT_1)	Population growth rate adjusted for density-dependence
1993	28.4	156	1.93	2.28
1995	25.5	102	2.18	2.40
1996	6.27	899	-1.96	0.03
1997	14.3	127	0.87	1.15
1998	3.39	303	0.33	1.00
1999	4.94	420	0.72	1.65
2000	13.34	864	-0.13	1.78
2001	10.6	756	-0.23	1.45
2002	11.4	603	-1.47	-0.13
2003	103	139	0.41	0.72
2004	38.8	210	-1.04	-0.58
2005	27.3	74	-1.01	-0.84
2006	8.3	27	0.42	0.48

SUMMARY OUTPUT

ln(FMWT/FMWT_1)=a+b*cumulative salvage index+c*FMWT_1

Regression Statistics	
Multiple R	0.5387
R Square	0.2902
Adjusted R Square	0.1483
Standard Error	1.1390
Observations	13

ANOVA

	df	*SS*	*MS*	*F*
Regression	2	5.3046	2.6523	2.0445
Residual	10	12.9728	1.2973	
Total	12	18.2774		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	0.9687	0.6714	1.4428	0.180
cum. salvage index	-0.0041	0.0134	-0.3053	0.766
FMWT year-1	-0.0022	0.0011	-1.9665	0.078

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. Statistical significance was determined using standard regession theory (Draper, N. and H. Smith. 1981. Applied Regression Analysis, 2nd edition. Wiley, New York). Population growth rate is defined as the logarithm of the ratio (R/S) (also defined as relative population growth rate, Owen-Smith (2007, p. 29), which is written as *ln*(R/S). Adding to *ln*(R/S) the estimated density-dependent term in a Ricker model (say c*S) one obtains the quantity "population growth rate adjusted for density-dependence."

Neither the cumulative salvage index nor the density-dependent term (FMWT year-1) are statistically significant (that is, P-values of 0.766 and 0.78, respectively, for the two terms are above the significance level of 0.05). The 0.05 significance level is a standard benchmark in applied statistics (Sigler, S. 2008. Fisher and the 5% level. Chance 21(4). Springer New York).

A reduced model was applied in which the only candidate explanatory variable was the cumulative salvage index. The reduced model was applied because the density-dependent term (FMWT year-1) was not statistically significant. The results confirm that the actual salvage rate was not statistically significant because the P-value of 0.419 is above the 0.05 significance level as seen in the results tabled below.

SUMMARY OUTPUT

ln(FMWT/FMWT_1)=a+b*cumulative salvage index

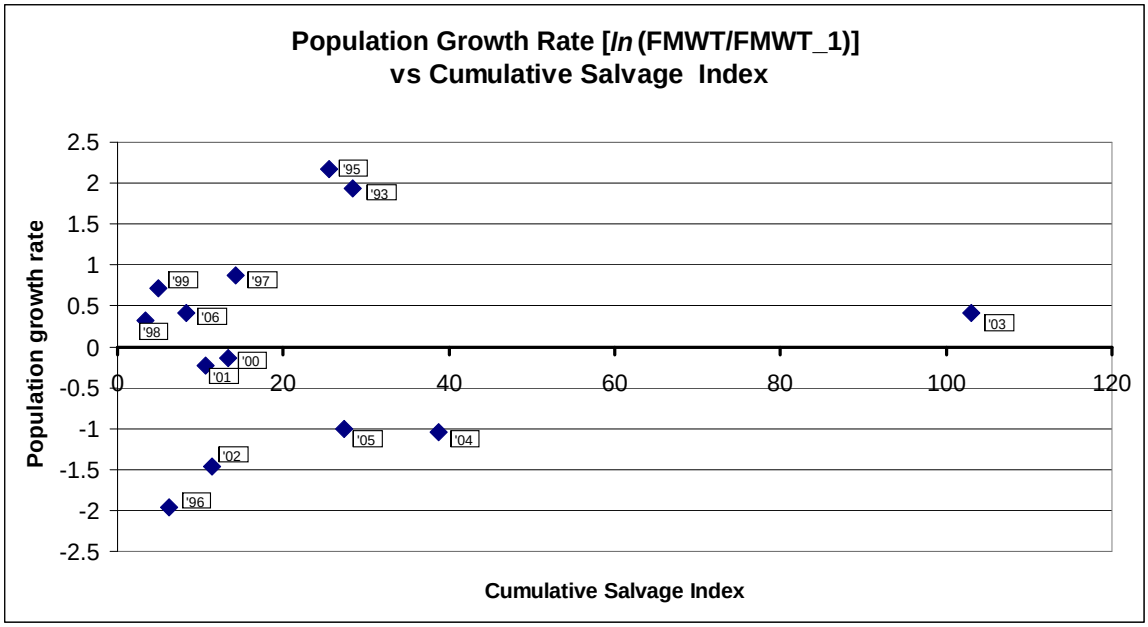
Regression Statistics	
Multiple R	0.125
R Square	0.016
Adjusted R Square	-0.074
Standard Error	1.279
Observations	13.000

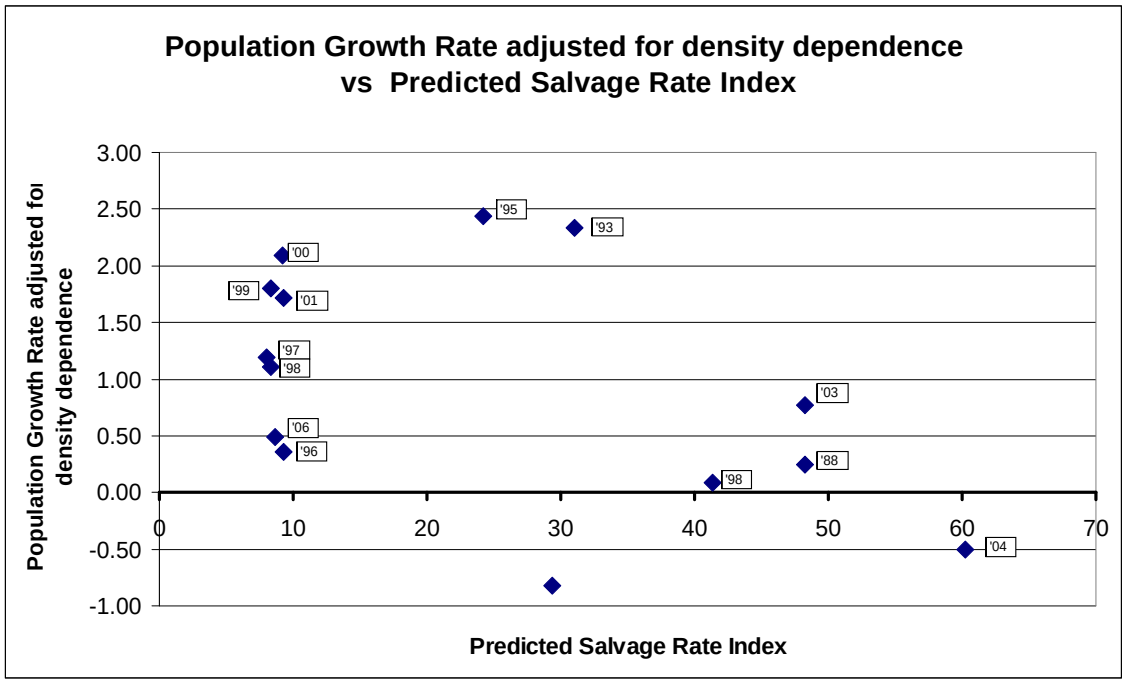
ANOVA

	df	*SS*	*MS*	*F*
Regression	1.000	0.288	0.288	0.176
Residual	11.000	17.990	1.635	
Total	12.000	18.277		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	-0.055	0.476	-0.115	0.911
Cum. salvage index	0.006	0.014	0.419	0.683

As a visual aid, population growth rate and cumulative salvage index are graphed below. If there had been a strong negative effect of salvage index on population growth then the graph would have been expected to show a pronounced negative slope. Instead the graph shows no trend in population growth rate as the salvage index increases.





Year	Predicted salvage rate	*S* = FMWT year-1	*ln*(R/S) = ln(FMWT_0/FMWT_1)	Pop growth rate adjusted for density dependence
1988	48.23	280	-0.48	0.24
1993	31.05	156	1.93	2.33
1995	24.18	102	2.18	2.44
1996	9.30	899	-1.96	0.36
1997	8.00	127	0.87	1.20
1998	8.30	303	0.33	1.11
1999	8.32	420	0.72	1.80
2000	9.24	864	-0.13	2.09
2001	9.31	756	-0.23	1.72
2002	41.36	603	-1.47	0.08
2003	48.23	139	0.41	0.77
2004	60.25	210	-1.04	-0.50
2005	29.33	74	-1.01	-0.82
2006	8.67	27	0.42	0.49

SUMMARY OUTPUT

ln(FMWT/FMWT_1)=a+b* predicted salvage rate+c*FMWT_1

Regression Statistics	
Multiple R	0.652
R Square	0.425
Adjusted R Square	0.320
Standard Error	0.985
Observations	14.000

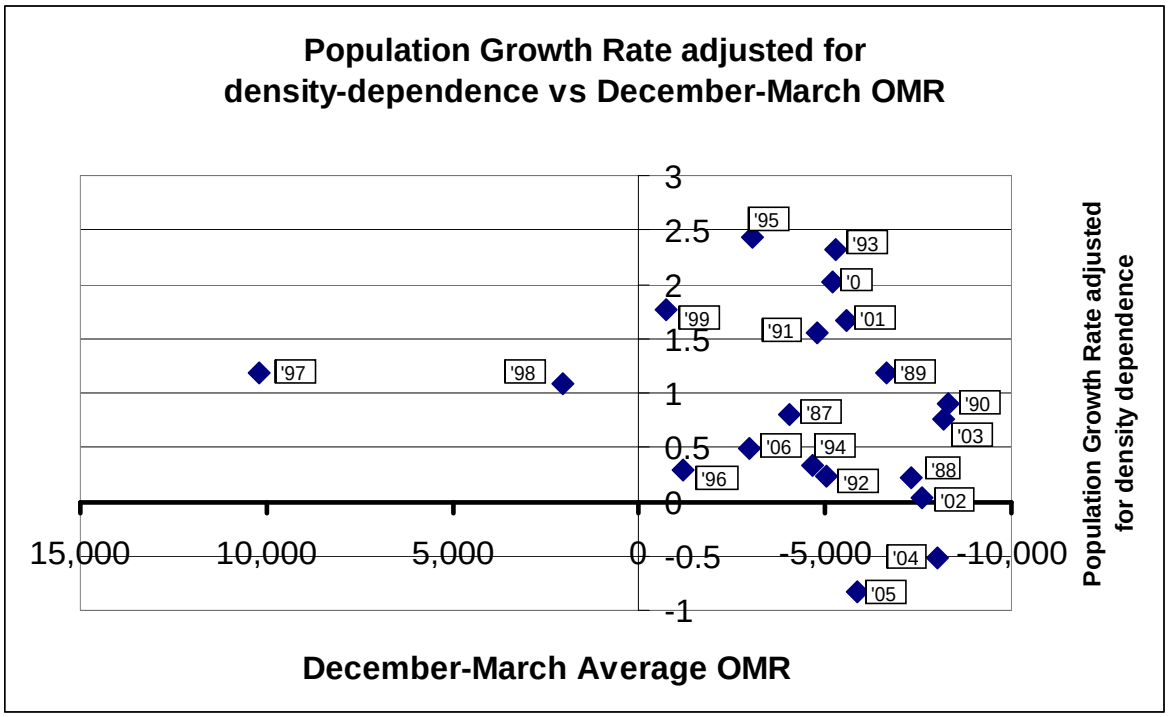
ANOVA

	df	*SS*	*MS*	*F*
Regression	2.000	7.881	3.940	4.058
Residual	11.000	10.682	0.971	
Total	13.000	18.563		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	1.609	0.642	2.506	0.029
predicted salvage rate	-0.027	0.016	-1.726	0.112
FMWT year-1	-0.003	0.001	-2.704	0.020

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. The density-dependent term is statistically significant (P-value = 0.020 is below the 0.05 level). Predicted salvage rate is not statistically significant (that is, P-value 0.112 is above the significance level of 0.05).

Point 3.



Year	Dec-Mar Average OMR	FMWT year-1 (= FMWT_1)	FMWT year (= FMWT_0)	ln(FMWT_0/FMWT_1)	Population growth rate adjusted for density-dependence
1987	-4054.2	212	280	0.278	0.807
1988	-7319.8	280	174	-0.476	0.223
1989	-6647.8	174	366	0.744	1.178
1990	-8313	366	364	-0.005	0.908
1991	-4775	364	689	0.638	1.546
1992	-5037.4	689	156	-1.485	0.233
1993	-5279.8	156	1078	1.933	2.322
1994	-4656.2	1078	102	-2.358	0.331
1995	-3031.5	102	899	2.176	2.431
1996	-1181.7	899	127	-1.957	0.286
1997	10188.7	127	303	0.870	1.186
1998	2046.5	303	420	0.327	1.082
1999	-740.2	420	864	0.721	1.769
2000	-5178.4	864	756	-0.134	2.022
2001	-5558.7	756	603	-0.226	1.660
2002	-7615.3	603	139	-1.467	0.037
2003	-8161.1	139	210	0.413	0.759
2004	-8004.5	210	74	-1.043	-0.519
2005	-5858.4	74	27	-1.008	-0.824
2006	-2975.7	27	41	0.418	0.485

SUMMARY OUTPUT

ln(FMWT/FMRT_1)=a+b*(Dec-Mar OMR)+c*FMWT_1

Regression Statistics	
Multiple R	0.692
R Square	0.478
Adjusted R Square	0.417
Standard Error	0.915
Observations	20.000

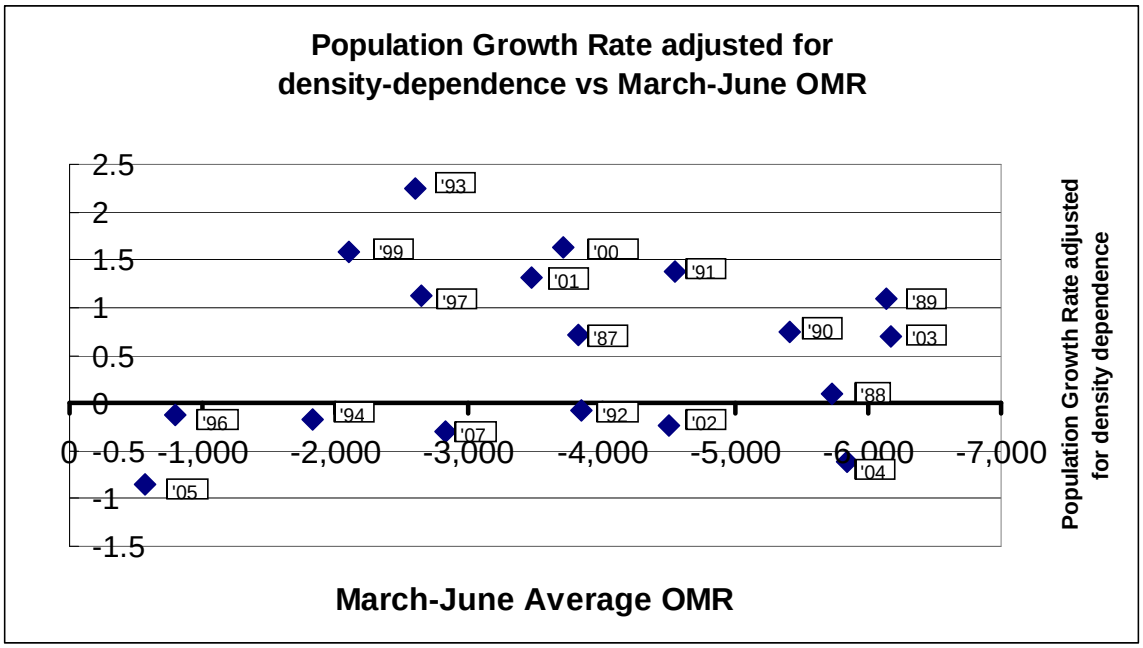
ANOVA

	df	*SS*	*MS*	*F*
Regression	2.000	13.034	6.517	7.792
Residual	17.000	14.218	0.836	
Total	19.000	27.253		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	1.102	0.377	2.920	0.010
Dec-Mar OMR	0.000	0.000	1.023	0.321
FMWT year-1	-0.002	0.001	-3.705	0.002

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. The density-dependent term is statistically significant (P-value = 0.002 is below the 0.05 level). December-March Average OMR is not statistically significant (that is, P-value 0.321 is above the significance level of 0.05).

Point 4.



Year	Mar-Jun OMR	S=FMWT year-1 (= FMWT_1)	FMWT year (= FMWT_0)	ln(FMWT_0/FMWT_1)	Population growth rate adjusted for density dependence
1987	-3828.3	212	280	0.28	0.71
1988	-5732.3	280	174	-0.48	0.10
1989	-6132.3	174	366	0.74	1.10
1990	-5414.7	366	364	-0.01	0.74
1991	-4545.3	364	689	0.64	1.38
1992	-3847.1	689	156	-1.49	-0.08
1993	-2599.1	156	1078	1.93	2.25
1994	-1824.1	1078	102	-2.36	-0.16
1996	-798.1	899	127	-1.96	-0.12
1997	-2641.2	127	303	0.87	1.13
1999	-2100.9	420	864	0.72	1.58
2000	-3712.4	864	756	-0.13	1.63
2001	-3466.7	756	603	-0.23	1.32
2002	-4499.5	603	139	-1.47	-0.24
2003	-6174.4	139	210	0.41	0.70
2004	-5841.3	210	74	-1.04	-0.61
2005	-567.6	74	27	-1.01	-0.86
2007	-2828.7	41	28	-0.38	-0.30

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.613
R Square	0.376
Adjusted R Square	0.293
Standard Error	0.938
Observations	18

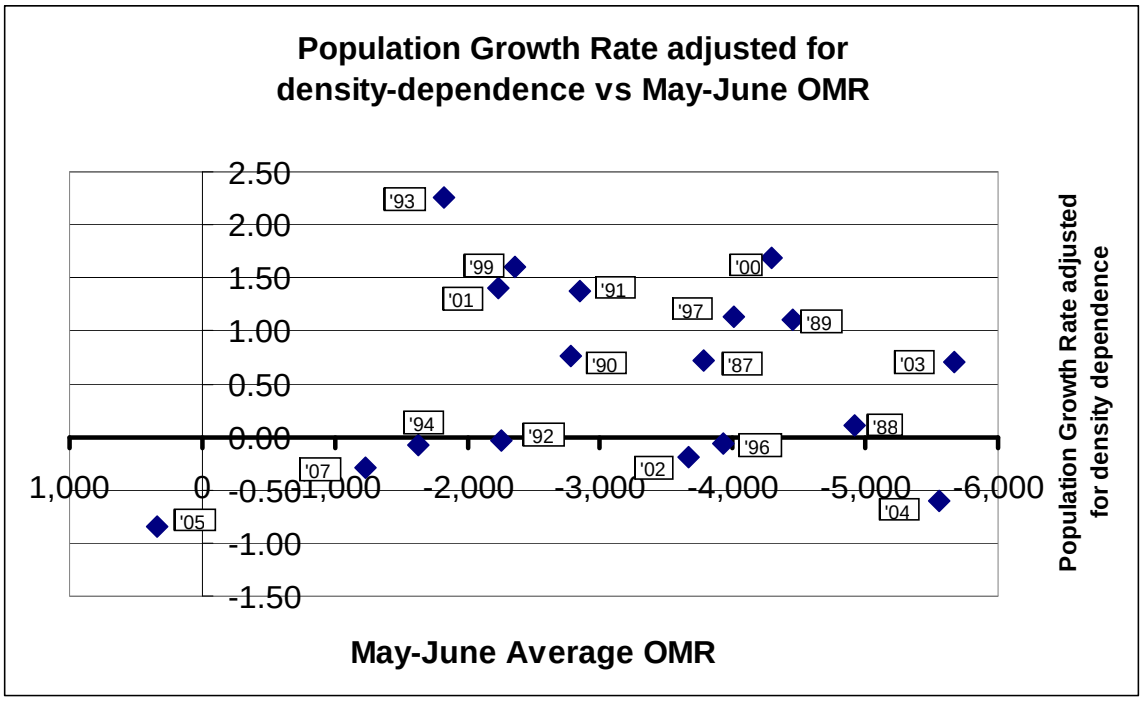
ln(FMWT/FMWT_1)=a+b*OMR+cS

ANOVA

	df	*SS*	*MS*	*F*
Regression	2	7.961	3.981	4.525
Residual	15	13.196	0.880	
Total	17	21.157		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	0.374	0.690	0.541	0.596
Mar-Jun OMR	-0.000052	0.000135	-0.389	0.703
S=FMWT year-1	-0.002035	0.000739	-2.754	0.015

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. The density-dependent term is statistically significant (P-value = 0.015 is below the 0.05 level). March-June average OMR is not statistically significant (that is, P-value 0.703 is above the significance level of 0.05).



Year	May-June OMR	FMWT year-1 (= FMWT_1)	FMWT year (= FMWT_0)	ln(R/S) or ln(FMWT_0/FMWT_1)	Population growth rate adjusted for density dependence
1987	-3777.0	212	280	0.28	0.72
1988	-4915.4	280	174	-0.48	0.11
1989	-4447.1	174	366	0.74	1.11
1990	-2777.1	366	364	-0.01	0.76
1991	-2236.3	364	689	0.64	1.40
1992	-2251.7	689	156	-1.49	-0.04
1993	-1819.5	156	1078	1.93	2.26
1994	-1629.8	1078	102	-2.36	-0.10
1996	-3932.3	899	127	-1.96	-0.07
1997	-4007.2	127	303	0.87	1.14
1999	-2353.8	420	864	0.72	1.60
2000	-4295.3	864	756	-0.13	1.68
2001	-2848.2	756	603	-0.23	1.36
2002	-3667.9	603	139	-1.47	-0.20
2003	-5673.5	139	210	0.41	0.70
2004	-5555.4	210	74	-1.04	-0.60
2005	343.3	74	27	-1.01	-0.85
2007	-1226.1	41	28	-0.38	-0.30

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.613
R Square	0.376
Adjusted R Square	0.293
Standard Error	0.938
Observations	18

ln(FMWT/FMWT-1)=a+b*OMR+cS

ANOVA

	df	*SS*	*MS*	*F*
Regression	2	7.963	3.982	4.527
Residual	15	13.194	0.880	
Total	17	21.157		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	0.421	0.589	0.714	0.486
May-June OMR	-0.00006	0.00014	-0.392	0.701
FMWT year-1	-0.00211	0.00071	-2.975	0.009

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. The density-dependent term is statistically significant (P-value = 0.009 is below the 0.05 level). May-June average OMR is not statistically significant (that is, P-value 0.701 is above the significance level of 0.05).

Point 5.

A Ricker stock-recruitment model was applied to stock and recruitment data in which the juvenile summer townet survey index (TNS) and FMWT take the role of recruitment and stock, respectively. Fall X2 data were obtained from the IEP web site http://www.iep.ca.gov/dayflow/output/index.

Year	X2 year-1	S= FMWT year-1	TNS year	*ln*(TNS)	*ln*(R/S)= *ln*(TNS/FMWT_1)
1987	78.67	212	1.4	0.3	-5.020
1988	90.09	280	1.2	0.2	-5.452
1989	90.58	174	2.2	0.8	-4.371
1990	91.06	366	2.2	0.8	-5.114
1991	89.45	364	2	0.7	-5.204
1992	90.00	689	2.6	1.0	-5.580
1993	87.57	156	8.2	2.1	-2.946
1994	82.06	1078	13	2.6	-4.418
1995	86.14	102	3.2	1.2	-3.462
1996	74.00	899	11.1	2.4	-4.394
1997	78.05	127	4	1.4	-3.458
1998	81.70	303	3.3	1.2	-4.520
1999	68.74	420	11.9	2.5	-3.564
2000	83.44	864	8	2.1	-4.682
2001	85.00	756	3.5	1.3	-5.375
2002	83.66	603	4.7	1.5	-4.854
2003	84.68	139	1.6	0.5	-4.464
2004	83.65	210	2.9	1.1	-4.282
2005	82.61	74	0.3	-1.2	-5.508
2006	82.17	27	0.4	-0.9	-4.212
2007	82.52	41	0.4	-0.9	-4.630

SUMMARY OUTPUT

1987-2007 for all analyses below
ln(R/S)=a+bX2+cS

Regression Statistics	
Multiple R	0.490
R Square	0.240
Adjusted R Square	0.155
Standard Error	0.674
Observations	21.000

ANOVA

	df	*SS*	*MS*	*F*
Regression	2.000	2.579	1.289	2.841
Residual	18.000	8.170	0.454	
Total	20.000	10.748		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	0.317	2.310	0.137	0.892
X2 year-1	-0.055	0.027	-2.017	0.059
FMWT year-1	-0.001	0.000	-1.534	0.143

Neither the X2 variable or the density-dependent term, FMWT_(year-1) were statistically significant because their P-values of 0.059 and 0.143, respectively, are greater than the 0.05 significance level.

The density-dependent term was not significant so a reduced survival model was then analyzed which omitted the density-dependent term.

SUMMARY OUTPUT

ln(R/S)= a+bX2

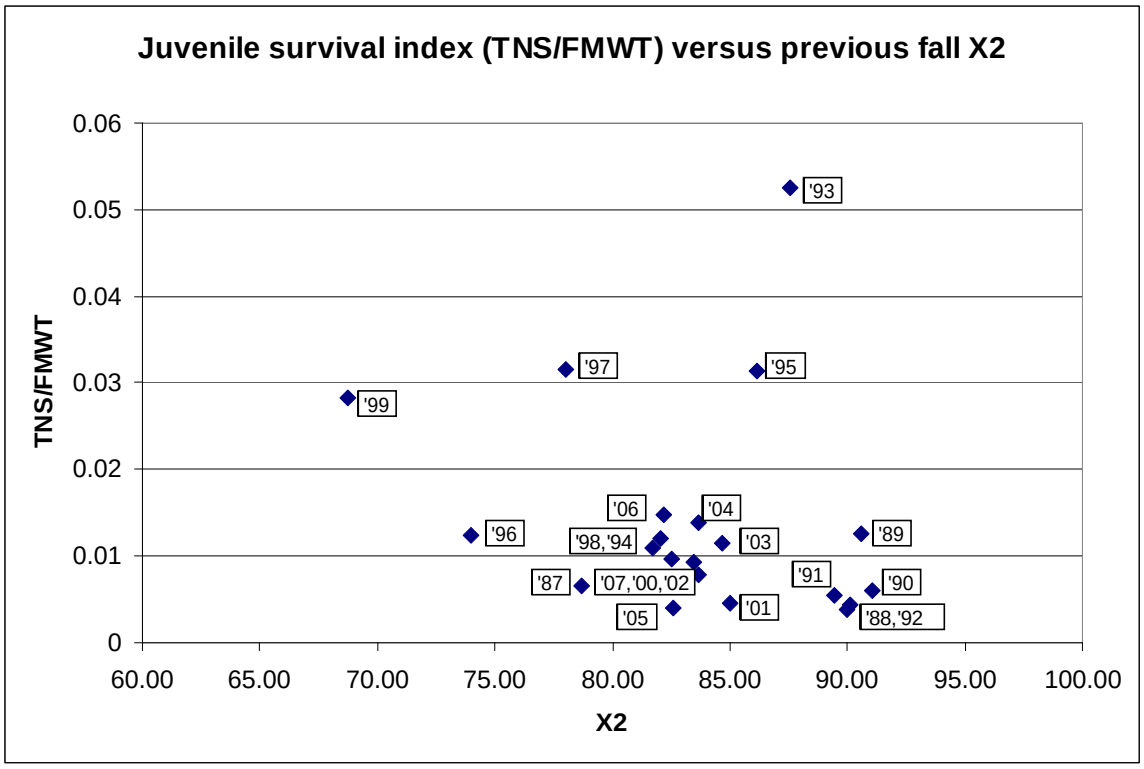
Regression Statistics	
Multiple R	0.375
R Square	0.141
Adjusted R Square	0.095
Standard Error	0.697
Observations	21.000

ANOVA

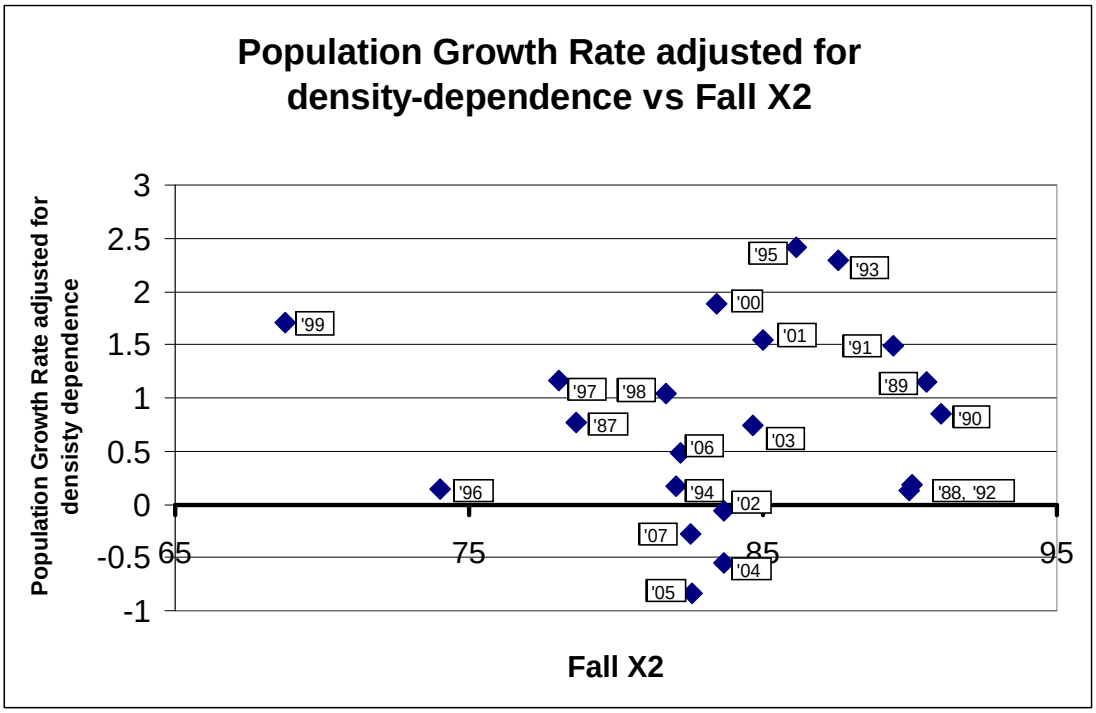
	df	*SS*	*MS*	*F*
Regression	1.000	1.511	1.511	3.108
Residual	19.000	9.237	0.486	
Total	20.000	10.748		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	-0.438	2.336	-0.188	0.853
X2 year-1	-0.049	0.028	-1.763	0.094

The X2 term is not statistically significant in the reduced model since P-value 0.094 is greater than the 0.05 significance level. The graph below is included as a visual aid to allow the reader to see that there is not a relationship between an index of juvenile survival (TNS/FMWT_1) and X2. If there had been a strong negative effect of X2 on juvenile survival then the graph would have been expected to show a pronounced negative slope. Instead the graph shows no trend in juvenile survival as X2 increases.



Point 6.



Year	Fall X2 year-1	S= FMWT year-1 (= FMWT_1)	FMWT year (= FMWT_0)	ln(FMWT_0/FMWT_1)	Population growth rate adjusted for density-dependence
1987	78.67	212	280	0.28	0.77
1988	90.09	280	174	-0.48	0.18
1989	90.58	174	366	0.74	1.15
1990	91.06	366	364	-0.01	0.85
1991	89.45	364	689	0.64	1.49
1992	90.00	689	156	-1.49	0.13
1993	87.57	156	1078	1.93	2.30
1994	82.06	1078	102	-2.36	0.16
1995	86.14	102	899	2.18	2.41
1996	74.00	899	127	-1.96	0.15
1997	78.05	127	303	0.87	1.17
1998	81.70	303	420	0.33	1.04
1999	68.74	420	864	0.72	1.70
2000	83.44	864	756	-0.13	1.89
2001	85.00	756	603	-0.23	1.54
2002	83.66	603	139	-1.47	-0.06
2003	84.68	139	210	0.41	0.74
2004	83.65	210	74	-1.04	-0.55
2005	82.61	74	27	-1.01	-0.84
2006	82.17	27	41	0.42	0.48
2007	82.52	41	28	-0.38	-0.29

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.634
R Square	0.402
Adjusted R Square	0.335
Standard Error	0.953
Observations	21.000

ln(FMWT/FMWT-1)=a+b(Fall X2)+cS

ANOVA

	df	*SS*	*MS*	*F*
Regression	2.000	10.985	5.493	6.046
Residual	18.000	16.353	0.908	
Total	20.000	27.338		

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	0.249	3.269	0.076	0.940
Fall X2 year-1	0.006	0.038	0.165	0.870
FMWT year-1	-0.002	0.001	-3.418	0.003

The analysis was made by first applying a logarithmic transformation to the Ricker model to obtain equation (3.33) in Quinn and Deriso (1999), which is then treated as a multiple linear regression equation. The equation applied is shown in the table above. The density-dependent term is statistically significant (P-value = 0.003 is below the 0.05 level). Fall X2 is not statistically significant (that is, P-value 0.870 is above the significance level of 0.05).

Population growth rate is defined as the logarithm of the ratio (R/S) (also defined as relative population growth rate, Owen-Smith (2007, p. 29), which is written as *ln*(R/S). Adding to *ln*(R/S) the estimated density-dependent term in a Ricker model (say c*S) one obtains the quantity “population growth rate adjusted for density-dependence.”

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UNITED STATES DISTRICT COURT

EASTERN DISTRICT OF CALIFORNIA

THE DELTA SMELT CASES, SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. SALAZAR, *et al.* (Case No. 1:09-cv-407) STATE WATER CONTRACTORS v. SALAZAR, *et al.* (Case No. 1:09-cv-422) COALITION FOR A SUSTAINABLE DELTA, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-480) METROPOLITAN WATER DISTRICT v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-631) STEWART & JASPER ORCHARDS, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-892)	1:09-cv-407 OWW GSA 1:09-cv-422 OWW GSA 1:09-cv-631 OWW GSA 1:09-cv-892 OWW GSA PARTIALLY CONSOLIDATED WITH: 1:09-cv-480 OWW GSA **REPLY DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF MOTION FOR INTERIM RELIEF/PRELIMINARY INJUNCTION** Date: January 20, 2010 Time: 9:00 a.m. Ctrm: 3 Judge: Hon. Oliver W. Wanger

I, Dr. Richard B. Deriso, declare:

I. INTRODUCTION 1

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A. The Studies Cited by Defendants Do Not Support the Conclusion That Entrainment Affects the Population Growth Rate 2

1. Manly and Chotkowski (2006) 2

2. Interagency Ecological Program's 2007 Synthesis Report on the Pelagic Organism Decline 4

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B. There Are No Significant "Episodic" Effects From Entrainment 11

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I. INTRODUCTION

1. I have reviewed the Federal Defendants' Opposition to Plaintiffs' Motion for Interim Relief/Preliminary Injunction, Docket #469 ("Fed. Def. Opp."), the Declaration of Cay Collette Goude in support thereof, Docket #470 ("Goude Decl."), and the Defendant-Intervenors' Opposition to Plaintiffs' Motion for Interim Relief/Preliminary Injunction, Docket #473 ("Def. Int. Opp."), filed on December 29, 2009. I am also aware of other declarations filed later by Defendants in this case, including the Declaration of Ken B. Newman, Docket #484. My understanding is that those subsequent declarations were not filed in opposition to the Motion for Interim Relief/Preliminary Injunction. Therefore, in this reply declaration for the motion, my comments herein are addressed solely to the Opposition briefs and the Goude Declaration.

II. ENTRAINMENT DOES NOT AFFECT THE DELTA SMELT POPULATION GROWTH RATE

2. In my previous declarations, I used standard principles of quantitative fish population dynamics to explain that salvage and Old and Middle River ("OMR") flows do not have a statistically significant effect on population growth rate. This conclusion applies to both winter OMR flows and spring OMR flows.

3. Federal Defendants' criticisms of my methodology are inaccurate. They are based on mischaracterizations of both my work and several studies cited in the 2008 Biological Opinion ("BiOp"). Defendants misuse and misquote these studies in an attempt to find support for the flawed conclusion in the BiOp that certain salvage and OMR flows are likely to jeopardize the continued existence of the delta smelt. Defendants do not point to any quantitative statistical analysis that would support those conclusions. A review of the studies reveals that they do not provide support for Defendants' position. Further, they do not negate my prior work showing that salvage and OMR flows do not have a statistically significant effect on population growth rate.

A. The Studies Cited by Defendants Do Not Support the Conclusion That Entrainment Affects the Population Growth Rate

4. On page 18 of the Federal Defendants' Opposition, several studies are cited for the proposition that there are "statistically significant" effects to the smelt population from entrainment. Fed. Def. Opp. at 18:2-28. These studies are:

- Manly and Chotkowski (2006)
- The Interagency Ecological Program's 2007 Synthesis Report
- Kimmerer (2008)
- Rose (2000)

A review of those studies shows that they have been misrepresented by Federal Defendants.

1. Manly and Chotkowski (2006)

5. Defendants make the false assertion that Manly and Chotkowski (2006) "found a statistically significant relationship between exports and smelt abundance as measured by Fall Midwater Trawl ("FMWT") catches." Fed. Def. Opp. at 18:2-4; *see also* Def. Int. Opp. at 28:11-

14. Manly and Chotkowski drew no such conclusion. Indeed, Dr. Manly in his declaration stated flatly that the above-quoted statement "is incorrect." *See* Docket #489 at 2:19-3:28. Manly and Chotkowski were not testing for the statistical significance of exports, or any other hydrology variable, on abundance. Rather, their 2006 study is a methods paper. In it, the authors attempted to improve the ability to detect when regime changes have occurred. They define "regime change" as a change in the functional relationship between estimated abundance and the underlying model. *See* Docket #489 at 3:9-10 ("the focus of the article was not about the reasons for the recent decline in delta smelt numbers"). Defendants mischaracterize how exports are used in the paper. Exports are not used as a single variable, tested for significance. Rather, exports are incorporated into the models as one part of a multi-part variable used as a measure of gross hydrology.

6. In the paper's first application, the measure of hydrology is a quadratic polynomial of a gross hydrology variable defined as average daily flow for the Sacramento and San Joaquin Rivers minus flow from other Delta rivers from January to September each year. The paper finds that expected values in the first regime change analysis for models with and without variables for gross hydrology are very similar after 1980. *See* Administrative Record ("AR") at 019681. In the paper's second application, the authors also add a quadratic polynomial of gross hydrology as a variable. Unlike the first application, they do not discuss whether the expected values for models with and without variables for gross hydrology look similar. However, a review of the models in the study, and particularly Figure 4, shows that they are similar. *See* AR at 019683.

7. In his declaration, Dr. Manly himself explained the results of the 2006 study as follows: "gross hydrology did not appear to have an effect on delta smelt subsequent abundance. Instead, in this and other work I did preceding this 2006 article, predictions of delta smelt abundances from the models used were almost the same whether hydrological variables, including exports, were in the models or not." Docket #489 at 3:25-28.

8. At bottom, the paper does not provide any statistical analysis to determine whether exports themselves are statistically significant. Defendants' reliance on this methods paper to

somehow support their conclusions about the significance of export effects on abundance is misplaced.

2. Interagency Ecological Program's 2007 Synthesis Report on the Pelagic Organism Decline

9. Defendants next refer to the Interagency Ecological Program's 2007 Synthesis Report on the Pelagic Organism Decline ("IEP (2007)"), by asserting:

> Moreover, the Interagency Ecological Program's 2007 Synthesis Report on the Pelagic Organism Decline Team stated that ". . . entrainment of adults and larvae (top-down effects) are particularly important to the delta smelt population . . . ."

Fed. Def. Opp. at 18:4-7. The use of ellipses by the Defendants is rather disturbing. Without the use of ellipses, the report actually states:

> *We hypothesize that* entrainment of adults and larvae (top-down effects) are particularly important to the delta smelt population . . . .

AR at 0016957 (emphasis added). Defendants appear to have excerpted the quote to state a hypothesis as a conclusion. A hypothesis is commonly defined as "a *proposed* explanation for an observable phenomenon" that is to be tested—a hypothesis is not a scientifically established result. *See, e.g.*, Wikipedia, http://en.wikipedia.org. To the extent the Federal Defendants' Opposition uses the report as support for the flow restrictions in the BiOp, that use of nothing more than a "hypothesis" is misplaced.[1]

[1] The misuse of a hypothesis for ecological purposes was specifically addressed in the published journal piece, Elner, R.W. and R.L. Vadas, Sr., *Inference in Ecology: the Sea Urchin Phenomenon in the Northwestern Atlantic*, The American Naturalist, Vol. 136., No. 1 (July 1990). The authors explained: "there appears a need for more rigor in conducting and interpreting ecological research. We contend that, because of the lack of rigor and guidelines, the tendency to rely on 'weak' inference and 'common sense' is pervasive, resulting in a propensity to cling uncritically to 'pet' concepts rather than to test multiple hypotheses (Chamberlin 1897). Such a soft approach has promoted circular reasoning, aided in the development of paradigms, and retarded ecological discovery." *Id.* at 108. That circular reasoning is evident, for example, by FWS's reliance on the Kimmerer (2008) paper—Kimmerer simply assumed a relationship between OMR flows and salvage, but then FWS uses Kimmerer as a basis for justifying the imposition of flow restrictions to protect the smelt.

3. Kimmerer (2008)

10. Defendants next refer to Kimmerer's 2008 study. *See* Fed. Def. Opp. at 18:8-20:15; *see also* Def. Int. Opp. at 28:8-11, 14-17. This study requires some explanation.

11. In Kimmerer's paper, he created estimates of entrainment of delta smelt in order "to place these losses in a population context." AR at 018854. The estimates were generated and then compared to population abundance (using survey results from the corresponding year) to come up with a proportion of the population lost to entrainment.

12. In order to develop his entrainment estimates, Kimmerer developed equations that include OMR flows as a variable—that is to say, his estimates build in a correlation between OMR flows and entrainment. Kimmerer's study did not set out to test whether such a correlation exists (or, more importantly, whether OMR flows impact the population from one year to the next). Thus, a critical element that should frame any discussion of Kimmerer (2008) is that he *assumed* a relationship between OMR flows and abundance, which is stated plainly in the study itself: "Despite the lack of evidence for population-level effects, a strong influence of the south Delta export facilities on populations of estuarine and anadromous fish has been *assumed* for several reasons." *See* AR at 018855 (emphasis added). Defendants ignore this basic assumption that underlies Kimmerer's work, and make a series of mischaracterizations that are revealed through a close review of the 2008 study.

13. Kimmerer repeatedly explains that the influence of export pumping on the population is an assumption. For his analysis of adult smelt, he explains: "Principal assumptions were: . . . Entrainment is proportional to the combined southward flow in Old and Middle River flows." *See* AR at 018865. The same applies for juveniles: "Principal assumptions for calculating daily loss for each survey were: . . . The relevant flow toward the export facilities is the southward flow in Old and Middle Rivers." AR at 018868. Thus, for both adults and larvae/juveniles, Kimmerer assumes a proportional relationship.

14. The analysis of the data contained in my declaration, however, tests this assumption, and can be found at Docket #401 at 24-26, Docket #455 at 7. The data shows that the assumption Kimmerer made is not statistically supported for flows below -6,100 cfs with

respect to adults, and is not statistically supported at all for larvae/juveniles. Docket #401 at 24-25; Docket #455 at 7. Indeed, Kimmerer even seems to recognize this himself—one of the three "reasons" Kimmerer gives for making this assumption has more to do with practical considerations than scientific analysis. He states that "manipulations of flow patterns in the Delta provide the only apparent tool for managing some fish populations such as delta smelt." AR at 018855.

15. After making these key assumptions, Kimmerer then estimates the effects of pumping on delta smelt "mechanistically" instead of through a correlative analysis—i.e., he has assumed the existence of a mechanism, such as negative OMR flows causing entrainment, then he calculates the loss by deriving an equation based on that mechanism.

16. Relying on Kimmerer's estimates for determining where to set flows, as FWS has in the BiOp, is fraught with problems because the estimates are derived using the assumption that flows and entrainment are correlated. Kimmerer acknowledges this for larvae and juvenile estimates when he states, "The variation in annual loss was related to flow conditions (Pl = -0.4 + (1.7 $\pm$ 0.6) Qsd, r^2 = 0.79, 9 df), but this relationship is *tautological*, since *Old and Middle River flow was used explicitly in the calculations*." AR at 018875-018876 (emphasis added). Here again, Kimmerer bases his study on a foundational assumption—one that is ignored by Defendants.

17. This also creates problems with any X2 analysis, as Kimmerer states, "The relationship of proportional loss to Old and Middle River flow (by assumption) and inflow and export flow (Figure 16) guarantees a relationship with X2." AR at 018876.

18. The Defendants (and to some extent Kimmerer) then suggest that the inability to show an effect on the population growth rate is due to variability in the population between summer and fall, and that the effects are likely masked by this high variation. These arguments about the effect of pumping being masked, however, are belied by the results Kimmerer reaches regarding food supply. He observes that, "The summer-fall index of survival varied over a range of 50-fold, and was significantly related to summer zooplankton biomass in the low-salinity zone (Figure 17). This may indicate food-limited survival." AR at 018877. If high variability was

masking the effects of the pumps, one would expect it to mask any other significant sources of impacts to the population. However, because Kimmerer is able to detect a significant relationship between adult abundance and zooplankton (smelt survival and zooplankton biomass are strongly correlated), the argument about masked effects by other causes—such as pumping—is circumspect. If high variability does not mask significant sources of impacts such as food availability, one could certainly conclude that the variability is only masking insignificant sources. Thus, if pumping were significant, it would be reflected by an analysis of the data just as food availability is.

19. Kimmerer (2008) should also be read in light of its final conclusions—ones that succumb to practical considerations: "Management of delta smelt should incorporate any opportunities that arise to improve habitat or food supply and to reduce any negative impacts of predation or toxic contamination. However, current evidence does not provide a clear path toward improving the status of the delta smelt using these factors. Manipulating export flow (and, to some extent, inflow) is the only means to influence the abundance of delta smelt that is both feasible and supported by the current body of evidence, even though export effects are relatively small." AR at 018878. This "practical" conclusion is best informed by Kimmerer's repeated acknowledgments that "no effect of export flow on subsequent midwater trawl abundance is evident," and that "[i]f this variability is uncorrelated with entrainment losses, then these losses will contribute little to the variability in fall abundance index," and that there is a "lack of evidence for population-level effects." AR at 018855, 018878.

20. Defendants also seem to imply that Kimmerer has determined that the analysis of correlative relationships is improper. *See* Fed. Def. Opp. at 18:8-15, 18-21. Defendants fail to acknowledge, however, that Kimmerer conducted a correlative analysis in his own 2008 study. *See* AR at 018877 (Figure 17). Not only does he conduct this analysis for survival and biomass, but he finds that they are "significantly related." *Id*. Thus, Kimmerer (2008) does not support Defendants' sweeping assertion that conducting a correlative analysis is not the best available science; Kimmerer in fact performs one himself.

21. Defendants also ignore other key findings in Kimmerer's study that undermine the BiOp's reliance on this work to justify flow restrictions. For estimates of adult delta smelt losses, Kimmerer qualifies that the highest value of 50 percent "may have been biased upward." AR at 018854. Overall, he concludes that the effect of losses on population abundance "was obscured" by "subsequent 50-fold variability in survival from summer to fall"—meaning, ultimately, that any effect is an undetected assumption. *See* AR at 018854.

22. In sum, Defendants improperly rely on Kimmerer (2008) to try and support their position that entrainment effects are significant and that exports should be controlled to reduce losses. Defendants misuse Kimmerer by failing to recognize the several assumptions and tautologies that are built into the study and expressly acknowledged by Kimmerer. Kimmerer's assumptions cannot be used to counter the quantitative statistical analysis I conducted in my previous declarations, because I used the actual data, rather than making assumptions about significance.

4. Rose (2000)

23. Defendants next misuse Rose (2000), characterizing Rose's work as using "several individual-based models to show how multiple interacting stressors can result in fish population declines that would not be readily discernible using linear regression-based approaches." Fed. Def. Opp. at 18:28-19:2. Rose, however, does not show that conventional fisheries population dynamics models—such as the Ricker model—would fail to detect the impacts of stressors on population declines. In fact, Rose argues that the time series regression that he applied in one of his examples is appropriate. AR at 020016. That is the only example where such a regression was done in Rose (2000), and the results are not a basis for rejecting time series analysis as a useful tool for fisheries population analysis.[2]

24. Defendants then characterize the content of my previous declarations as a "narrow statistical approach" in comparison to Rose. *See* Fed. Def. Opp. at 19:2. In my previous declarations, I applied a nonlinear Ricker stock-recruitment model with multiple candidate

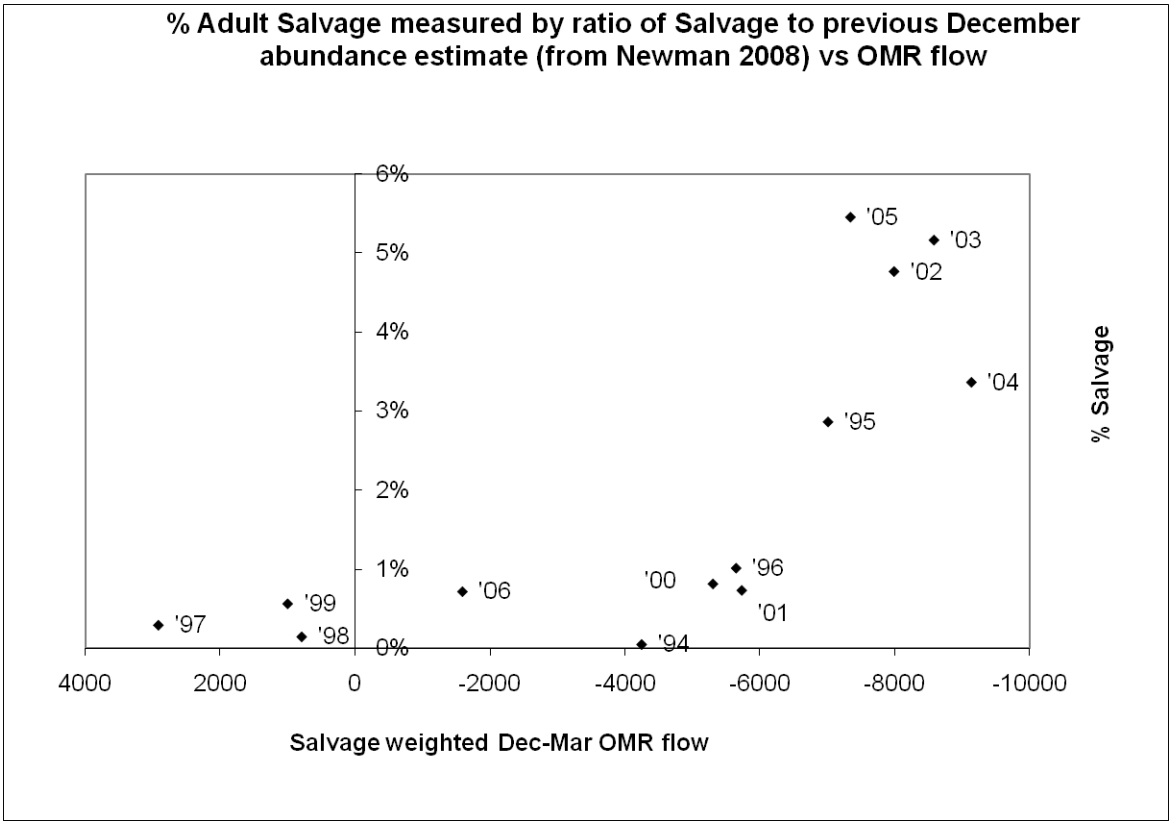
[2] It should also be noted that Rose (2000) was not a study involving delta smelt.

variables. It is a mischaracterization to call this a straightforward correlative analysis. This type of analysis is commonly used, and should have been employed by FWS in developing the BiOp, as I explained in my prior declarations. In fact, the approaches and methodologies I presented are similar to what Rose used in his subsequent 2008 study. It should also be noted that I have been working with others to conduct a full life stage model which is preliminarily confirming the results I reached in my previous work—namely, that OMR flows do not have a statistically significant effect on population growth rate.

5. *Family Farm Alliance v. Salazar*

25. There is a fifth piece referenced in the Opposition papers, even though the paper was put together after the BiOp was issued. This paper is titled an "Independent Peer Review" of the BiOp conducted by PBS&J as part of the U.S. Fish and Wildlife Service's ("FWS") response to the Family Farm Alliance's Information Quality Act Appeal ("FFA Peer Review"), which is cited in the Fed. Def. Opp. at 19 n. 7 and the Def. Int. Opp. at 20 n. 13, 21:5-9, 30:15-22.

26. Table 1 in the FFA Peer Review contains data for winter salvage, population estimates, and salvage as a percentage of total population for the years 1994-2006 (each year includes data from the prior months leading up to March, such that salvage from December 1993 to March 1994 is listed as 1994). I plotted a curve comparing the latter variable—salvage as a percentage of total population—against salvage weighted December-March average OMR flow (taken from Figure B-13 in the BiOp at 348 (AR at 000363)).



27. The following data, with the abundance estimates from the FFA Peer Review, was used for the above figure:

Year	Salvage weighted average Dec-Mar OMR	Salvage	December abundance estimate (in 1000s) (from Newman 2008)	% adult salvage
1994	-4242.011186	447	866	0.05%
1995	-7006.202454	2608	91	2.87%
1996	-5642.794285	5634	554	1.02%
1997	2909.257659	1828	618	0.30%
1998	784.0915287	1027	691	0.15%
1999	992.4281581	2074	366	0.57%
2000	-5298.918733	11493	1405	0.82%
2001	-5726.576409	8003	1087	0.74%
2002	-7984.825346	6865	144	4.77%
2003	-8576.809158	14305	277	5.16%
2004	-9132.953117	8148	242	3.37%
2005	-7338.401388	2018	37	5.45%
2006	-1599.518519	324	45	0.72%

28. As can be seen in the figure above, all of the higher salvage percentages occurred with average OMR flows more negative than -7,000 cfs. Thus, even the data used by the FFA Peer Review supports the same conclusions I reached previously, namely, that OMR flows do not have a significant effect on adult smelt until flows become very negative.

29. I also wish to note that there appear to be many other problems in the FFA Peer Review, but I have limited my discussion here to only what was raised in the Oppositions. *See* Fed. Def. Opp. at 19 n. 7; Def. Int. Opp. at 20 n. 13, 21:5-9, 30:15-22.

B. There Are No Significant "Episodic" Effects From Entrainment

30. Beyond the general misuse of the studies and pieces described above, the Oppositions also suggest that the lack of effects to the population growth rate somehow overlooks "episodic" effects. *See* Fed. Def. Opp. at 18:18-22; Def. Int. Opp. at 28:19-27. For this "episodic" theory, Defendants again cite to Kimmerer (2008). Defendants rely on this theory as support for the reasonable and prudent alternatives ("RPAs") using the erroneous assumption that even though year over year trends show no impact to population, the sporadic occurrence of a large salvage count in a given year could still somehow harm the population and therefore justify the OMR flow restrictions. *See* Fed. Def. Opp. at 18:18-19:7.

31. The problem with Defendants' assertion is that even an "episodic" effect should be reflected in the population growth rate if it has somehow impacted the population. If the episodes of large entrainment were significant, they would appear as such in a statistical model testing the significance of entrainment. However, because the data shows that OMR flows do not have such an effect, the "episodic" argument is not sustainable.

32. An explanation of Kimmerer's analysis of larvae/juveniles is illustrative. The annual percent loss of larvae/juveniles is presented in Figure 15 of Kimmerer's paper, which I digitized and then plotted against March-June average OMR flow. As would be expected given his assumptions, a significant correlation exists between Kimmerer's estimates of entrainment percent loss and negative OMR flow (R = -0.83, P-value = 0.005). Kimmerer's assumptions drive the entire estimation procedure for the spring—for example, at flows of approximately -4,800 cfs, more than 25 percent of the population is estimated by Kimmerer to be lost. Thus, an

"episodic" event translates merely into episodes of highly negative OMR flows in the spring. But as I have shown in my application of the Ricker model, such events do not have a significant detectable impact on the population growth rate.

C. The Lack of a Spatial Distribution Variable Is Not a Valid Critique

33. Defendants' criticisms of the absence of a spatial distribution variable in my previous declarations also have no merit. *See* Fed. Def. Opp. at 20:5-15. Like the argument about "episodic" effects, one would still expect to see an impact to the population growth rate regardless of whether spatial distribution was an important consideration. And as I have explained, there is no such effect.

34. This spatial distribution argument is also a red herring in that Defendants ignore the analysis in the BiOp itself at Figure B-13, which does not account for spatial distribution. With regard to adults, the BiOp, in its formulation of RPA Component 1, develops flow guidelines that are apparently based on the relationship of salvage to OMR flows. *See* BiOp at 348, 350 (Figures B-13 and B-14) (AR at 000363, 000365). Those graphs and any results based on those graphs do not explicitly consider the spatial distribution of delta smelt. Rather, those graphs offer the single "explanatory" variable of salvage weighted December-March average OMR flow. In my previous work, I used the same data from Figures B-13 and B-14 in the BiOp to show that the cumulative salvage index and OMR flows do not have a statistically significant effect on the population growth rate.

35. With regard to larvae and juveniles, the BiOp's discussion is based largely on Kimmerer (2008). On this point, it is worth noting that Kimmerer estimates entrainment losses of larvae/juveniles with a method that takes into account explicitly the spatial distribution of delta smelt as measured by the spring 20-mm survey. His equations use nearfield density terms, incorporating the number of fish caught specifically in the south Delta. AR at 018866-018868.

36. As I described previously, Kimmerer's estimation method also relies heavily on the assumption that the larvae/juvenile population percent daily loss is itself proportional to OMR flow if the flow is negative. *See* AR at 018868 (Equation 19). That assumption has such a strong influence on the overall results that Kimmerer writes, "this relationship is tautological, since Old

and Middle River flow was used explicitly in the calculations." AR at 018875-018876. With such a dominant assumption, additional information on spatial distribution of delta smelt is simply not needed. All that was required was to evaluate spring salvage versus OMR flow, which did not provide statistical support for the assumption that entrainment losses (as measured by an index of salvage rates (salvage/20-mm survey index)) have a statistically significant relationship to OMR flow. Moreover, spring OMR flow did not have detectable impacts on the population growth rate. The spatial distribution argument, therefore, is again confounded by the lack of population growth rate effects.

D. The Data Used in My Prior Declarations Was Based on FWS's Freedom of Information Act Response and Analyses Set Forth in My Technical Appendices

37. Defendants' criticism that my prior submissions were "unaccompanied by the raw data purportedly relied upon" is inaccurate. *See* Fed. Def. Opp. at 19:11-13. I displayed tables of the data I used and the analyses I conducted in the technical appendices to my declarations. *See* Docket #401, Appx. 1-1 to 1-18; Docket #455, Appx. 1-1 to 1-2. Much of that was data provided by FWS in its response to a Freedom of Information Act request from the Metropolitan Water District of Southern California and in the BiOp itself. *See* Docket #455 at 1:26-2:1.

E. My Prior Declarations Addressed Squarely Johnson's "Break-point"

38. Defendants make the false assertion that "Plaintiffs' extra-record evidence fails to address the statistical analyses that were actually provided in the BO" in reference to the BiOp's "regression analysis to determine the break-point in the OMR-salvage relationship." *See* Def. Int. Opp. at 30:11-13; *see also* Fed. Def. Opp. at 12:19-22, Goude Decl. at 12:15-19. To the contrary, the work conducted in my prior declarations explains the analysis in the BiOp and specifically the OMR-salvage relationship and "break-point." I evaluated FWS's analysis of that relationship as depicted in Figures B-13 and B-14 of the BiOp. *See* Docket #401 at 16:9-21:10. I explained that the figures were incorrect in that they relied on raw salvage as the quantity to be predicted by OMR flow. As I further explained in my declaration, the appropriate quantity to be predicted by OMR flow is the cumulative salvage index (i.e., an index of the proportion of the population removed by salvage). Using the cumulative salvage index showed that the appropriate break

point is -6,100 cfs, rather than the -1,162 cfs in the erroneously constructed Figure B-14 (Johnson's analysis). Suggesting that I somehow failed to address the statistical analyses, and specifically the "break point" regression analysis, in the BiOp is simply wrong.

III. THE ADULT AND JUVENILE INCIDENTAL TAKE STATEMENT IS NOT STATISTICALLY VALID

39. Finally, Defendants claim that the use of an unrepresentative data point in calculating the Incidental Take Statement ("ITS")—even they refer to it as "imperfect data" (Fed. Def. Opp. at 30:23)—was nevertheless appropriate. The errors FWS committed in calculating the ITS fall outside the range of scientific reasonableness, and they are not entitled to deference. As I described in my prior declarations, to calculate the ITS for adults, FWS averaged the salvage rate from three years—2006, 2007, 2008—which it chose because the salvage data from those years "best approximate[d] expected salvage under the RPA Component 1." BiOp at 386 (AR at 000401). Yet the model upon which RPA Component 1 is based (Figure B-13) excludes the year 2007 because salvage was unrepresentatively low that year due to low turbidity. BiOp at 348 (AR at 000363). For FWS to make use of the 2007 salvage data in calculating the ITS because it "best approximate[d] expected salvage under the RPA Component 1," after earlier deciding that the exact same salvage data could not be used to calculate flow levels for RPA Component 1, was per se unreasonable and cannot be entitled to deference. FWS failed to adhere to the basic scientific principle that data should be used consistently throughout all parts of an analysis. *See* Docket #401 at 6:17-20.

40. Similarly, FWS included an unrepresentative year in the juvenile ITS. To calculate the juvenile ITS, FWS followed the same methodology that it used for adults in choosing representative salvage years—2005-2008. The year 2006 had extremely low salvage due to *positive* average OMR flows. FWS included 2006 despite its earlier assertion that "positive OMR is usually associated with no, or very low, entrainment"—making years with positive OMR flow unrepresentative for purposes of calculating the ITS. *See* BiOp at 163 (AR at 000178).

I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on January 26, 2010 at Del Mar, California.

DR. RICHARD B. DERISO

CERTIFICATE OF SERVICE

I hereby certify that on January 26, 2010, I electronically filed the foregoing with the Court by using the Court's CM/ECF system.

Participants in the case who are registered CM/ECF users will be served by the Court's CM/ECF system.

I further certify that the court-appointed experts are not registered CM/ECF users. I have emailed the foregoing document to the following:

REPLY DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF MOTION FOR INTERIM RELIEF/PRELIMINARY INJUNCTION

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I declare under penalty of perjury under the laws of the State of California the foregoing is true and correct and that this declaration was executed on January 26, 2010, at San Francisco, California.

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UNITED STATES DISTRICT COURT

EASTERN DISTRICT OF CALIFORNIA

THE DELTA SMELT CASES, SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. SALAZAR, *et al.* (Case No. 1:09-cv-407) STATE WATER CONTRACTORS v. SALAZAR, *et al.* (Case No. 1:09-cv-422) COALITION FOR A SUSTAINABLE DELTA, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-480) METROPOLITAN WATER DISTRICT v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-631) STEWART & JASPER ORCHARDS, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-892)	1:09-cv-407 OWW GSA 1:09-cv-422 OWW GSA 1:09-cv-631 OWW GSA 1:09-cv-892 OWW GSA PARTIALLY CONSOLIDATED WITH: 1:09-cv-480 OWW GSA **DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF PLAINTIFFS' MOTION FOR INJUNCTIVE RELIEF** Ctrm: 3 Judge: Hon. Oliver W. Wanger

I, Dr. Richard B. Deriso declare:

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IV. AN INCIDENTAL TAKE LIMIT (ITL) FOR ADULT DELTA SMELT SHOULD BE SET AT THE 80% UPPER CONFIDENCE INTERVAL UNDER LOG-NORMAL DISTRIBUTION 9

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I. INTRODUCTION

1. In my previous declarations, dated July 31, 2009, November 13, 2009, December 7, 2009, January 26, 2010, and March 1, 2010, I set forth my comprehensive explanation of the analysis that the United States Fish and Wildlife Service ("FWS") performed in its 2008 Delta Smelt Biological Opinion ("BiOp"), including its clear, fundamental errors in its analysis of OMR flows, Fall X2, and the incidental take levels. See Doc. 167; Doc. 401; Doc. 455; Doc. 508; Doc. 605.

2. In this declaration, I specifically focus on management measures for Old and Middle River ("OMR") flows that will reduce entrainment events during the smelt adult period from what has historically occurred. I have also developed revised incidental take limit ("ITL") calculations, based on these management measures, for the adult period. I also propose a revised ITL for juvenile smelt.

3. The management measures proposed are based on turbidity. The data reveals that turbidity measurements can be a powerful "trigger" for setting OMR flows to avoid entrainment. In other words, turbidity is used as the controlling factor for setting OMR flows because of the

strong relationship between turbidity and entrainment. I have developed a mathematical model (a formula) and fitted it to normalized delta smelt salvage (salvage/previous FMWT) for the period December through March 1988-2009 as a function of turbidity at Clifton Court and OMR flow.

4. In this declaration, I have provided results for a three-day model, in which the previous three-day average turbidity at Clifton Court is used to estimate the daily OMR flow limit for the current day that would provide substantial reduction in daily normalized salvage of adult delta smelt.

5. In developing the three-day model, predicted normalized salvage was highly statistically significantly correlated with observed normalized salvage (p-value < 0.00001). This means that the model performed very well in using prior data on turbidity and OMR flow to predict the historic entrainment events that occurred over the December through March 1988-2009 record. Because the model can predict entrainment events, it can be used in managing the projects to avoid or reduce such events in the future.

6. At the end of this declaration, I also introduce and explain the life cycle model that I developed with Dr. Mark Maunder, which shows that entrainment is not a significant factor impacting the smelt population growth rate, but that several other environmental factors are.

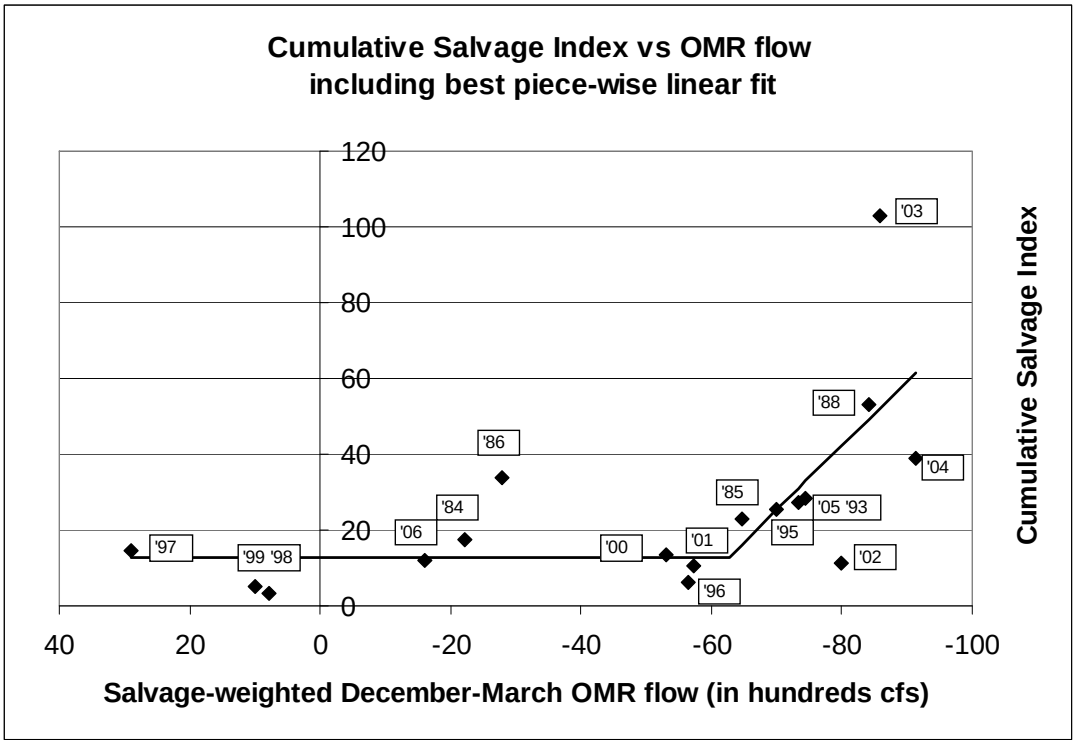
7. My qualifications and experience are set forth in my previous declaration, Doc. #401 ¶¶ 5-10 and Exhibits A and B thereto.

II. TURBIDITY AND OMR FLOW DATA CAN BE USED TO CONSTRUCT A NORMALIZED SALVAGE MODEL PREDICTING WINTER SALVAGE RATES

8. In developing the turbidity approach model for adult salvage, I modified the analysis from my previous declaration (Doc. 455 ¶ 16) that was presented as a prediction of normalized winter salvage (salvage/previous FMWT). That original analysis graphed adult normalized salvage (y-axis) against salvage-weighted average OMR flow for the December through March time period (x-axis). The graph consisted of a flat line for flows less negative than an OMR salvage-weighted average of -6,100 cfs, as shown below in Figure 1. Therefore, those results suggested that salvage rates, when graphed only against OMR flows, do not increase

until flows are more negative than -6,100 cfs; the OMR flow where salvage rates begin to increase is defined as the OMR trigger.

Figure 1.



9. That prior analysis only looked at two variables—OMR flow and normalized salvage.[1] The advanced approach that I have developed for this declaration allows the OMR trigger to be dependent on an additional variable—turbidity. A model utilizing OMR limits based on the level of turbidity predicts normalized salvage far better than a simple piece-wise model, such as Figure 1, which did not depend on turbidity. The model used in this analysis can be written as:

$$S = a + (1 - p)[b(OMR - OMR^*)]$$

$$p = 1, OMR > OMR^*; \; p = 0, otherwise.$$

$$OMR^* = a' + (1 - p')[b'(TUR - TUR^*)]$$

$$p' = 1, TUR > TUR^*; \; p' = 0, otherwise.$$

[1] I purposefully limited my prior declaration to reviewing the approach contained in the Smelt Biological Opinion.

where OMR^* is the OMR trigger, TUR^* is the turbidity trigger, (a, a', b, b') are constants, OMR is daily OMR flow, TUR is previous 3-day average Clifton Court turbidity, and *S* is the daily normalized salvage (specific parameter estimates used for the model set forth in this declaration are referenced below in ¶11, Table 2).

10. Parameters for the normalized salvage model were estimated by non-linear least-squares minimization of the difference between predicted and observed normalized salvage for each daily time period within the months of December through March of 1988-2009, provided that the data were available to the minimum specifications detailed below.[2]

III. THE MANAGEMENT OF OMR FLOWS BETWEEN DECEMBER AND MARCH TO PROTECT PRE-SPAWNING ADULT DELA SMELT SHOULD UTILIZE THREE-DAY AVERAGE TURBIDITY DATA AND CORRESPONDING OMR FLOW LIMITS

11. The results of the model show that predicted normalized salvage is highly correlated with observed normalized salvage using the previous three-day average turbidity (p-value < 0.00001). As a comparison, I also fitted a linear regression model of turbidity and OMR flow to normalized salvage, and the results of that model were also statistically significant. However, the three-day analysis that I ran performed measurably better. Comparing the three-day model to the linear model, the three-day model's Akaike Information Criteria (AIC) score was more that 400 lower than the linear fit.[3] Paraphrasing the seminal text on AIC scores by Burnham and Anderson,[4] models that are 10 or more AIC units above the best model have essentially no

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[2] Data on OMR flows, turbidity, and salvage were obtained by the Metropolitan Water District of Southern California ("MWD") from a Freedom of Information Act ("FOIA") request to FWS and from certain websites. The FOIA request was submitted by MWD to FWS on August 10, 2009. FWS responded to the FOIA request by providing data through March 2006 in an excel worksheet titled "Take Analysis.xls" (see Chart 3). Data for dates after March 2006 were obtained from the following websites: turbidity (http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=CLC); OMR (http://waterdata.usgs.gov/ca/nwis/sw; salvage: http://www.usbr.gov/mp/cvo/fishrpt.html); salvage (http://www.usbr.gov/mp/cvo/fishrpt.html). The FMWT data used to normalize salvage was obtained from http://www.dfg.ca.gov/delta/data/fmwt/charts.asp. Two days of Middle River flows were estimated using a correlation between Old and Middle River flows. See data points for 12/21 and 12/22 of the 2008 OMR data set at http://waterdata.usgs.gov/ca/nwis/sw.

[3] AIC represents a measure of the goodness of fit of an estimated statistical model and is utilized as a tool for model selection. To interpret AIC scores, one compares the AIC values for a set of models fit to the same data set. The model with the lowest AIC score (in this case, the 3-day model) is the preferred model.

[4] Burnham, K. P. and Anderson, D.A. 2004. Multimodel inference, understanding AIC and BIC in model selection, Socio. Methods & Res. 33(2): 261-304.

support. Therefore, the linear model has essentially no support when compared to the three-day model I developed, as it is more than 400 units above the three-day model. In simplest terms, the three-day turbidity model that I have presented here is far superior to a linear regression model of turbidity. Table 1, below, demonstrates the AIC score results between the linear regression model and the three-day model version. Table 2 contains the parameter estimates used for the coefficients in the three-day model formula.

Table 1. AIC score comparison: fits to daily normalized salvage

Model	**Linear**	**Three-day model version**
Number of Parameters	4	6
Number of observations	1880	1880
RSS	234	186
ln(likelihood)	-5,128	-4,914
AIC	**10,263**	**9,840**
Difference in AIC		**- 423**

Table 2.

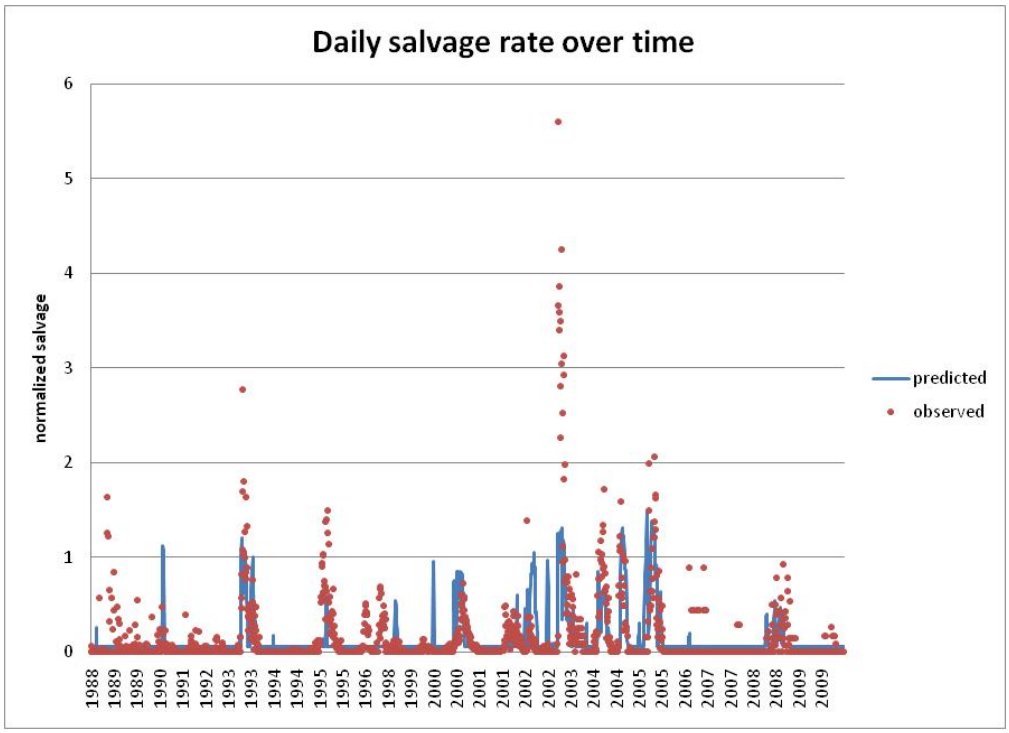
Coefficient	**Three-day average**
a	0.061
b	-0.00021
b'	402.21
TUR*	28.747
a'	-3590

12. Statistics fitting the three-day average turbidity and daily OMR flow in a multiple linear regression model to daily normalized salvage are calculated in Appendix 1. As seen in the tabled outputs, both turbidity and OMR flow are highly statistically significant covariates.

13. The huge improvement in AIC score (more than 600 units) by increasing model complexity (by adding the additional variable of turbidity and going non-linear) to the basic piece-wise approach described in paragraph 8 is statistically well-supported. Figure 2, below, plots both the actual observed daily normalized salvage of delta smelt for December-March 1988-2009, and also the normalized salvage that the three-day model would have predicted using the historic turbidity data. Predictions are based on the best fit of the model with prior three-day

average turbidity at Clifton Court and daily OMR flow to observed normalized salvage. As seen in Figure 2, the model predicts most of the days with increased normalized salvage (defined as salvage rate in the figure).

Figure 2.

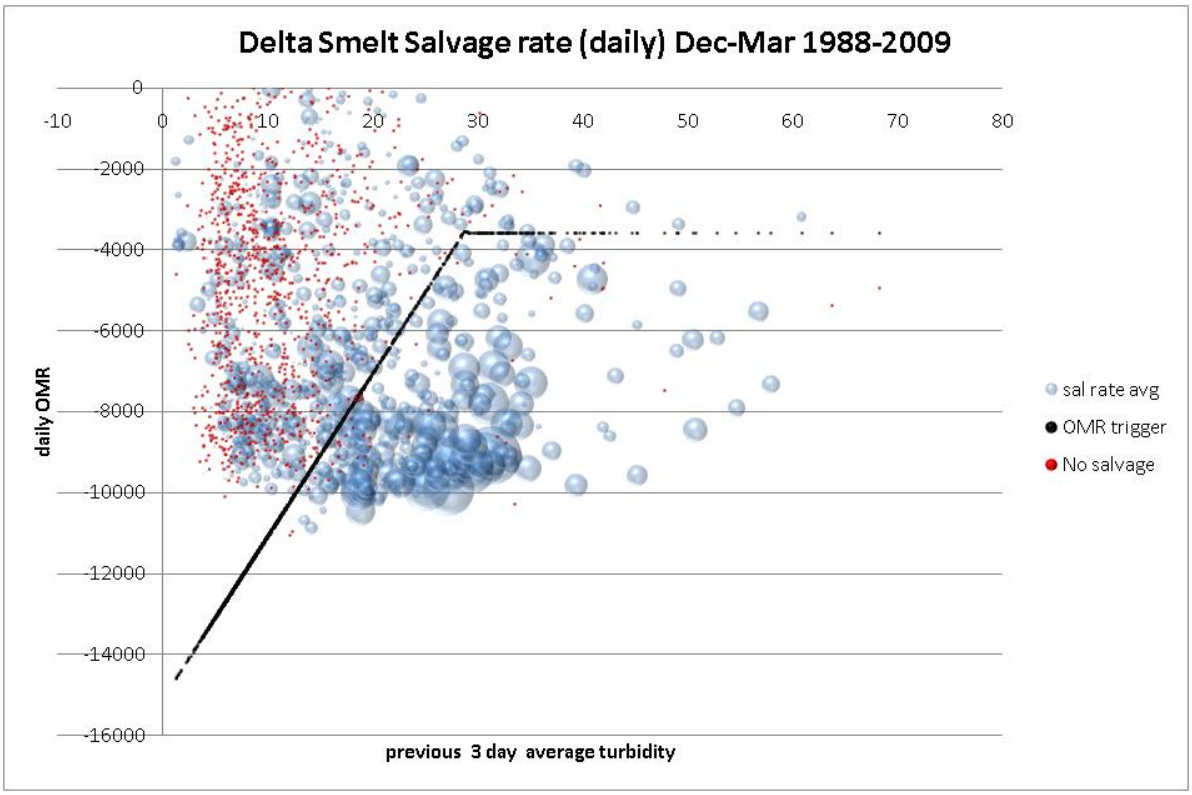


14. Figure 2 shows that the model using turbidity has a powerful ability to predict when salvage events will occur.

15. Figure 3, below, shows a bubble plot in which the OMR trigger is shown on the Y-axis as a function of prior three-day average turbidity on the X-axis, along with observed normalized salvage (the bubbles). Data is shown only if there are three previous days with turbidity estimates and it is restricted to days with negative daily OMR flow (for a total of 1880 days). The size of the bubbles is proportional to the amount of observed daily normalized salvage; the bigger the bubble, the larger the percentage of the population salvaged. As seen in Figure 3, most of the larger normalized salvage events (the larger bubbles) lie in the region that

the data suggests would be avoided by using the proposed OMR limits (i.e., the events in the region below and to the right of the OMR trigger would be avoided).

Figure 3.



16. Table 3, below, provides the specific numerical values of the proposed individual flow limits (based on the OMR trigger) for each unit of turbidity. The table also places the OMR flow limits in five-unit "bins." More specifically, a median OMR flow limit is shown for each five-unit range of turbidity levels greater than 15 and less than 30 (i.e., one flow limit is proposed for turbidity values of 16-20 and another for turbidity 21-25). These "bin" values are shown because it is my understanding they may be more operationally feasible than constantly changing flow limits with every single change in turbidity value. Limits are given for use with the previous three-day turbidity model, and the OMR flow limits were constrained at -9,000 for purposes of this table. While the OMR limit at turbidity levels of 15 and less would be more negative than -9000 cfs, this is based on an assumption that the projects would not be restricted in any other

way. I am informed, in fact, that there are a number of other limitations and practical restrictions that would necessarily limit OMR flows.[5] Thus, for purposes of Table 3, I constrained OMR limits to -9000 cfs for turbidity levels 1-15.

Table 3.

	Three-day turbidity model	
Bin size:	1-unit	5-unit
Turbidity	OMR limit	OMR limit
1-15	-9,000	-9,000
16	-8,717	-7,913
17	-8,315	
18	-7,913	
19	-7,510	
20	-7,108	
21	-6,706	-5,902
22	-6,304	
23	-5,902	
24	-5,499	
25	-5,097	
26	-4,695	-4,012
27	-4,293	
28	-3,891	
29	-3,590	
30+	-3,590	-3,590

17. The expected salvage rate corresponding to all OMR limits in Table 3 is 5.02 (i.e., the median salvage rate for the years 1988-2009 using the turbidity model). That is, we expect that about half of the time salvage rates will be above 5.02 if the daily flow controls are followed.

18. The three-day operational approach provides an approximate 58% reduction in adult normalized salvage when compared to the historical average for 1988-2009 (December through March). Stated another way, assuming the projects had been run historically according to

[5] I also understand that there are instances where turbidity may be isolated in Clifton Court Forebay, and that in these particular conditions smelt may not arrive at the project pumps. For instance, current conditions at Clifton Court Forebay show high levels of turbidity but no salvage has been occurring. My understanding is that the proposed interim remedy order submitted by Plaintiffs deals with this circumstance by providing for specific turbidity levels to be met at Prisoner's Point, Victoria Canal, and Holland Cut, in keeping with the use of those three monitoring stations in the Biological Opinion.

this proposal, the model predicts that the normalized salvage would have been 58% lower than what did occur. For the purpose of comparison, this reduction is better than the estimated 57% reduction in normalized salvage that would have occurred if flows had been continually limited to a flat -3,000 cfs (based on the average normalized salvage for daily OMR flows between -2,500 cfs and -3,500 cfs during December through March of 1988-2009). Therefore, this proposal provides for much more water, but also substantially reduces and avoids entrainment.

19. Based on my analyses, the data persuasively demonstrates that daily OMR flow limits are accurately calculated by utilizing three-day turbidity data and corresponding OMR flow limits.

IV. AN INCIDENTAL TAKE LIMIT (ITL) FOR ADULT DELTA SMELT SHOULD BE SET AT THE 80% UPPER CONFIDENCE INTERVAL UNDER LOG-NORMAL DISTRIBUTION

20. An incidental take limit is an amount of salvage that is greater than what is expected under normal operations and which requires consultation with the agency when and if it is exceeded. This paper proposes a method for calculating a proper ITL for adult smelt. In developing the proposed limit, I followed a two-part approach: i) estimate what the expected salvage rate would be in the future, and ii) find an amount above the expected rate that could serve as a trigger for further consultation.

21. My adult Delta smelt ITL calculations are based on the assumption that future daily flow controls are limited to those specified in my OMR recommendations in Section III above. The estimated salvage rates that would have occurred by following the daily flow controls were calculated for a subset of days[6] in the December through March time frame for the years 1988-2009. The average of the daily estimated salvage rates for a given water year were then multiplied by the total number of days in the time period December-March to obtain a season total salvage rate. Those rates are listed below in Table 4.

[6] The subset consisted of days in which the previous three days had turbidity measurements and the current day had negative OMR flow.

Table 4. Winter adult salvage rates obtained by following daily flow controls and that are used in the calculation of confidence intervals

Year	Estimated Salvage Rate
1988	1.67
1989	12.28
1990	3.67
1991	3.40
1992	2.37
1993	9.21
1994	0.54
1995	23.46
1996	8.98
1997	25.20
1998	3.30
1999	2.44
2000	8.13
2001	9.50
2002	4.90
2003	14.30
2004	8.84
2005	4.93
2006	9.30
2007	0.93
2008	9.00
2009	1.10
Median Salvage Rate	5.02

22. With respect to this proposal, the median salvage rate for those 22 years using the turbidity model is 5.02. Given that 5.02 is the median, we expect that about half of the time salvage rates will be above 5.02 if the daily flow controls are followed.[7] This median is lower than the median in the smelt BiOp (i.e., more protective) because the three-day turbidity model is more effective at reducing and avoiding entrainment.

23. In order to determine a reasonable incidental take limit based on salvage rates, I propose using an upper one-sided confidence interval of 80% as an acceptable level of risk. I

[7] The ITL in the 2008 smelt BiOp is calculated using the average cumulative salvage index (BiOp at 287). That means that consultation will be triggered about 50% of the time, or roughly every other year.

understand that in discussions over acceptable levels of risk for various species, NMFS has relied upon 80%, and that this is a conservative number that favors the species relative to higher confidence intervals.[8] Using an 80% confidence level results in a salvage rate of 12.4. Correspondingly, the likelihood that the salvage rate for any given future year will exceed 12.4 is about 20% of the time provided the daily flow limit proposal is implemented.

24. That leads to the following proposed ITL:

Adult Incidental Take Limit = 12.4 * Prior year's FMWT index

To calculate the percentage of the population entrained at this take limit, I conservatively relied on the same estimates from a publication that was relied on in the BiOp, namely the Kimmerer 2008 study. I took the ratio of Kimmerer's estimates of annual adult entrainment to the annual normalized salvage for the years 1995-2006 (following the date range he used in his study) and calculated the median of those annual ratios. That median ratio is the coefficient used to scale the salvage rates into a percentage entrainment of the adult population.[9] When this estimate is performed, the proposed take limit effectively equates to 4.80% of the smelt population.

25. The above analysis demonstrates that based on my estimates of what expected salvage rates will be in the future, an ITL for adult Delta smelt should be set at the 80% upper confidence interval under log-normal distribution. Using an 80% upper confidence level will result in monitoring take levels and initiating reconsultation action in instances where take exceeds a modest 4.80%.

V. AN INCIDENTAL TAKE LIMIT (ITL) FOR JUVENILE DELTA SMELT SHOULD BE SET AT THE 80% UPPER CONFIDENCE INTERVAL UNDER LOG-NORMAL DISTRIBUTION

26. In my previous declaration (Doc. #455, ¶¶ 23-29), I presented several analyses that demonstrate there is no statistically significant relationship between OMR flows and juvenile Delta smelt salvage rates (juvenile salvage/20-mm survey index). The graph from page 13 of my

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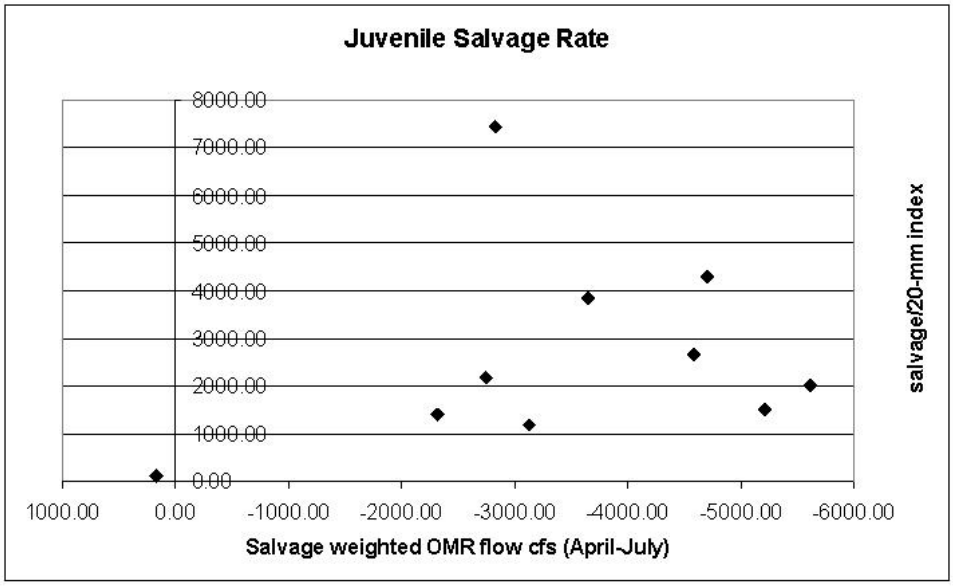
[8] Pers. comm. with Dr. Kenneth Burnham.

[9] While the underlying assumption of Kimmerer that entrainment is proportional to OMR flow remains unsupported for all the reasons set forth in my prior declarations (see Doc. 401 ¶¶ 71-76; Doc. 455 ¶16; Doc. 508 ¶¶ 10-22), Kimmerer's proportionality co-efficient, which contains expanded salvage data that includes other sources of mortality in Clifton Court Forebay, provides one way to translate the ITL into a percentage of the population.

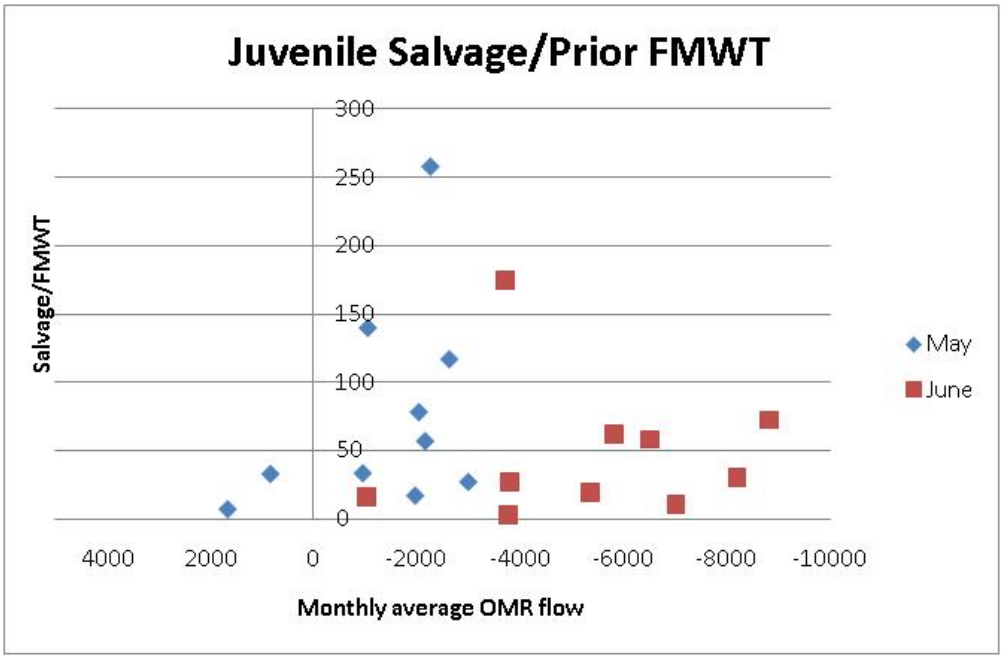
previous declaration is reproduced below as Figure 4 to show visually that there is no relationship between juvenile salvage rates and OMR flows.

Figure 4.



27. In Figure 5, below, I plotted monthly data for May and June, the two months where most salvage occurs. The y-axis is monthly salvage/previous FMWT (which is the juvenile salvage rate). OMR flows are given on the x-axis. As seen in Figure 5, there is no visual relationship between the monthly juvenile salvage rate and OMR.

Figure 5.



28. To calculate the Juvenile Salvage Index (JSI), I followed the approach discussed in the BiOp (page 389), which defined the Juvenile Salvage Index as:

Monthly Juvenile Salvage Index (JSI) = cumulative seasonal salvage ≥ 20 mm by month end divided by current WY FMWT Index

29. I constructed Table 5, below, to show the average JSI for years in which OMR flow in the spring was negative. Given that the data do not evidence a relationship between negative OMR flow and juvenile salvage rates, salvage rates located near the average value would be expected in the future, irrespective of any OMR flow controls that may be implemented. This leads to a proposed ITL calculation of:

Juvenile Incidental Take Limit = (upper 80% confidence interval JSI)* Prior year's FMWT index

Table 5. NOTE: The zero value for April 2005 was not used in the log-normal calculation.

Year	prior FMWT		Juvenile Salvage/prior FMWT				
			April	May	June	July	Apr-Jul
1995	102						
1996	899		0.12	33.81	10.50	0.16	44.60
1997	127		9.13	258.49	62.02	4.25	333.88
1998	303						
1999	420		1.02	140.31	174.69	47.20	363.21
2000	864		2.02	57.29	58.44	1.72	119.47
2001	756		0.69	17.42	3.20	0.01	21.31
2002	603		0.62	78.54	19.78	0.04	98.98
2003	139		3.63	117.33	72.63	0.09	193.68
2004	210		1.31	27.38	30.44	0.09	59.21
2005	74		0.00	7.39	15.96	0.00	23.35
2006	27						
2007	41		0.59	10.44	36.80	17.27	65.10
2008	28		0.14	33.21	27.04	0.50	60.89
2009	23		0.00	18.39	13.65	0.00	32.04
	Average		1.61	66.67	43.76	5.94	117.98
	stand dev		2.59	73.97	46.74	13.89	118.10
	JSI		1.61	68.27	112.03	117.98	117.98
			JSI for corresponding upper confidence interval of 80% under log-normal distribution				
	JSI Upper confidence interval of 80%		3.1	109.1	175.4	184.9	184.9
2011	Juvenile Incidental take limit based on 80% confidence interval and previous FMWT		89	3,164	5,087	5,362	5,362

30. All of the above analyses demonstrate that based on my estimates of what expected salvage rate will be in the future, and the calculation of a trigger for further consultation above that expected rate, ITLs for adult and juvenile Delta smelt should be set at the 80% upper confidence interval under log-normal distribution.

VI. LIFE CYCLE MODELING SHOWS THAT ENTRAINMENT IS NOT A SIGNIFICANT FACTOR IMPACTING THE SMELT POPULATION GROWTH RATE BUT THAT SEVERAL ENVIRONMENTAL FACTORS ARE

31. The foregoing discussion is designed to monitor and address entrainment of Delta smelt. The important issue remains over what is causing, and what may remedy, the population decline of the species. As both I and others have previously explained, a life cycle model is the common tool used for this type of population analysis.

32. Dr. Mark Maunder and I have used available data on the Delta smelt and developed a life cycle model; the results of the model provide important information that may be used for future management of the species. Specifically, the model indicates that food abundance, temperature, predator abundance, and density dependence are the most critical factors impacting the Delta smelt population—not entrainment from water export operations. See Exhibit A. (Mark Maunder and Richard Deriso, "A state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt" (Dec. 27, 2010) (under review) (hereinafter "Maunder and Deriso")).

33. The model Dr. Maunder and I developed represents the different life cycle stages of the species (adult, larval, juvenile) and how the population abundance changes between stages. It models survival from one life stage to the next, as well as the stock-recruit relationship between adults and larvae. It allows multiple factors or covariates (including factors relating to environmental conditions and mortality rates based on entrainment) to influence the survival and stock-recruit relationships. Each factor represents a hypothesis about what conditions or events make a difference for smelt survival and recruitment.

34. The survey data upon which the model is based spans the period 1972 to 2006. It comes from Manly 2010[10] and Nations 2007,[11] and includes: the 20mm trawl survey (1995 to 2006) [larvae]; the Summer tow net survey (1972 to 2006) [juveniles]; and the Fall mid-water trawl survey (1972 to 2006, but no data for years 1974 and 1979) [pre-adults]. The Spring Kodiak trawl survey was not used because it was only recently initiated and does not go back enough years. The environmental data examined with the model were taken from Manly 2010, with the exception of secchi depth data, which Dr. Manly provided in a personal communication. All survey and environmental data is set forth in Tables S1 and S2 in Maunder and Deriso. Maunder and Deriso at pps. 69-74. Entrainment rates (i.e., normalized salvage) were

[10] Manly, B.F.J. 2010. Initial analyses of delta smelt abundance changes from Fall to Summer, Summer to Fall, and Fall to Fall. Western EcoSystems Technology, Inc. 2003 Central Avenue, Cheyenne, Wyoming, 82001, unpublished report.

[11] Nations, C. 2007. Variance in Abundance of Delta Smelt from 20 mm Surveys. Western EcoSystems Technology, Inc. 2003 Central Avenue, Cheyenne, Wyoming, 82001, unpublished report.

conservatively estimated by fitting regression models based on OMR flow to the entrainment estimates in Kimmerer (2008).[12]

35. We fit the model to the data, and used a model selection procedure to determine which factors (covariates) are important for explaining changes in smelt survival and recruitment. That procedure involved using Akaike Information Criterion (AIC) to rank models that included different mixes of co-variates based on the strength of evidence in the data for including each co-variate in the better models.

36. Through this winnowing process, testing multiple co-variates and multiple combinations of co-variates, we determined that of all the factors we tested, food abundance, temperature, predator abundance, and density dependence are the most important factors controlling the population dynamics of delta smelt. Maunder & Deriso at p. 31. Survival is positively related to food abundance and negatively related to temperature and predator abundance. Maunder & Deriso at p. 31. The model selection procedure did not select entrainment in the larval-juvenile life stage as an important factor affecting the population growth rate. While we found some support for adult entrainment as a factor affecting the population growth rate, it was not one of the main factors and the coefficient was unrealistically high and highly negatively correlated with the coefficient for water clarity. Maunder & Deriso at p. 31. Impact analysis further showed that if adult entrainment has any effect on smelt population growth rate, it is minor. Maunder & Deriso at p. 24.

37. These results indicate that the use of the turbidity-based approach for limiting increases in the adult smelt entrainment rate, described above, is a conservative approach that errs on the side of protecting the species. More generally, the data shows that imposing restrictions on the projects to avoid entrainment is not a sensible approach to improving the smelt population and that, instead, efforts should be focused on addressing environmental conditions affecting the species, such as its food supply.

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[12] Kimmerer, W.J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary Watershed Science 6(2): 1-27.

I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on January 28, 2011 at Del Mar, California.

DR. RICHARD B. DERISO

Appendix

Appendix

Appendix 1. Statistics Fitting the Average Turbidity and Daily OMR Flow in a Multiple Linear Regression Model to Daily Normalized Salvage

Statistics fitting the three-day average turbidity and daily OMR flow in a multiple linear regression model to daily normalized salvage are shown below in Table 1. As seen in the tabled outputs, both turbidity and OMR flow are highly statistically significant covariates.

Table 1. SUMMARY OUTPUT for linear regression of daily normalized salvage

Regression Statistics				
Multiple R	0.44		multiple linear regression	
R Square	0.20		for normalized salvage	
Adjusted R Square	0.20			
Standard Error	0.35			
Observations	1880			
ANOVA				
	df	*SS*	*MS*	*F*
Regression	2	57.16	28.58	229.33
Residual	1877	233.91	0.12	
Total	1879	291.07		
	Coefficients	*Standard Error*	*t Stat*	***P-value***
Intercept	-2.74E-01	2.25E-02	-1.22E+01	**6.78E-33**
turbidity 3-day average	1.69E-02	9.48E-04	1.78E+01	**6.87E-66**
Daily OMR	-3.29E-05	3.05E-06	-1.08E+01	**2.54E-26**

Appendix 2. Details on the Calculation of Upper Confidence Intervals

The one-sided confidence interval I calculated for the proposed ITL is based on a t-test statistic for testing whether the means of two distributions are equal. The test statistic is based on the assumptions that the two distributions have equal variances and samples are of different sample size. In this application, one of the distributions represents salvage rate in a future year for a single year. The other distributions are historical samples. The test statistic is:

$$t = \frac{(x_2 - \bar{x}_1)}{S\sqrt{1 + \frac{1}{N}}}$$

In the above calculation, the sample mean of the historical data is $\bar{x}_1$, the standard deviation of the historical data is *S*, the single sample from a future year is x_2, and sample size is *N*. The t-statistic has N-1 degrees of freedom. The application in this paper uses the equation above for a given *t* value to solve for the corresponding x_2. For example, with N=9 and upper one-sided confidence interval probability of 0.95, the *t* value is 1.86. Substitute 1.86 in the equation above along with estimates of the sample mean and standard deviation then solve for the x_2 which would be the salvage rate at the upper one-sided 95% confidence interval. For the log-normal distribution the data were log-transformed to calculated confidence intervals which were then back transformed.

CERTIFICATE OF SERVICE

I hereby certify that on January 28, 2011, I electronically filed the foregoing with the Court by using the Court's CM/ECF system.

Participants in the case who are registered CM/ECF users will be served by the Court's CM/ECF system.

I further certify that the court-appointed experts are not registered CM/ECF users. I have emailed the foregoing document to the following:

DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF PLAINTIFFS' MOTION FOR INJUNCTIVE RELIEF

SERVICE LIST

Dr. André Punt University of Washington School of Aquatic and Fishery Sciences P.O. Box 355020 Seattle, WA 98195 *ThePuntFam@aol.com*	Dr. Thomas Quinn University of Washington School of Aquatic and Fishery Sciences P.O. Box 355020 Seattle, WA 98195 *TQuinn@U.Washington.edu*

I declare under penalty of perjury under the laws of the State of California the foregoing is true and correct and that this declaration was executed on January 28, 2011, at San Francisco, California.

/s/ Jennifer P. Doctor
Jennifer P. Doctor
JDoctor@mofo.com

Exhibit A

Exhibit A

A state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt

Mark N. Maunder[a,c] and Richard B. Deriso[b,d]

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[b]Scripps Institution of Oceanography, La Jolla, CA 92093-0203, USA

[c]Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive

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Abstract

Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of populations. To provide appropriate management advice, the data should be used to determine which factors are important and what life stages they impact. It is also important to consider density dependence because it can modify the impact of some factors. We develop a state-space multi-stage life cycle model that allows for density dependence and environmental factors to impact different life stages. Models are ranked using a two-covariate-at-a-time stepwise procedure based on AICc model averaging to reduce the possibility of excluding factors that are detectable in combination, but not alone. Impact analysis is used to evaluate the impact of factors on the population. The framework is illustrated by application to delta smelt, a threatened species that is potentially impacted by multiple anthropogenic factors. Our results indicate that density dependence and a few key factors impact the delta smelt population. Temperature, prey, and predators dominated the factors supported by the data and operated on different life stages. The included factors explain the recent declines in delta smelt abundance and may provide insight into the cause of the pelagic species decline in the San Francisco Estuary.

Key words: delta smelt; density dependence; model selection; population dynamics; state-space model;

Introduction

Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of natural populations. To provide appropriate management advice, the available data should be used to determine which factors are important and what life stages they impact. It is also important to consider density dependent processes because they can modify the impact of some factors and the strength of density dependence can vary among life stages. Management can then better target limited resources to actions that are most effective. Unfortunately, the relationships among potential factors, the life stages that they influence, and density dependence are often difficult to piece together through standard correlation or linear regression analyses.

Life cycle models are an essential tool in evaluating factors influencing populations of management concern (Buckland et al. 2007). They can evaluate multiple factors that simultaneously influence different stages in the presence of density dependence. They also link the population dynamics from one time period to the next propagating the information and uncertainty. This link allows information relating to one life stage (i.e., abundance estimates) to inform processes influencing other life stages and is particularly important when data is not available for all life stages for all time periods. The life cycle model should be fit to the available data to estimate the model parameters, including parameters that represent density dependence, and determine the data based evidence of the different factors that are thought to influence the population dynamics. Finally, the model should be used to direct research or provide management advice.

Deriso et al. (2008) present a framework for evaluating alternative factors influencing the dynamics of a population. It extends earlier work by Maunder and

Watters (2003), Maunder and Deriso (2003), and Maunder (2004) and is similar to approaches taken by others (e.g., Besbeas et al. 2002; Clark and Bjornstad 2004; Newman et al. 2006). The Deriso et al. framework involves several components. First, the factors to be considered are identified. Second, the population dynamics model is developed to include these factors and then fitted to the data. Third, hypothesis tests are performed to determine which factors are important. Finally, in order to provide management advice, the impact of the factors on quantities of management interest, are assessed. They illustrate their framework using an age-structured fisheries stock assessment model fit to multiple data sets. Their application did not allow for density dependence in the population dynamics, except through the effect of density on the temporal variation in which ages are available to the fishery.

Inclusion of density dependence is important in evaluating the impacts on populations. Without density dependence, modeled populations can increase exponentially. This is unrealistic and can also cause computational or convergence problems in fitting population dynamics models to data. Density dependence can also moderate the effects of covariates. This is important because factors affecting density independent survival may be much less influential in the presence of density dependence compared to factors that affect carrying capacity (e.g., habitat). It is also important to correctly identify the timing of when the factors influence the population with respect to the timing of density dependence processes and available data. The approach also provides a framework for amalgamating the two paradigms of investigating population regulation outlined by Krebs (2002); the density paradigm and the mechanistic paradigm.

Here we develop a life cycle model that allows for density dependence at multiple life stages and allows for factors to impact different life stages. We apply the framework of Deriso et al. (2008) where the first component also includes identifying the life stages that are impacted by each factor and where density dependence occurs. We illustrate the framework by applying it to Delta smelt. Delta smelt is an ideal candidate to illustrate the modeling approach because there are several long-term abundance time series for different life stages and a range of hypothesized factors influencing its survival for which covariate data is available. Life cycle models have been recommended to evaluate the factors effecting delta smelt (Bennett 2005; Mac Nally et al. 2010; Thomson et al. 2010).

Delta smelt is of particular management concern due to declines in abundance and the myriad of anthropogenic factors that could be causing the decline. Delta smelt is endemic to the San Francisco Estuary, which has multiple stressors including habitat modification, sewage outflow, farm runoff, and water diversions, to name just a few. Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993. Several other pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Recent studies have investigated the factors hypothesized to have caused the declines at both the species and ecosystem level, but the results were not conclusive (Mac Nally et al. 2010; Thomson et al. 2010).

Materials and Methods

Model

The model is stage based with consecutive stages being related through a function that incorporates density dependence. For simplicity and to be consistent with the predominant dynamics of delta smelt, we assume an annual life cycle. However, it is straightforward to extend the model to a multiple year life cycle or to stages that cover multiple years (i.e., adding age structure; e.g., Rivot et al. 2004; Newman and Lindley 2006). Within a year the number of individuals in each stage is a function of the numbers in the previous stage. The number of individuals in the first stage is a function of the numbers in the last stage in the previous year (i.e., the stock-recruitment relationship), except for the numbers in the first stage in the first year, which is estimated as a model parameter. The functions describing the transition from one stage to the next are modeled using covariates. A state space model (Newman 1998; Buckland et al. 2004; Buckland et al. 2007) is used to allow for annual variability in the equation describing the transition from one life stage to the next. Traditionally, state space models describe demographic variability (e.g., using a binomial probability distribution to represent the number of individuals surviving based on a given survival rate; e.g., Dupont 1983; Besbeas et al. 2002) however environmental variability generally overwhelms demographic variability (Buckland et al. 2007) so we model the process variability (e.g., Rivot et al. 2004; Newman and Lindley 2006) using a lognormal probability distribution (Maunder and Deriso 2003). Our approach differs from modeling the log abundance and assuming additive normal process variability (e.g., Quinn and Deriso 1999, page 103) and the population dynamics function models the expected value rather than the median. The difference in the expectation will simply be a scaling factor ($\exp\left[-0.5\sigma^2\right]$) unless the variance of the process variability changes with time.

(1) $N_{t,s} \sim \text{Lognormal}\left(f\left(N_{t,s-1}\right), \sigma_{s-1}^2\right) \qquad s > 1$

(2) $N_{t,1} \sim \text{Lognormal}\left(f\left(N_{t-1,nstages}\right), \sigma_{nstages}^2\right)$

Where *t* is time, *s* is stage, *nstages* is the number of stages in the model, and σ_s is the standard deviation of the variation not explained by the model (process variability) in the transition from stage *s* to the next stage.

The three parameter Deriso-Schnute stock-recruitment model (Deriso 1980; Schnute 1985) is used to model the transition from one stage to the next. The Deriso-Schnute model is a flexible stock-recruitment curve in which the third parameter (γ) can be set to represent the Beverton-Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) stock-recruitment models (Quinn and Deriso 1999, page 95).

(3) $f(N) = aN(1 - b\gamma N)^{\frac{1}{\gamma}}$

where the parameter *a* can be interpreted as the number of recruits per spawner at low spawner abundance or the survival fraction at low abundance levels. In cases for which only the relative abundance at each stage can be modeled (as in the delta smelt example), *a* also contains a scaling factor from one survey to the next. The parameter *b* determines how the number of recruits per spawner or the survival rate decreases with abundance. Constraints can be applied to the parameters to keep the relationship realistic: $a \geq 0$, b ≥

0. The additional constraint $a \leq 1$ can be applied when the relationship is used to describe survival and the consecutive stages are modeled in the same units.

Covariates are implemented to influence the abundance either before density dependence [$g(N,x)$] or after density dependence [$h(x)$]. Although, when no density dependence is present the two methods are identical.

(4) $$f(N) = ag(N,x)(1 - b\gamma g(N,x))^{\frac{1}{\gamma}} h(x)$$

(5) $$g(N,x) = N \exp\left[\sum \lambda x\right]$$

(6) $$h(x) = \exp\left[\sum \beta x\right]$$

Where λ and β are the coefficients of the covariate (x) for before and after density dependence, respectively, and are estimated as model parameters.

For survival it might be important to keep the impact of the environmental factors within the range 0 to 1 and the logistic transformation can be used, e.g.,

(7) $$ag(N,x) = N \frac{\exp\left[a' + \sum \lambda x\right]}{1 + \exp\left[a' + \sum \lambda x\right]}$$

Where the parameter a' defines the base level of survival (i.e. $a = \frac{\exp[a']}{1 + \exp[a']}$) and replaces a of the density dependence function.

If the covariate values are all positive, the negative exponential can be used, e.g.,

(8) $$g(N,x) = N\exp\left[-\sum \lambda x\right] \qquad \lambda \geq 0 \quad x \geq 0$$

A combination of the above three options may be appropriate depending on the application.

The importance of the placement of the covariates (i.e., before or after density dependence) relates to both the timing of density dependence and the timing of the surveys, which provide information on abundance. Covariates could be applied to the other model parameters. For example, covariates that are thought to be related to the carrying capacity (e.g., habitat) could be used to model *b*.

The model is fit to indices of abundance ($I_{t,s}$). The abundance indices are assumed to be normally distributed, but other sampling distributions could be assumed if appropriate. Typically, if the index of abundance is a relative index and not an estimate of the absolute abundance, the model is fit to the index by scaling the model's estimate of abundance using a proportionality constant (*q*, often called the catchability coefficient) (Maunder and Starr 2003).

(9) $$I_{t,s} \sim \text{Normal}\left(qN_{t,s}, v_{t,s}^2\right)$$

However, the scaling factor is completely confounded with the *a* parameter of the Deriso-Schnute model and therefore the population is modeled in terms of relative abundance that is related to the scale of the abundance indices for each life stage and only makes

sense in terms of total abundance if the abundance indices are also in terms of total abundance. Therefore, the proportionality constant (q) should be set to one. Other data could also be used in the analysis if appropriate (e.g., information on survival from mark-recapture studies; Besbeas et al. 2002; Maunder 2004).

Model parameters to estimate

The model parameters estimated include the initial abundance of the first stage $N_{1,1}$, the parameters of the stock-recruitment model for each stage $\mathbf{a}, \mathbf{b}, \boldsymbol{\gamma}$, the coefficients of the covariates $\boldsymbol{\lambda}, \boldsymbol{\beta}$, the standard deviation of the process variability for each stage $\boldsymbol{\sigma}$, and the standard deviation of the observation error (used in defining the likelihood function) for each index of abundance $\mathbf{v}$. The observation error standard deviation, $\mathbf{v}$, is often fixed based on the survey design or restricted so that there is not a parameter to estimate for each survey and time period (e.g. Maunder and Starr 2003). The state space model can be implemented by treating the process variability as random effect parameters (de Valpine 2002). The likelihood function that is optimized is calculated by integrating over these parameters (Skaug 2002; Maunder and Deriso 2003). Therefore, they are not treated as parameters to estimate. However, realizations of the random effects can be estimated by using empirical Bayes methods (Skaug and Fournier 2006) so that the unexplained process variation can be visualized. The estimated parameters of the model are:

Parameters = $\{N_{1,1}, \mathbf{a}, \mathbf{b}, \boldsymbol{\gamma}, \boldsymbol{\lambda}, \boldsymbol{\beta}, \boldsymbol{\sigma}, \mathbf{v}\}$

Implementation in AD Model Builder

Dynamic models like the multistage life cycle model described here can be computationally burdensome if they are carried out in a state-space modeling framework (i.e., integrating over the state-space or equivalently the process variability) and efficient parameter estimation is needed if multiple hypotheses are being tested. Implementation is facilitated by the use of Markov chain Monte Carlo and related methods (Newman et al. 2009) and their use has increased in recent years (Lunn et al. 2009). In particular, authors have found a Bayesian framework convenient for implementation (Punt and Hilborn 1997). An alternative approach is to use the Laplace approximation to implement the integration (Skaug 2002). AD Model Builder (http://admb-project.org/) has an efficient implementation of the Laplace approximation using automatic differentiation (Skaug and Fournier 2006). The realizations of the random effects are estimated by using empirical Bayes methods adjusted for the uncertainty in the fixed effects (Skaug and Fournier 2006). ADMB was originally designed as a function minimizer and therefore likelihoods are implemented in terms of negative log-likelihoods and probability distributions are implemented in terms of negative log-probabilities. A more complete description of ADMB and its implementation of random effects can be found in Fournier et al. (in review).

The population is modeled using random effects to implement the state space model (de Valpine 2002)

(12) $$N_{t,s} = f\left(N_{t,s-1}\right)\exp\left[\sigma_{s-1}\varepsilon_{t,s-1} - 0.5\sigma_{s-1}^2\right]$$

(13) $$N_{t,1} = f\left(N_{t-1,nstages}\right)\exp\left[\sigma_{nstages}\varepsilon_{t-1,nstages} - 0.5\sigma_{nstages}^2\right]$$

(14) $$\varepsilon_{t,s} \sim N(0,1)$$

A penalty is added to the objective function to implement the random effects,

(15) $$\sum_{t,s}\varepsilon_{t,s}^2 \ .$$

The negative log-likelihood function for the abundance indices ignoring constants is

(16) $$-\ln[L] = \sum_{t,s}\ln[\nu_{t,s}] + \frac{\left(I_{t,s} - qN_{t,s}\right)^2}{2\nu_{t,s}^2}$$

Model selection

Model selection (Hilborn and Mangel 1997) can be used to determine if the data supports density dependence for a particular stage or the factors that impact the population dynamics. In our analysis different models are represented by different values of the model parameters. The relationship between one stage and the next is density independent if $b = 0$. Therefore, a test for density dependence tests if $b = 0$. When $b = 0$, γ has no influence on the results and unless a hypothesis about γ is made (i.e., Beverton-Holt, $\gamma = -1$ or Ricker, $\gamma \to 0$), testing between density independence and density dependence requires the estimation of two additional parameters (b, γ). A factor

has no influence on the model when its coefficient ($\lambda, \boldsymbol{\beta}$) is fixed at zero. Therefore, testing a factor requires estimating one parameter for each factor tested. There are a variety of methods available for model selection and hypothesis testing, each with their own set of issues (e.g., Burnham and Anderson 1998; Hobbs and Hilborn 2006). Given these issues, we rely on Akaike information criteria adjusted for sample size (AICc) and AICc weights to rank models and provide an idea of the strength of evidence in the data about an a priori set of alternative hypotheses (factors) but they are not used as strict hypothesis tests (Andersen et al. 2000; Hobbs and Hilborn 2006).

The AIC is useful for ranking alternative hypotheses when multiple covariates and density dependence assumptions are being considered. The AICc (Burnham and Anderson 2002), is given by

$$AIC_c = -2\ln L + 2K + \frac{2K(K+1)}{n-K-1} \tag{10}$$

where L is the likelihood function evaluated at its maximum, K is the number of parameters, and n is the number of observations. A better model fit is one with a smaller AICc score.

AIC weights are often used to provide a measure of the relative support for a model and to conduct model averaging (Hobbs and Hilborn 2006). AIC weights are essentially the rescaled likelihood penalized by the number of parameters, which is considered the likelihood for the model (Anderson et al. 2000).

$$w_i = \frac{\exp[-0.5\Delta_i]}{\sum_j \exp[-0.5\Delta_j]} \quad (11)$$

Where Δ is the difference in the AICc score from the minimum AICc score.

The correct modeling of observation and process variability (error) is important for hypothesis testing. If process variability is not modeled, likelihood ratio and AIC based tests are biased towards incorrectly accepting covariates (Maunder and Watters 2003). Other tests, such as randomization tests, should be used if it is not possible to model the additional process variability (e.g., Deriso et al. 2008). Incorrect sampling distribution assumptions (e.g., assumed values for the variance) can influence the covariate selection process and the weighting given to each data set can change which covariates are chosen (Deriso et al 2007). If data based estimates of the variance are not available, estimating the variances as model parameters or using concentrated likelihoods is appropriate (Deriso et al. 2007). Missing covariate data need to be dealt with appropriately, such as by using the methods described in Gimenez et al. (2009) and Maunder and Deriso (2010).

Parameter estimation of population dynamics models generally requires iterative methods, which take longer than calculations based on algebraic solutions, and therefore limit the number of models that can be tested (Maunder at al. 2009). This is problematic when testing hypotheses because, arguably, all possible combinations of the covariates and density dependent possibilities should be evaluated. All possible combinations should be used because a covariate by itself may not significantly explain process variation, but in combination they do (Deriso et al. 2008) and some covariates may only

be significant if density dependence is taken into consideration. However, modeling of process variability, as we suggest, may minimize this possibility. In many cases, time and computational resource limitations may prevent testing all possible combinations and therefore we suggest the strategy described in Table 1.

We stop evaluating covariates when the lowest AICc model in the current iteration is at least 4 AICc units higher than the model with the lowest overall AICc (step 2e). The approach is based on a compromise between eliminating models for which *there is definite, strong, or very strong evidence that the model is not the K-L best model* ($4 \leq \Delta$)) and the fact that there is a maximum Δ when adding covariates to the lowest AICc model. We have chosen to carry out the selection process by using the sum of the AICc weights over all models that include the corresponding factor (step 2d). This selection process chooses factors that have high support in general, work in combination with other factors, and are therefore less likely to preclude additional factors in subsequent steps. This approach embraces the multiple hypothesis weight of evidence framework and is somewhat consistent with model averaging. We also remove models for which any of the estimated covariate coefficients are the incorrect sign as assumed a priori (step 2b). Modification of this procedure may be needed depending on the available computational resources, the number of covariates and model stages, and the relative difference in the weight of evidence among models.

Burnham and Anderson (2002) note that in general, there are situations where choosing to make inferences using a model other than the lowest AICc model can be justified (page 330) based on professional judgment, but only after the results of formal selection methods have been presented (page 334). For example, model parameterizations

that do not make sense biologically might be eliminated from consideration. Burnham and Anderson (2002) give an example (page 197) where a quadratic model is rejected because it could not produce the monotonic increasing dose response that was desired. Sometimes AICc will select a model that fits to quirks or noise in the data but does not provide a useful model. The selected best model is a type of estimate, and so like a parameter estimate it can sometimes be a poor estimate (Ken Burnham, Colorado State University, personal communication).

Parameter estimates from stock recruitment models in integrated assessments are often biased towards extremely strong density dependent survival (recruitment is independent of stock size) (Conn et al. 2010) and this is unrealistic for stocks that have obtained very low population sizes. We therefore identify values of the Deriso-Shnute stock-recruitment relationship (for the Beverton-Holt and Ricker special cases) *b* parameter that are realistic (see Appendix). We assume that recruitment (or the individuals surviving) can't be greater than 80% of that expected from the average population size when the population is at 5% of the average population size seen in the surveys during the period studied. Models with unrealistic density dependence are given zero weight in that step of the model selection prodecure (step 2b).

Impact analysis

To determine the impact of the different factors on the stock, we conducted analyses using values of the covariates modified to represent a desired (e.g. null) effect. Following Deriso et al. (2008) these analyses were conducted simultaneously within the

code of the original analyses so that the impact assessments shared all parameter values with the original analyses. This allowed estimation of uncertainty in the difference between the models with the covariate included and with the desired values of the covariate. The results are then compared for the quantities of interest, which may be a derived quantity other than the covariate's coefficients. For example, if a covariate is related to some form of mortality, the coefficient is set to zero to determine what the abundance would have been in the absence of that mortality (e.g., Wang et al. 2009).

Application to Delta smelt

The multi-stage lifecycle model is applied to delta smelt to illustrate the application of the model, covariate selection procedure, and impact analysis. Delta smelt effectively live for one year and one spawning season. Some adults do survive to spawn a second year, but the proportion is low (Bennett 2005) and we ignore them in this illustration of the modeling approach. The delta smelt life cycle is broken into three stages (Figure 1). The model stages are associated with the timing of the three main surveys, (1) 20mm trawl (20mm), (2) summer tow net (STN), and (3) fall mid-water tow (FMWT), and roughly correspond to the life stages larvae, juveniles, and adults, respectively. The reason for associating the model stages with the surveys is because the surveys are the only data used in the model and therefore information is only available on processes operating between the surveys. The population is modeled from 1972 to 2006 because these are the years for which data for most of the factors are available. The STN abundance index is available for the whole time period. The FMWT abundance index is available for the whole time period except for 1974 and 1979. The 20mm abundance

index is only available starting in 1995. Other survey data are available (e.g., the Spring Kodiak trawl survey), but they are not used in this analysis.

The FMWT and STN survey indices of abundance are the estimates taken from Manly (2010b) tables 2.1 and 2.2. The standard errors were calculated by bootstrap procedures (Manly, 2010a). The 20mm survey index was taken from Nations (2007). The index values and standard errors are given in the supplementary material. The results of the bootstrap analysis suggest that the abundance indices are normally distributed (Manly 2010a).

Two types of factors are used in the model (Table 2). The first are standard factors relating to environmental conditions. The second are mortality rates based on estimates of entrainment at the water pumps. The mortality rates are converted to the appropriate scale to use in the model. Let u represent the mortality fraction such that the survival fraction is $1-u=\exp[\beta x]$ and x will be used as a covariate in the model. Setting $\beta=1$ gives $x=\ln[1-u]$.

Several factors were chosen for inclusion in the model (Table 3). These factors are used for illustrative purposes only and they may differ in a more rigorous investigation of the factors influencing delta smelt. The environmental factors are taken as those proposed by Manly (2010b). The entrainment mortality rates are calculated based on Kimmerer (2008); the rates were obtained by fitting a piece-wise linear regression model of winter Old Middle River (OMR) flow to his adult entrainment estimates and his larval/juvenile entrainment estimates were fitted to a multiple linear regression model with spring OMR flow and spring low salinity zone (as measured by X2). The values from Kimmerer (2008) were used for years in which they are available

and the linear regression predictions were used for the remaining years. Manly (2010b) provided several variables as candidates to account for the changes in delta smelt abundance from fall to summer and summer to fall. The fall to summer covariates could influence the adult and larvae stages, while the summer to fall covariates could influence the juvenile stage. The factors proposed by Manly (2010b) are those that are considered to act directly on delta smelt. There are many other proposed factors that act indirectly through these factors. We also include secchi disc depth as a covariate for water turbidity/clarity since it was identified as a factor by Thomson et al. (2010). Exports were also identified as an important factor and were assumed to be related to entrainment. However, we chose to use direct measures of entrainment. Interactions among the factors were not considered in the application. However, some of the covariates implicitly include interactions in their definition and construction.

Some manipulation of the data was carried out before use in the model (the untransformed covariates values used in the model are given in the supplementary material). Delta smelt average length was missing for 1972-1974, 1976, and 1979, and was set to the mean based on Maunder and Deriso (2010). The factors were normalized (mean subtracted and divided by standard deviation) to improve model performance, except for the covariates relating to predator abundance, which were just divided by the mean, and the entrainment mortality rates, which were not transformed. These exceptions are factors that are hypothesized to have a have a unidirectional impact and setting their coefficients to zero is needed for impact analysis. Setting the coefficient for the entrainment mortality rate covariates to one can be used to determine the impact if the entrainment estimates are assumed to be correct.

The standard approach outlined above and in table 1 is applied to the delta-smelt application. The Ricker model was approximated by setting $\gamma = -\exp[-10]$. We also constrained $\gamma < 0$ to avoid computational errors. It is difficult to scale the survey data to absolute abundance, so they are all treated as relative abundance and are not on the same scale. The scaling parameter a is not limited to $a \leq 1$ and the exponential model is used for all covariates. To illustrate the impact analysis, we implement three scenarios. In the first scenario, the covariates are all set to zero. This means that environmental conditions are average, predation is zero, and entrainment is zero. We implement the second scenario if one or both of the entrainment covariates are selected for inclusion in the model. In this case, only the entrainment coefficients are set to zero. In the third scenario we take the final set of covariates and add the entrainment covariates (or substitute them if they we already included in the model) with their coefficients set to one and rerun the model. In this case, only the entrainment coefficients are set to zero in the impact analysis.

Results

AICc values and weights were calculated for all possible combinations of density dependence that included no density dependence (No), a Beverton-Holt Model (BH), a Ricker model (R), and estimation of both b and γ (DD) (Table 3). Density dependence was clearly preferred for survival from juveniles to adults (J), but it is not clear if the density dependence is Beverton-Holt, Ricker, or somewhere in between. The Beverton-Holt and Ricker models for juvenile survival appear to be influenced by three consecutive data points (years 1976-1978) of high juvenile abundance with corresponding average

adult abundance (Figures 2 and 3). The evidence for and against density dependence is about the same for the stock-recruitment relationship from adults to larvae (A). With slightly more evidence for no density dependence if survival from juveniles to adults is Beverton-Holt and slightly more evidence for Beverton-Holt density dependence if the survival from juveniles to adults is Ricker. The evidence for no density dependence in survival from larvae to juveniles (L) is moderately (3 to 4 times) higher than for density dependence. Therefore, we proceed with four density dependence scenarios: (1) Beverton-Holt density dependence in survival from juveniles to adults (JBH); and (2) Beverton-Holt density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae (JBHABH); (3) Ricker density dependence in survival from juveniles to adults (JR); and (4) Ricker density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae (JRABH).

The number and the type of factors supported by the data depended on the assumptions made about density dependence (Tables 4 and 5). The models with density dependence for both survival from juveniles to adults and a stock recruitment relationship for adults to larvae included more covariates in the lowest AICc models (8 and 9 covariates for Beverton-Holt and Ricker density dependence in survival from juveniles to adults, respectively) than the models that included only density dependence for survival from juveniles to adults (5 covariates each). Several temperature, prey and predator covariates (TpAJ, EPAJ, EPJA, TpJul, Pred1) were selected in the first few steps and were included in all models. The April-June abundance of predators (Pred2) was selected in the first few steps in one model, but not selected at all in the others.

Overall, the model with Ricker density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae had better AICc scores than the other models (Table 5). This differs from the similarity in scores obtained when no covariates were included in the models (Table 3). For all density dependent assumptions, there were alternatives with more (or less) covariates than the lowest AICc model (within the models for that density dependence assumption), for which there was not *definite, strong, or very strong evidence that the model is not the K-L best model* ($4 \leq \Delta$) suggesting that these factors should also be considered as possible factors that influence the population dynamics of delta smelt (Table 5). Although, the asymmetrical nature of the AICc scores for nested models should be kept in mind.

The magnitude and the sign of the covariate coefficients are generally consistent across models (Table 6). The covariates were standardized so that the size of the coefficients are generally comparable across covariates. The coefficients are similar magnitudes for most covariates except those for water clarity (Secchi) and, particularly, adult entrainment (Aent), which had much larger effects. These both occurred before the stock-recruitment relationship from adults to larvae, which had a very strong density dependence effect. Pred2 had a small effect. The confidence intervals on the coefficients support inclusion of the covariates in the lowest AICc models except for Pred2 (Table 6). The effects for Secchi and Aent appear to be unrealistically large and their coefficients have a moderately high negative correlation. This appears to be a consequence of the unrealistically strong density dependence estimated in the stock-recruitment relationship from adults to larvae for those models (see Table S6).

The five lowest AIC_c models in iteration 6 of the two factors at a time procedure had a *b* parameter of the Beverton-Holt stock recruitment relationship from adult to larvae that was substantially greater than the critical value used to define realistic values of the parameter. The sixth model had an AIC of 812.53, which is worse than the lowest AICc model of iteration 5. The lowest AICc model with Beverton-Holt survival from juveniles to adults and Beverton-Holt stock recruitment relationship from adult to larvae also had an unrealistic *b* parameter and the next lowest AICc model had an AIC of 812.33. Therefore, the lowest AICc model after accounting for realistic parameter values is the lowest AICc model from iteration 5 with Ricker survival from juveniles to adults and Beverton-Holt stock recruitment relationship from adult to larvae with one additional covariate (Table 5, AICc = 808.47). The confidence intervals for the pred2 covariate for this model contained zero and removing the Pred2 covariate essentially had no effect on the likelihood. Therefore, we chose this model without the Pred2 covariate as the lowest AICc model (AICc = 806.63). Several models had an AICc score within 2 units of this model, which according to the Burnham and Anderson guidelines "*there is no credible evidence that the model should be ruled out"*. Therefore, to illustrate the sensitivity of results to the model choice we also provide results for the model with the fewest parameters that was within 2 AICc units of the lowest AICc model. This alternative model is that selected with two additional parameters in iteration 3 of the selection procedure (Table 5, AICc=810.20). Removing the Pred2 covariate improved the AICc score (808.63) so we also eliminated the Pred2 covariate from this model.

The models fit the survey data well (Figures 4 and 5), in fact better than expected from the survey standard errors, indicating that most of the variation in abundance was

modeled by the covariates or unexplained process variability. The unexplained process variability differed among the stages (Figure 6; Table 7). Essentially all the variability in survival between larvae and juveniles was explained by the covariates. The amount of variability in the survival from juveniles to adults explained was higher than in the stock-recruitment relationship, but they show similar patterns (Figure 6; Table 7).

The impact analysis of the selected covariates shows that the adult abundance under average conditions, with no predators, and entrainment mortality set to zero, differs moderately from that estimated in the original model (Figure 7). In particular, the recent decline is not as substantial under average conditions indicating that the covariates describe some of the decline, although there is still substantial unexplained variation and a large amount of uncertainty in the recent abundance estimates. Entrainment is estimated to have only a small impact on the adult abundance in either the lowest AICc model, which uses the estimated adult entrainment coefficient and the juvenile entrainment coefficient is zero, or the alternative model, in which both the juvenile and adult entrainment coefficients are set to one (Figure 8). The lowest AICc model with the two entrainment coefficients set at 1 did not converge and results are not shown for that analysis, although the results are expected to be similar.

Discussion

We developed a state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence. Application to delta-smelt detected strong evidence for a few key factors and density dependence operating on the population. Both environmental factors (e.g., Deriso et al. 2008) and density dependence (e.g., Brook and

Bradshaw 2006) have been detected in a multitude of studies either independently or in combination (e.g., Sæther 1997; Ciannelli et al. 2004). Brook and Bradshaw (2006) used long-term abundance data for 1198 species to show that density dependence was a pervasive feature of population dynamics that holds across a range of taxa. However, the data they used did not allow them to identify what life stages the density dependence operates on. Ciannelli et al. (2004) found density dependence in different stages of walleye Pollock. In our application we found evidence against density dependent survival from larvae to juveniles, strong evidence for density dependence in survival from juveniles to adults, and weak evidence for density dependence in the stock-recruitment relationship from adults to larvae, which includes egg and early larval survival. Other studies have suggested that density dependence is more predominant at earlier life stages (e.g., Fowler 1987; Gaillard et al. 1998), although the life history of these species differs substantially from delta smelt. The density dependence in survival from juveniles to adults found in our study was probably heavily influenced by three consecutive years of data. Unfortunately, this is a common occurrence in which autocorrelated environmental factors cause autocorrelation in abundance within a stage and this likely influences other studies as well. We only allowed factors to influence density independent survival, either before or after density dependence, however the factors could also influence the strength or form of the density dependence (Walters 1987). For example, Ciannelli et al. (2004) found that high wind speed induced negative density dependence in the survival of walleye Pollock eggs. Our analysis is one of the few, but expanding, applications investigating both density dependent and density independent factors in a rigorous statistical framework that integrates multiple data sets within a life cycle model. The

framework amalgamates the density and the mechanistic paradigms of investigating population regulation outlined by Krebs (2002) while accommodating the fact that most available data is observational rather than experimental. More detailed mechanistic processes could be included in the model if the appropriate observational or experimental data are available.

One factor is often erroneously singled out as the only major cause of population decline (e.g., over fishing; Sibert et al. 2006). However, there is a substantial accumulation of evidence that multiple factors interact to cause population declines. Our analysis found support for a variety of factors that influence delta smelt population dynamics. We also showed that together these factors explain the decline in the delta smelt population. Deriso et al. (2008) also found support that multiple factors influenced the decline and suppression of the Prince William Sound herring population, including one or more unidentified factors related to a particular year.

Three of the first four factors included in the delta smelt application acted on the survival between larvae and juveniles. This is also the period where no density dependence in survival occurred. The final model estimates that the factors explain all the variability in survival from larvae to Juveniles. The 20mm trawl survey, which provides information on juvenile abundance, only starts in 1995 so there is less data to explain and this may be partly why the unexplained process variability variance goes to zero. The process variability for the other stages may partly absorb the variability in survival from larvae to juveniles.

Deriso et al. (2008) showed that multiple factors influence populations and that analysis of factors in isolation can be misleading. We also found that multiple factors

influence the dynamics of delta smelt and that evaluating factors in isolation can produce different results than evaluating them in combination. The type of density dependence assumed also impacted what factors were selected. Specifically, one predator covariate (Pred2) would be the first selected covariate based simply on AICc for two of the density dependent assumptions, but was not selected by the two factor stepwise procedure (see supplementary material). However, this covariate was selected in the first step of the two factor stepwise procedure for another density dependent assumption, which happened to be the final model with the lowest AICc. In the final model the confidence intervals on the coefficient indicate that this factor should not be included in the model. Exploratory analysis showed that this covariate had about a 0.6 correlation with a temperature (TpAJ) and a prey covariate (EPAJ) that were consistently selected in the first or seconds steps, which operated on the same stage (larvae), when these covariates were combined together. The covariate was also highly correlated with time (see supplementary material). We did find, to some extent, which other covariates were included in the model and the order in which they were included changed depending on the density dependence assumptions. However, apart from the one predator covariate, the four density dependence assumptions tended to select the same factors in the first few steps of the model selection procedure, although the order of selection differed.

There was substantial correlation among estimated parameters (see supplementary material). The parameters of the density dependence function were highly positively correlated as previously observed for stock-recruitment relationships (Quinn and Deriso 1999) and reparameterization might improve the estimation algorithm. The relative number of larvae in the first year is negatively correlated with parameters influencing

larval survival including the survival fraction at low abundance (*a*), the standard deviation of the process variability, and the prey covariate coefficients. The coefficients for the prey and temperature covariates influencing larval survival are correlated. This is partly related to the fact that some of these covariates are also correlated. The coefficients for water clarity (Secchi) and adult entrainment (Aent) in the lowest AIC model were highly negatively correlated and were correlated with the parameters of the adult density dependence survival function. The coefficient for adult entrainment is also unrealistically large suggesting that the model including water clarity and adult entrainment is unreliable.

The covariates were included in the model as simple log-linear terms. There may be more appropriate relationships between survival and the covariates. For example, good survival may be limited to a range of covariate values so a polynomial that describes a dome shape cure may be more appropriate. There may also be interactions among the covariates. Neither of these was considered in the delta smelt application. Although, some of the covariates were developed based on combining different factors such as water clarity and predator abundance. Some of the covariates were highly correlated (see supplementary material), but those with the highest correlations were either for different stages or not selected in the final models.

Density dependence and environmental factors could influence other population processes (e.g. growth rates) or the ability (catchability) of the survey to catch delta smelt. Modeling of catchability has been extensively researched for indices of abundance based on commercial catch data (Maunder and Punt 2004) and results have shown that the relationship between catch-per-unit-effort and abundance can be nonlinear (Harley et

al. 2001; Walters 2003). Rigorous statistical methods have been developed to account for habitat quality in the development of indices of abundance from catch and effort data (Maunder et al. 2006). Methods have been developed to integrate the modeling of catchability within population dynamics models as a random walk (Fournier et al. 1998) or as a function of covariates (Maunder 2001; Maunder and Langley 2004). Surveys are less likely to be effected by systematic changes in catchability because sampling effort and survey design tend to be more consistent over time than effort conducted by commercial fishing fleets. Most fisheries stock assessments assume that there are no systematic changes in survey catchability unless there is an obvious change (e.g. change in survey vessel). However, catchability may changes due to factors such as changes in the spatial distribution of the species or population density. Similar methods as used for survival can be used to model catchability as a function of density or environmental factors. Random influences on catchability beyond those caused by simple random sampling can be accommodated by estimating the standard deviation of the likelihood function used to fit the model to the survey data (Maunder and Starr 2003). However, the fit to the delta smelt data appears better than expected from the bootstrap confidence intervals suggesting that the observation error is smaller than estimated by the bootstrap procedure. Systematic and additional random variation in catchability could bias the evaluation of strength and statistical significance of density dependence and environmental factors (Deriso et al. 2007).

The estimates of the *b* parameter of the Beverton-Holt stock-recruitment relationship between adults and larvae produced density dependence that was unrealistically strong in a few models. Consequently, this caused estimates of some

651 coefficients that were also unrealistic (e.g., the coefficient for adult entrainment was
652 nearly two orders of magnitude higher than expected). Even when a model was selected
653 for which the *b* parameter was considered reasonable, the coefficient for adult
654 entrainment was still an order of magnitude greater than expected. This illustrates that
655 naively following AICc model selection without use of professional judgment is not
656 recommended. We could have included all models in the sum of the AICc weights by
657 bounding the *b* parameter in the parameter estimation process (the parameter would
658 probably be at the bound), but we considered inference based on models with a parameter
659 at the bound inappropriate. An alternative approach would be to use an informative prior
660 for *b* (Punt and Hilborn 1997) to pull it away from unrealistic values, but we did not have
661 any prior information that was considered appropriate.

662 Andersen et al. (2000) warn against data dredging as a method to test factors that
663 influence population dynamics. In their definition of data dredging they include the
664 testing of all possible models, unless, perhaps, if model averaging is used. This provides
665 somewhat of a dilemma when using a multi-stage life cycle model because there are often
666 multiple candidate factors for each life stage and they may only be detectable if included
667 in the model together. For this reason, we use an approximation to all possible models
668 and rely on AICc and AICc weights to rank models and provide an idea of the strength of
669 evidence in the data about the models and do not apply strict hypothesis tests. Some form
670 of model averaging using AICc weights might be applicable to the impact analysis,
671 although the estimates of uncertainty would have to include both model and parameter
672 uncertainty. The estimates of uncertainty in our impact analysis under estimate
673 uncertainty because they do not include model selection uncertainty and use of model

averaging might provide better estimates of uncertainty (Burnham and Anderson 2002). In addition, we use symmetric confidence intervals and approaches that provide asymmetric confidence intervals may be more appropriate (e.g., based on profile likelihood or Bayesian posterior distribution).

Our results suggest that of all the factors that we tested, food abundance, temperature, predator abundance and density dependence are the most important factors controlling the population dynamics of delta smelt. Survival is positively related to food abundance and negatively related to temperature and predator abundance. There was also some support for a negative relationship with water clarity and adult entrainment, and a positive relationship with the number of days where the water temperature was appropriate for spawning. The first variables to be included in the model were those related to survival from larvae to juveniles, followed by survival from juveniles to adults, and finally the stock-recruitment relationship. Mac Nally et al. (2010) also found that high summer water temperatures had an inverse relationship with delta smelt abundance. Thomson et al. (2010) found exports and water clarity as important factors. We did not include exports, but included explicit estimates of entrainment. We found some support for adult entrainment, but it was not one of the main factors and the coefficient was unrealistically high and highly correlated with the coefficient for water clarity. Mac Nally et al. (2010) and Thomson et al. (2010) only used the FMWT data and did not look at the different life stages, which probably explains why the factors supported by their analyses differ from what we found.

We found strong evidence for density dependence in survival from juveniles to adults, some evidence for density dependence for the stock-recruitment relationship from

adults to larvae and evidence against density dependence in survival from larvae to juveniles. This might be surprising since the population is of conservation concern due to low abundance levels. However, the available data covers years, particularly in the 1970s, where the abundance was high and data for these years provide information on the form and strength of the density dependence. At the recent levels of abundance, density dependence is probably not having a substantial impact on the population and survival is impacted mainly by density independent factors. Previous studies only found weak evidence for a stock-recruitment relationship and suggested that density independent factors regulate the delta smelt population (e.g., Moyle et al. 1992). Bennett (2005) found that the strongest evidence for density dependence was between juveniles and pre-adults. Mac Nally et al. (2010) found strong support for density dependence, but Thomson et al. (2010) did not.

Several pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Thomson et al. (2010) used Bayesian change point analysis to determine when the declines occurred and included covariates to investigate what caused the declines. They were unable to fully explain the decline and unexplained declines were still apparent in the early 2000s. The impact analysis we applied to delta smelt suggests that the factors included in the model explain the low levels of delta smelt in the mid 2000s. Although, there is still substantial annual variation in the delta smelt abundance and uncertainty in the estimates of abundance for these years.

The theory for state-space stage-structured life cycle models is well developed (Newman 1998; de Valpine, P. 2002; Maunder 2004), they have been promoted

(Thomson et al. 2010; Mac Nally et al. 2010), they facilitate the use of multiple data sets (Maunder 2003), provide more detailed information about how factors impact a population, and we have shown that they can be implemented. Therefore, we recommend that they are an essential tool for evaluating factors impacting species of concern such as delta smelt.

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Appendix: Calculating realistic values for the *b* parameter of the Beverton-Holt and Ricker versions of the Deriso-Schnute stock-recruitment model.

The third parameter (γ) of the Deriso-Schnute stock-recruitment model (Deriso 1980; Schnute 1985)

$$f(N) = aN(1 - b\gamma N)^{\frac{1}{\gamma}}$$

can be set to represent the Beverton-Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) models (Quinn and Deriso 1999, page 95), which correspond to

$$f(N) = \frac{aN}{1 + bN} \text{ and } f(N) = aN \exp[-bN]$$

The recruitment at a given reference abundance level (e.g., the carrying capacity N_0) can be calculated as

$$R_0 = \frac{aN_0}{1 + bN_0} \text{ and } R_0 = aN_0 \exp[-bN_0]$$

The recruitment when the abundance is at a certain fraction (p) of this reference level can be calculated as

$$R_p = \frac{apN_0}{1+bpN_0} \text{ and } R_p = aN_0 \exp[-bpN_0]$$

A standard reference in fisheries is the recruitment as a fraction of the recruitment in the absence of fishing (the carrying capacity) that is achieved when the abundance is 20% of the abundance in the absence of fishing (steepness).

$$h = \frac{R_{0.2}}{R_0} = \frac{1/N_0 + b}{5/N_0 + b} \text{ and } h = \frac{R_{0.2}}{R_0} = 0.2\exp[0.8bN_0]$$

To set b for a given steepness

$$b = \frac{5h-1}{N_0 - hN_0} \text{ and } b = \frac{\ln[5h]}{0.8N_0}$$

The 20% reference level was probably chosen because the objective of fisheries management has traditionally been to maximize yield and it is generally considered that when a population falls below 20% of its unexploited level the stock cannot sustain that level of yield. In the delta smelt application the concern is about low levels of population abundance and we do not estimate the unexploited population size. Therefore, a more appropriate reference level might be 5% of the average level observed in the surveys.

$$h_{0.05} = \frac{R_{0.05}}{R_{ave}} = \frac{1/N_{ave} + b}{20/N_{ave} + b} \text{ and } h_{0.05} = \frac{R_{0.05}}{R_{ave}} = 0.05\exp[0.95bN_{ave}]$$

$$b = \frac{20h_{0.05} - 1}{N_{ave} - h_{0.05}N_{ave}} \text{ and } b = \frac{\ln[20h_{0.05}]}{0.95N_{0.05}}$$

This specification is also more appropriate when considering both the Beverton-Holt and Ricker models because the Ricker model reduces at high abundance levels and the recruitment at an abundance level that is 20% of the carrying capacity could be higher than the recruitment at carrying capacity. We restrict the models to those that have *b* estimates such that the expected recruitment when the population is at 5% of its average level (over the survey period) is equal to or less than 80% of the recruitment expected when the population is at its average level (Table A1). This is equivalent to a Beverton-Holt $h_{0.2} = 0.95$ based on the abundance reference level being the average abundance from the surveys, which is probably conservative is the sense of not rejecting high values of *b*.

Appendix References

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Table A1. Maximum values of the parameter *b* for inclusion of models in the model selection process.

	Maximum *b*		
	Average abundance	Beverton-Holt	Ricker
20mm (larvae)	7.99	9.3867	0.3653
STN (juveniles)	6140	0.0122	0.0005
FMWT (adults)	459	0.1634	0.0064

Table 1. Algorithm for evaluating covariates for the delta smelt application.

1) Evaluate density dependence

a) Calculate all combinations of density dependent processes without the inclusion of factors.

Combinations include: a) density independent; b) Beverton-Holt; c) Ricker; and d) estimate both b and γ. These can be at any of the three stages.

b) Choose the density dependence combination that has the lowest AICc or if there are several that have similar support, choose multiple combinations.

2) Evaluate covariates

a) For each densitity dependence scenario chosen in (1b) run all possible one and two covariate combinations

b) For each combination, set the AICc weight to zero if the sign is wrong for either of the coefficients in the combination or if the b parameter of a density dependence function is unrealistically high.

c) Sum AICc weights for a given covariate across all models that include that covariate

d) Select the two covariates with the highest summed AICc weights to retain for the next iteration

e) Iterate a-d until the AICc value of the best model in the current iteration is more than 4 units higher than the lowest AICc model

3) Double check all included covariates

a. Check confidence intervals of the estimated coefficients for all included covariates to see if they contain zero.

b. For all coefficients that contain zero remove the associated covariate and see if the AICc is degraded. If the AICc is not degraded, exclude that covariate from the model.

Table 2. The variables used as candidates to account for the changes in delta smelt abundance. A = occurs between adult and larval stages, L = occurs between larval and juvenile stages, J = occurs between juvenile and adult stages. Norm = subtract mean and divide by standard deviation, Mean = divide by mean, Raw = not scaled. The covariate is attributed to after density dependence unless it is known to occur before density dependence. This is because density dependence generally reduces the influence of the covariate. *= the effect of entrainment on survival is negative, but the covariate is formulated so setting the coefficient to 1 implies the assumption that entrainment is known without error, so the coefficient should be positive.

Factor	Name	Covar	Stage	B(efore)/ A(fter)	Sign	Description	Data scaling	Justification
1	SpDys	1	A	B	+	Days where temperature is in	Norm	This measures the number of days of

						the range 11-20C		spawning—the longer the spawning season, presumably the better chance of survival.
2	TpAJ	2	L	B	- or +	Average water temperature Apr-Jun in delta smelt habitat	Norm	Temperature affects growth rate and survival of early life stages.
3	TpAJ	2	A	A	- or +			
4	TpJul	3	L	A	-	Average water temperature July in delta smelt habitat	Norm	Higher water temperatures can be lethal. Could also include August temperature.
5	EPAJ	4	L	B	+	Minimum eurytemora and pseudodiaptomus density April-Jun	Norm	Measures height of food "gap" in spring, as eurytemora falls from spring maximum and pseudodiaptomus rises from ~0.
6	EPAJ	4	A	A	+			
7	EPJul	5	L	A	+	Average eurytemora and pseudodiaptomus density July	Norm	Measures food availability in summer until STN survey, identified as problem by Bennett based on smelt condition.
8	Pred1	6	J	A	-	Sep-Dec abundance other	Mean	Predation is a source of direct mortality,

						predators		measured as the product of relative density from beach seine data with the square of average sechi depth
9	Pred1	6	A	B	-			
10	Pred1	6	A	A	-			
11	StBass	7	J	A	-	Sep-Dec abundance striped bass	Mean	A major predator, whose abundance is measured as actual number of adults.
12	StBass	7	A	B	-			
13	StBass	7	A	A	-			
14	DSLth	8	L	A	+	Delta smelt average length	Norm	See Bennett (2005) for length vs fecundity relationship, linear for 1-year-olds.
15	DSLth	8	J	A	+			
16	DSLth	8	A	A	+			
17	TpJS	9	J	A	-	Maximum 2-week average temperature Jul-Sep	Norm	Measure of whether lethal temperature is reached in hot months.
18	EPJA	10	J	A	+	Average eurytemora	Norm	Measures food availability in summer between

						and pseudodiaptomus density July-August		STN and FMWT surveys, identified as problem by Bennett based on smelt condition.
19	Secchi	11	A	B	-	Jan-Feb Weighted Secchi depth	Norm	Protection from predators
20	Secchi	11	A	A	-			
21	Jent	12	L	A	+ *	Juvenile entrainment	Raw	Entrained in by water pumps
22	Aent	13	A	B	+ *	Adult entrainment	Raw	Entrained in by water pumps
23	Pred2	14	L	B	-	Apr-Jun abundance other predators	Mean	Predation is a source of direct mortality, measured as the product of relative density from beach seine data with the square of average sechi depth
24	Pred2	14	A	A	-			

Table 3. AICc weights for all possible density dependence models without covariates. L = survival from larvae to juveniles; J = survival from juveniles to larvae; A = the stock recruitment relationship from adults to larvae; No = no density dependence, BH = Beverton-Holt density dependence; R = Ricker density dependence; DD = Deriso-Schnute density dependence (i.e. estimate γ)

		J-No	J-BH	J-R	J-DD	Sum
L-No	A-No	0.000	0.079	0.062	0.027	0.168
	A-BH	0.000	0.075	0.067	0.026	0.168
	A-R	0.000	0.059	0.052	0.020	0.131
	A-DD	0.000	0.069	0.064	0.023	0.156
	Sum	0.000	0.281	0.245	0.096	0.622
L-BH	A-No	0.000	0.022	0.017	0.007	0.047
	A-BH	0.000	0.020	0.018	0.007	0.045

	A-R	0.000	0.016	0.014	0.005	0.035
	A-DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L-R	A-No	0.000	0.022	0.017	0.007	0.047
	A-BH	0.000	0.020	0.018	0.007	0.045
	A-R	0.000	0.016	0.014	0.005	0.035
	A-DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L-DD	A-No	0.000	0.006	0.005	0.002	0.013
	A-BH	0.000	0.005	0.005	0.002	0.012
	A-R	0.000	0.004	0.004	0.001	0.009
	A-DD	0.000	0.004	0.004	0.001	0.010
	Sum	0.000	0.020	0.017	0.006	0.043

Table 4.

Order of inclusion of factors into the analysis. JBH = Beverton-Holt density dependence from the Juvenile to Adult stage; JBHABH = Beverton-Holt density dependence from the juvenile to adult stage and Beverton-Holt density dependence from the adult to larvae stage (the stock-recruitment relationship); JR = Ricker density dependence from the Juvenile to Adult stage; JRBH = Ricker density dependence from the juvenile to adult stage and Beverton-Holt density dependence from the adult to larvae stage (the stock-recruitment relationship). See Tables 2 and 3 for definitions. *This covariate was excluded from the final model because the confidence interval of its coefficient included zero and including the covariate degraded the AICc.

Factor	name	Stage	B(efore)/A(fter)	JBH	JBHABH	JR	JRABH
2	TpAJ	L	B	1	1	2	2
4	TpJul	L	A	2	2	2	3
5	EPAJ	L	B	1	1	1	1
7	EPJul	L	A		4		5
8	Pred1	J	A	2	2	3	3
18	EPJA	J	A	3	3	1	2
19	Secchi	A	B		3		4
22	Aent	A	B		4		4
23	Pred2	L	B				1*

Table 5. AICc values for each step in the model selection process. Shaded values are the lowest AICc for that density dependence configuration. See Table 4 for definitions.

	Step 1		Step 2		Step 3		Step 4		Step 5		Step 6		Step 7	
	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
JBH	841.06	833.44	827.58	824.00	823.01	823.30	824.61	825.95	828.28	831.08				
JBHABH	832.46	824.68	818.25	815.18	813.92	814.32	814.17	811.85	812.33	814.75				
JR	841.80	833.67	826.25	821.40	820.00	821.10	822.58	823.71	826.26	828.86				
JRBH	833.16	824.93	817.96	814.72	811.60	810.20	810.72	810.38	808.47	809.23	810.86	813.39	817.03	820.83

Table 6. Estimates of coefficients (and 95% confidence intervals) from the lowest AICc models for each density dependence assumption. Definitions of abbreviations and a description of the covariates can be found in Table 2 and the density dependence configurations in Table 4. The alternative model is the model that has the fewest covariates and the AICc is less than 2 AICc units greater than the lowest AICc model.

Factor	name	Stage	B/A	JBH	JBHABH	JR	JRABH	JRABH no Pred2	Alternative
2	TpAJ	L	B	-0.32 (-0.46, -0.18)	-0.21 (-0.36, -0.07)	-0.32 (-0.45, -0.19)	-0.20 (-0.34, -0.06)	-0.22 (-0.36, -0.09)	-0.31 (-0.44, -0.18)
4	TpJul	L	A	-0.29 (-0.50, -0.08)	-0.30 (-0.49, -0.12)	-0.28 (-0.49, -0.07)	-0.28 (-0.47, -0.09)	-0.32 (-0.50, -0.13)	-0.30 (-0.50, -0.11)
5	EPAJ	L	B	0.39 (0.15, 0.63)	0.40 (0.18, 0.62)	0.37 (0.13, 0.61)	0.32 (0.09, 0.55)	0.36 (0.14, 0.58)	0.47 (0.23, 0.71)
7	EPJul	L	A		0.32 (0.07, 0.58)		0.31 (0.05, 0.56)	0.33 (0.07, 0.59)	
8	Pred1	J	A	-0.45 (-0.84, -0.06)	-0.49 (-0.90, -0.08)	-0.37 (-0.71, -0.03)	-0.42 (-0.77, -0.07)	-0.44 (-0.78, -0.09)	-0.40 (-0.75, -0.05)
18	EPJA	J	A	0.21 (0.00, 0.42)	0.22 (0.00, 0.45)	0.44 (0.21, 0.66)	0.46 (0.22, 0.69)	0.46 (0.22, 0.69)	0.46 (0.23, 0.69)
19	Secchi	A	B		-1.08 (-1.97, -0.19)		-1.24 (-2.27, -0.22)	-1.15 (-2.11, -0.20)	
22	Aent	A	B		9.50 (0.62, 18.38)		10.97 (0.93, 21.01)	10.32 (0.99, 19.65)	
23	Pred2	L	B				-0.19 (-0.52, 0.13)		
	a	L		396 (334, 458)	451 (373, 529)	396 (337, 456)	593 (307, 879)	454 (376, 532)	410 (340, 481)
	a	J		0.74 (0.01, 1.48)	0.77 (-0.02, 1.56)	0.39 (0.18, 0.6)	0.42 (0.19, 0.65)	0.43 (0.2, 0.66)	0.41 (0.19, 0.63)
	a	A		0.03 (0.02, 0.04)	0.2 (-0.13, 0.53)	0.03 (0.02, 0.04)	0.27 (-0.24, 0.78)	0.25 (-0.18, 0.67)	0.08 (0, 0.16)
	b	L		0	0	0	0	0	0
	b (10^{-4})	J		8.38 (-0.19, 16.95)	7.95 (-0.57, 16.48)	1.43 (1.01, 1.84)	1.42 (1.01, 1.84)	1.44 (1.02, 1.85)	1.43 (1.01, 1.84)

b (10^{-2})	A	0	1.48 (-1.41, 4.38)	0	2.35 (-2.77, 7.47)	1.93 (-1.96, 5.81)	0.52 (-0.34, 1.39)
γ	L						
γ	J	-1	-1	0	0	0	0
γ	A		-1		-1	-1	-1
σ	L	0.07 (-0.32, 0.45)	0 (-0.35, 0.35)	0.04 (-0.5, 0.59)	0 (-0.35, 0.35)	0 (-0.26, 0.26)	0.1 (-0.2, 0.39)
σ	J	0.52 (0.36, 0.67)	0.55 (0.39, 0.71)	0.46 (0.31, 0.6)	0.48 (0.32, 0.63)	0.48 (0.32, 0.63)	0.47 (0.32, 0.62)
σ	A	0.79 (0.57, 1.01)	0.61 (0.45, 0.77)	0.82 (0.59, 1.04)	0.61 (0.45, 0.77)	0.62 (0.46, 0.78)	0.71 (0.52, 0.9)
$h_{0.05}$	L	1	1	1	1	1	1
$h_{0.05}$	J	0.24 (0.09, 0.4)	0.24 (0.08, 0.4)	0.11 (0.09, 0.14)	0.11 (0.09, 0.14)	0.12 (0.09, 0.14)	0.11 (0.09, 0.14)
$h_{0.05}$	A	1	0.29 (-0.06, 0.64)	1	0.38 (-0.09, 0.85)	0.34 (-0.07, 0.75)	0.15 (0, 0.3)

Table 7. Estimates of standard deviation of the process variation and the percentage of the process variation explained by the covariates for the lowest AICc model.

	Standard deviation without covariates	Standard deviation with covariates	%variation explained
Larvae	0.72	0.00	100%
Juvenile	0.63	0.48	43%
Adult	0.71	0.62	24%

Figure captions

Figure 1. Life cycle diagram of delta smelt with survey, entrainment, and density dependence timing.

Figure 2. Relationship among stages in the model for the lowest AICc model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship. Points are the model estimates of abundance, lines are the estimates from the stock recruitment models without covariates or process variation, crosses are the estimates without covariates.

Figure 3. Relationship among stages in the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model). Points are the model estimates of abundance, lines are the estimates from the stock recruitment models without covariates or process variation, crosses are the estimates without covariates.

Figure 4. Fit (line) to the survey abundance data (circles) for the lowest AICc model that includes Ricker survival between juveniles and adults and a Beverton-Holt stock-recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.

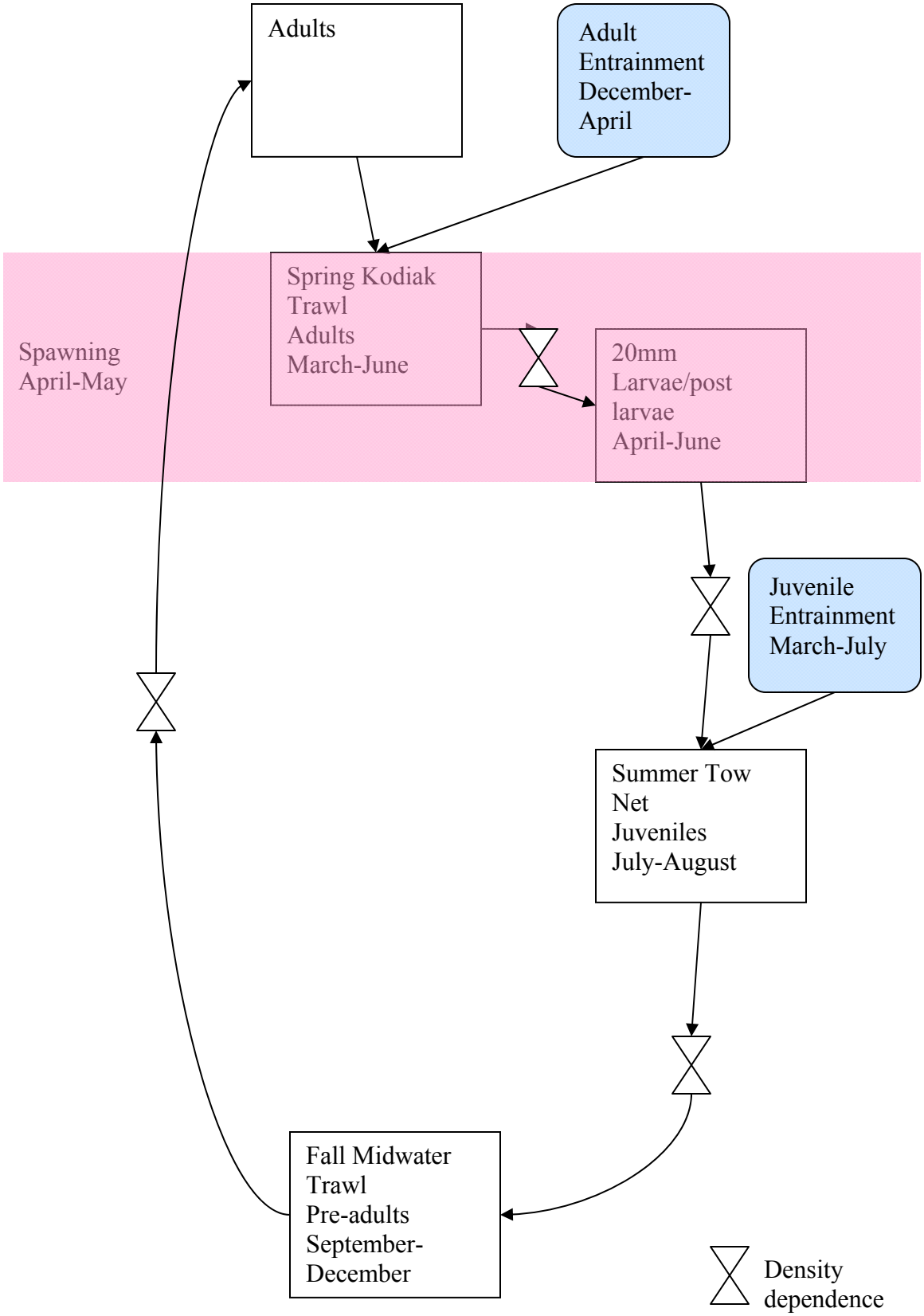
Figure 5. Fit (line) to the survey abundance data (circles) for the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) that includes Ricker survival from juveniles to adults and a Beverton-Holt stock recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.

Figure 6. Estimates of the realizations of the process variation random effects ($\exp\left[\sigma_s \varepsilon_{t,s} - 0.5\sigma_s^2\right]$) for the lowest AICc model that includes Ricker survival between juveniles and adults and a Beverton-Holt stock-recruitment relationship (top) and the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (bottom).

Figure 7. Estimates of abundance with and without covariates (coefficients of the covariates set to zero) (top) and ratio of the two with 95% confidence intervals (bottom, y-axis limited to show details) from the lowest AICc (left panels) model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship and the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (right panels).

Figure 8. Estimates of the adult abundance with and without adult entrainment (top) and the ratio of adult abundance without adult entrainment to with adult entrainment (bottom, y-axis limited to show details) from the lowest AICc model (left panels) with Ricker

survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship and the alterative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (right panels).


Adults
Adult Entrainment December-April
Spawning April-May
Spring Kodiak Trawl Adults March-June
20mm Larvae/post larvae April-June
Juvenile Entrainment March-July
Summer Tow Net Juveniles July-August
Fall Midwater Trawl Pre-adults September-December
Density dependence

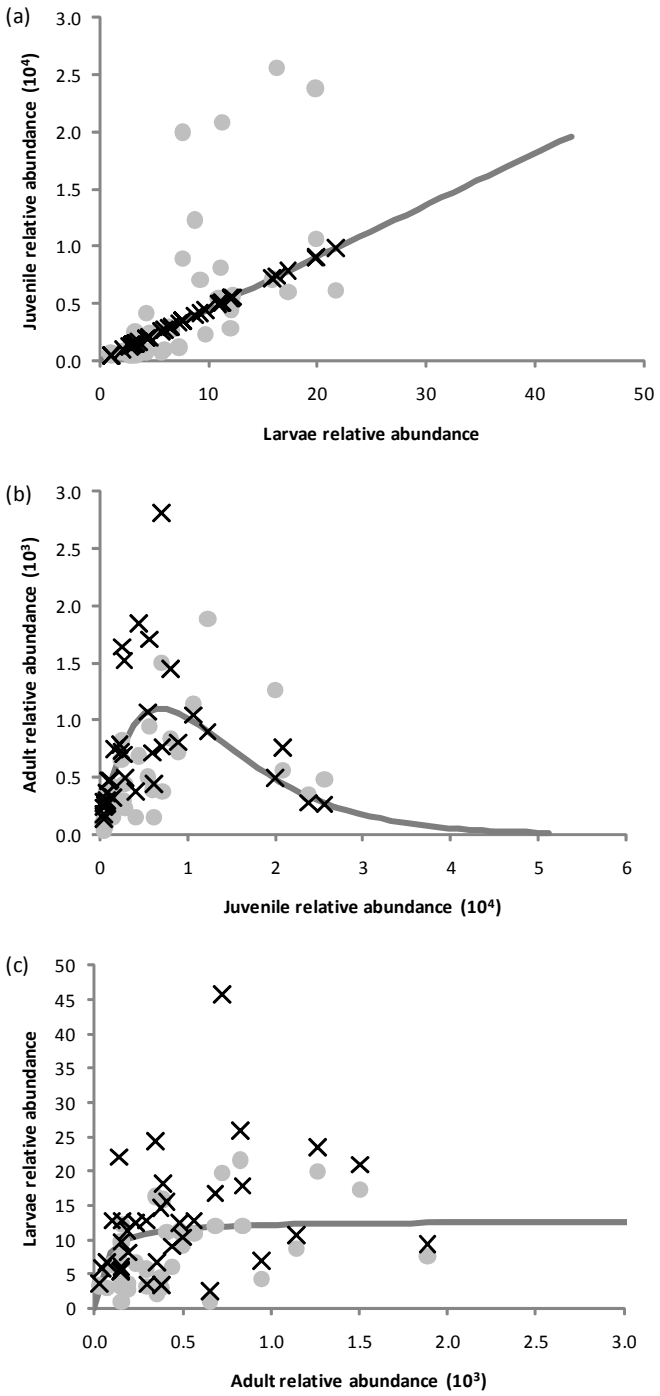

(a)
Juvenile relative abundance (10⁴)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
50
Larvae relative abundance
(b)
Adult relative abundance (10³)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
Juvenile relative abundance (10⁴)
(c)
Larvae relative abundance
50
45
40
35
30
25
20
15
10
5
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Adult relative abundance (10³)

Figure 2.

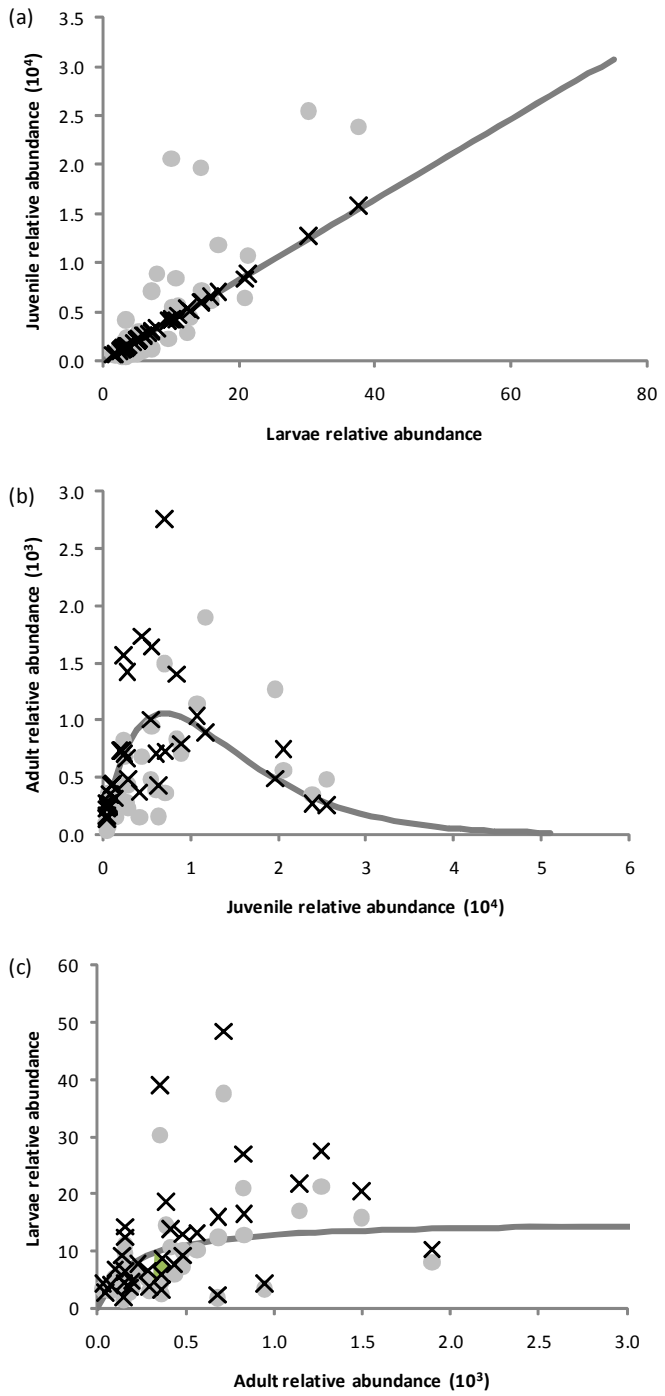

(a)
Juvenile relative abundance (10⁴)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
Larvae relative abundance
(b)
Adult relative abundance (10³)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
Juvenile relative abundance (10⁴)
(c)
Larvae relative abundance
60
50
40
30
20
10
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Adult relative abundance (10³)

Figure 3.

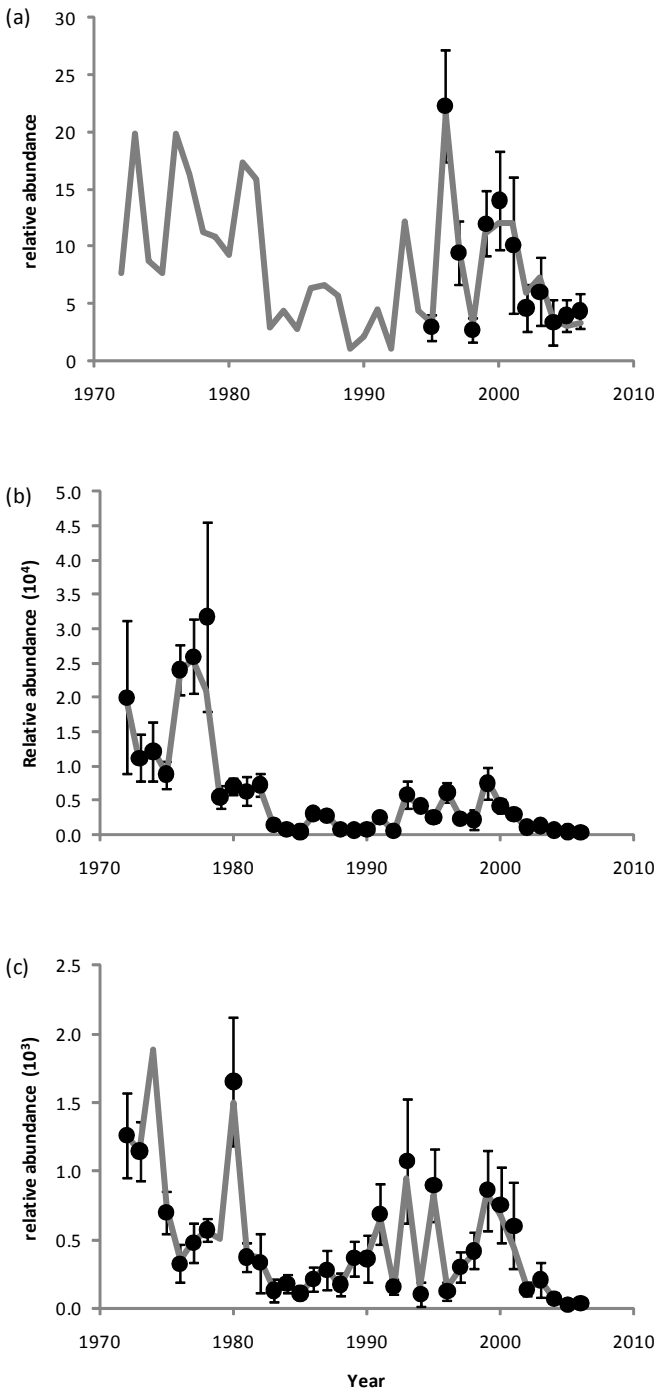

(a)
relative abundance
30
25
20
15
10
5
0
1970
1980
1990
2000
2010
(b)
Relative abundance (10⁴)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
(c)
relative abundance (10³)
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 4.

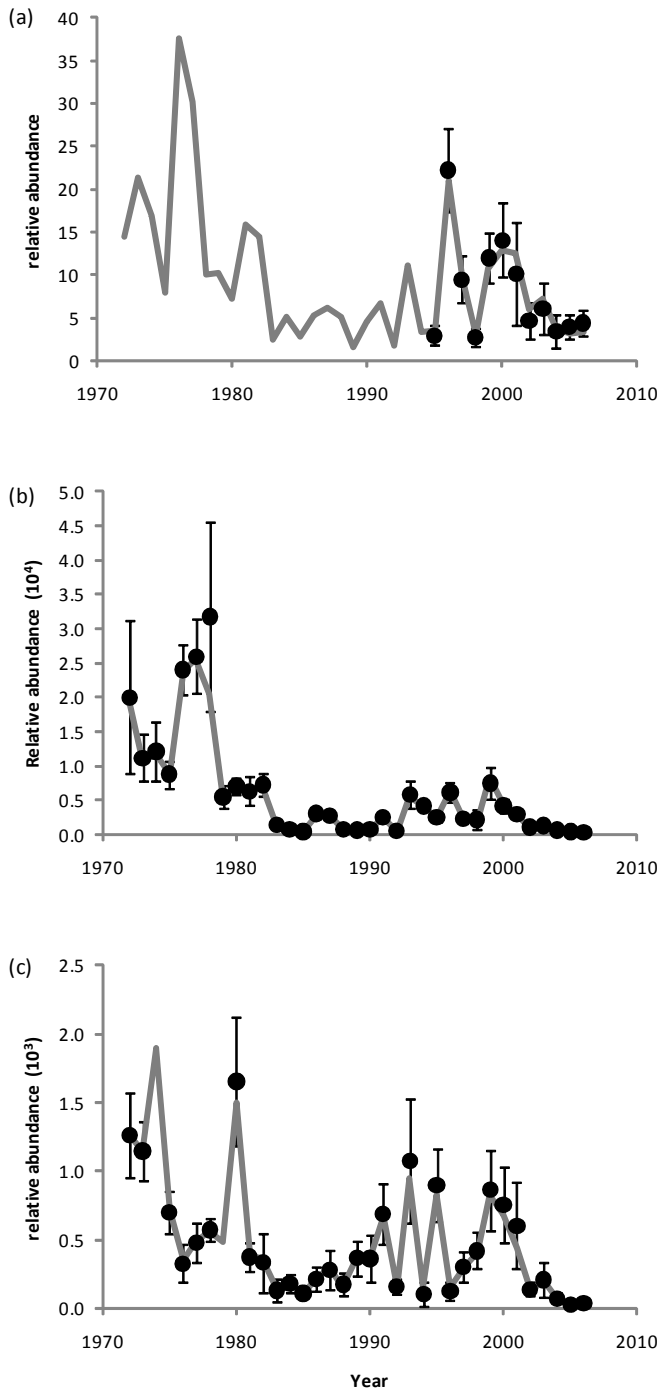

(a)
relative abundance
40
35
30
25
20
15
10
5
0
1970
1980
1990
2000
2010
(b)
Relative abundance (10⁴)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
(c)
relative abundance (10³)
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 5.

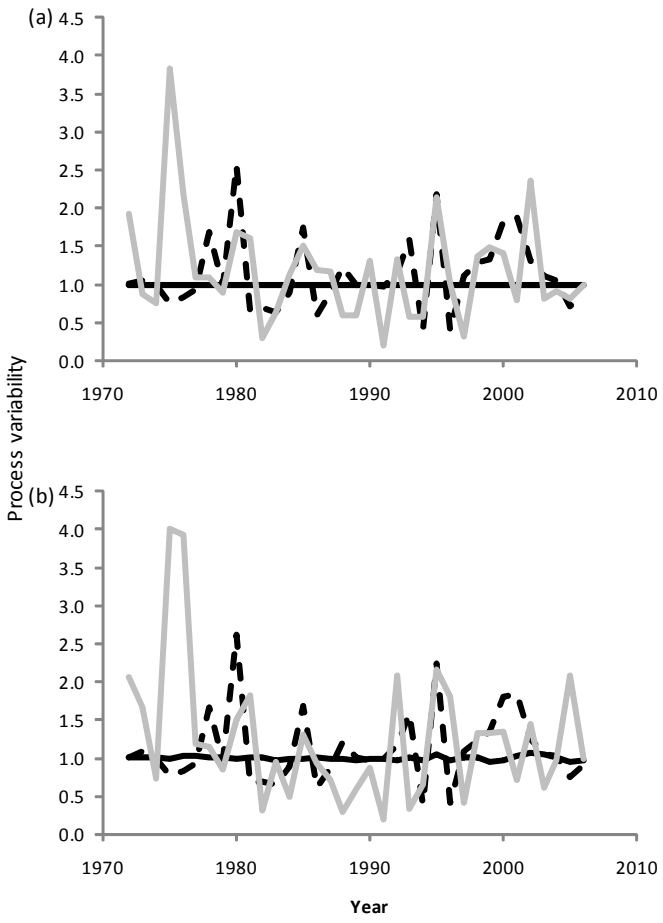

(a)
(b)
Process variability
Year
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010

Figure 6.

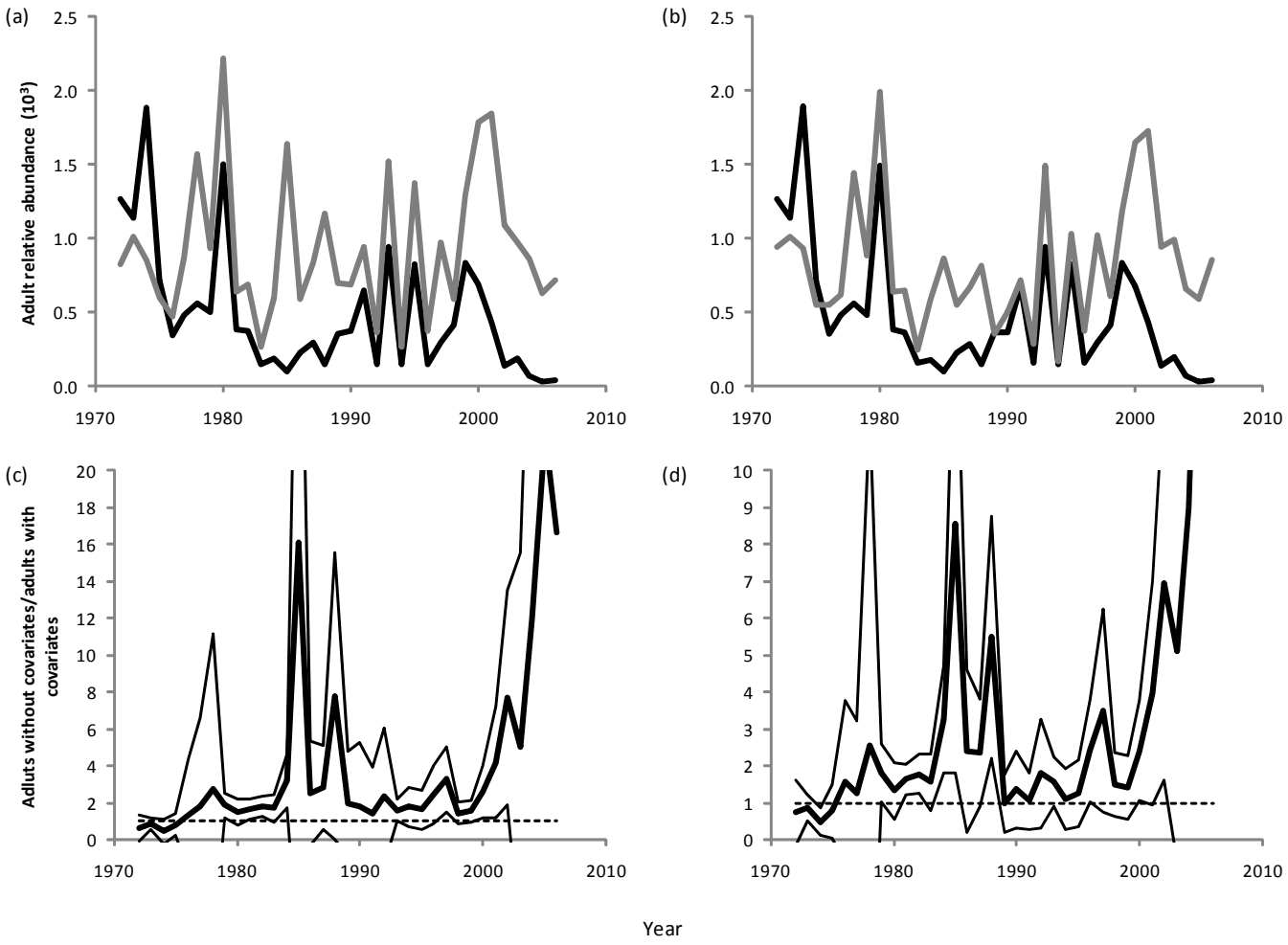

(a)
(b)
(c)
(d)
Adult relative abundance (10³)
Adluts without covariates/adults with covariates
Year
2.5
2.0
1.5
1.0
0.5
0.0
20
18
16
14
12
10
8
6
4
2
0
9
7
5
3
1
1970
1980
1990
2000
2010

Figure 7.

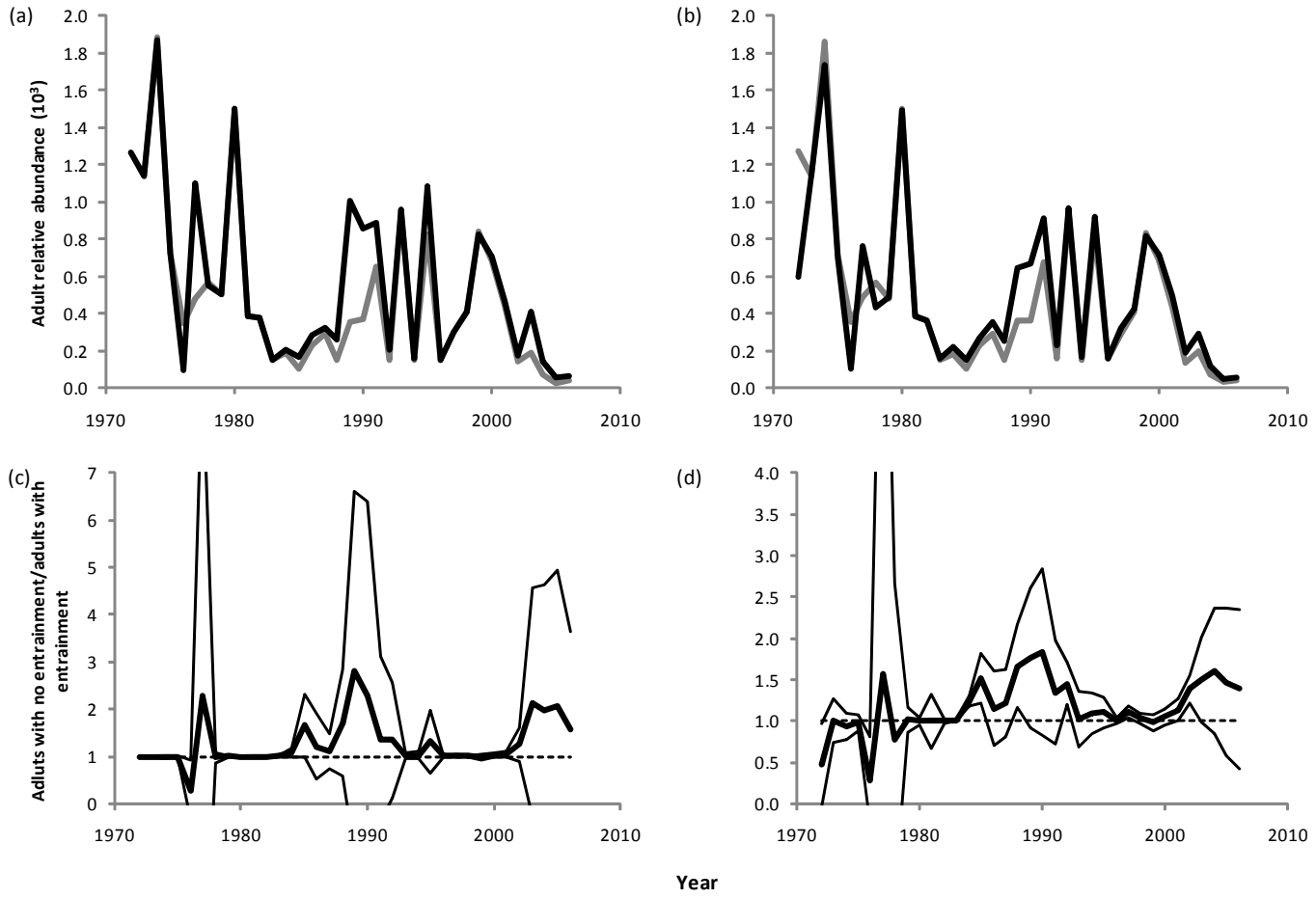

(a)
(b)
(c)
(d)
Adult relative abundance (10³)
Adluts with no entrainment/adults with entrainment
Year
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
7
6
5
4
3
2
1
0
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010

Figure 8.

Supplementary material

The following tables provide the data used in the analysis, a complete set of results for all the covariates evaluated in the analysis, and correlation matrices for the factors and estimated parameters.

Table S1. Indices of abundance and standard errors used in the delta smelt application.

	20mm		STN		FMWT	
Year	value	SE	value	SE	value	SE
1972			20005	5577	1265	155
1973			11185	1722	1145	108.7
1974			12147	2175		
1975			8786	989	697	77.8
1976			24000	1802	328	67.7
1977			25965	2681	480	69.7
1978			31758	6867	572	41.2

1979	5484	853		
1980	7068	646	1654	235.6
1981	6300	1043	374	49.9
1982	7242	820	333	108.5
1983	1390	279	132	43.6
1984	779	147	182	35.2
1985	387	67	110	21.6
1986	3057	406	212	42.7
1987	2743	227	280	71
1988	764	129	174	40.7
1989	647	52	366	63.7
1990	747	125	364	83.3
1991	2486	334	689	108.8
1992	471	68	156	27.8
1993	5763	996	1078	226.6
1994	4156	380	102	45.4

1995	2.933692	0.563774	2490	307	899	132.6
1996	22.25453	2.437344	6162	701	127	31
1997	9.437214	1.371236	2362	353	303	55
1998	2.704639	0.526823	2209	694	420	67
1999	12.00716	1.428904	7478	1142	864	146.2
2000	14.02919	2.160034	4178	519	756	139.9
2001	10.10347	2.983169	2897	332	603	156.2
2002	4.63569	1.04671	1115	163	139	25.2
2003	6.043828	1.479269	1329	174	210	64.9
2004	3.380115	0.967356	649	113	74	19
2005	3.981609	0.693923	393	97	27	6.6
2006	4.372327	0.779492	352	117	41	11.9

Table S2. Untransformed covariate values. See Table 2 for definitions.

Year	SpDys	TpAJ	TpJul	EPAJ	EPJul	Preds1	StBass	DSLth	TpJS	EPJA	Secci	JEnt	AEnt	Preds2
1972	110	17.8	21.3	1243.77	4725	586	36498		21.8	4303	50	0.28136	0.02626	354
1973	104	18.6	21.3	754.234	1547	1041	27596		21.9	2082	26	0.1174	0.02626	793
1974	85	17.7	21.0	614.313	4202	850	32314		22.5	3799	44	0.0814	0.02626	446
1975	92	17.2	20.1	479.507	1520	735	41650	65.1	21.5	1545	44	0.06449	0.02626	280
1976	130	17.6	21.4	666.081	4125	19410	65427		21.9	2895	74	0.31567	0.0952	6118
1977	118	17.0	21.1	581.151	4194	22324	40655	65.6	21.5	3972	59	0.35274	0.02626	7095
1978	110	17.8	21.1	1457.95	2082	14726	28399	65.3	22.4	1391	13	0	0.02626	8423
1979	90	18.0	21.0	516.84	947	37712	25761		22.1	722	34	0.15945	0.02626	18631
1980	137	16.8	20.5	428.147	548	20360	20254	70.3	22.5	647	11	0.03108	0.02626	15120
1981	108	18.7	21.8	787.671	922	22248	20621	67.2	22.8	724	42	0.22261	0.02626	17070
1982	105	17.0	20.6	19.4272	636	30605	21560	66.2	21.4	670	31	0.00746	0.02626	23570
1983	102	17.3	20.7	271.066	530	28422	31059	62.2	22.2	544	28	0	0.02626	13957
1984	100	18.3	22.4	251.49	1560	29082	35459	69.5	22.8	1545	50	0.20125	0.02626	20444

1985	105	18.5	22.0	134.587	548	62483	46997	69.1	22.5	543	76	0.26546	0.06687	30364
1986	122	18.1	21.2	648.516	626	30255	22752	68.1	21.5	534	60	0	0.02626	22921
1987	102	19.0	20.6	534.328	392	42089	41144	64.8	21.3	519	65	0.26078	0.02626	26771
1988	125	17.8	22.4	119.215	364	36828	30207	69.5	23.1	360	46	0.3583	0.16922	26668
1989	108	17.9	21.1	383.708	2558	38551	29441	67.8	21.7	3641	67	0.27032	0.13226	24067
1990	100	18.4	22.0	200.219	3616	57128	32336	63.9	22.7	3837	46	0.36378	0.22385	26671
1991	108	17.2	21.3	150.931	2542	63209	39881	62.5	21.8	3059	87	0.3181	0.02626	23754
1992	99	19.2	21.3	531.604	2733	89736	44102	57.9	22.5	2828	82	0.28653	0.04369	42138
1993	112	17.8	21.5	602.607	1184	48487	27938	54.7	22.2	1425	23	0.06506	0.05702	25301
1994	102	17.8	21.1	1112	965	61942	32635	62.9	21.4	856	75	0.21454	0.02626	53729
1995	142	17.0	21.5	573.935	2366	59091	34966	58.5	22.0	1431	27	0	0.18	38412
1996	115	18.3	21.4	380.924	533	72056	44927	55.1	22.6	731	38	0.01	0.025	52547
1997	104	19.3	21.2	369.14	590	64436	56551	57.6	21.8	800	22	0.14	0.025	33056
1998	117	16.3	21.3	271.886	1002	25623	32979	59.3	22.6	842	30	0	0.01	21106
1999	112	17.3	21.3	751.657	1308	29853	42465	59.1	22.0	1091	56	0.07	0.03	21961
2000	118	18.9	20.8	411.035	825	74907	60639	59.3	22.2	1007	64	0.13	0.05	50114
2001	73	19.5	21.3	423.892	758	81186	48811	63.5	22.0	484	57	0.19	0.05	50992

2002	108	18.6	21.8	105.105	641	75565	32632	62.2	22.2	462	36	0.26	0.16	59540
2003	106	18.0	22.2	136.244	787	86509	40081	58.6	23.2	1525	35	0.17	0.22	56424
2004	108	19.1	21.3	153.943	354	109036	82253	62.0	22.3	1012	37	0.21	0.19	50151
2005	123	18.1	22.0	57.0556	849	119419	58943	59.6	22.8	466	49	0.03	0.09	68310
2006	95	17.8	22.6	121.846	1321	116848	41977	58.0	23.7	884	39	0	0.03	53328

Table S3a. AICc weights for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	Name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.01	0.05	0.17	0.33	#
2	TpAJ	L	B	0.63	#	#	#	#
3	TpAJ	A	A	0.02	0.04	0.08	0.15	0.25
4	TpJul	L	A	0.31	0.68	#	#	#
5	EPAJ	L	B	0.56	#	#	#	#
6	EPAJ	A	A	0.01	0.00	0.00	0.00	0.00
7	EPJul	L	A	0.01	0.03	0.12	0.30	#
8	Pred1	J	A	0.13	0.43	#	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.00

10	Pred1	A	A	0.00	0.00	0.00	0.00	0.00
11	StBass	J	A	0.01	0.06	0.08	0.17	0.25
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.03	0.09	0.19	0.24
15	DSLth	J	A	0.00	0.03	0.00	0.00	0.00
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00
17	TpJS	J	A	0.00	0.02	0.06	0.00	0.00
18	EPJA	J	A	0.06	0.27	0.41	#	#
19	Secchi	A	B	0.01	0.08	0.23	#	#
20	Secchi	A	A	0.01	0.08	0.23	*	*
21	Jent	L	A	0.01	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.03	0.08	0.16	0.33
23	Pred2	L	B	0.18	0.06	0.10	0.18	0.25
24	Pred2	A	A	0.00	0.03	0.06	0.00	0.00

Table S3b. AICc weights for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.00	0.01	0.04	0.08	0.26
2	TpAJ	L	B	0.40	#	#	#	#
3	TpAJ	A	A	0.02	0.03	0.06	0.07	0.14
4	TpJul	L	A	0.05	0.71	#	#	#
5	EPAJ	L	B	0.89	#	#	#	#
6	EPAJ	A	A	0.04	0.03	0.11	0.13	0.17
7	EPJul	L	A	0.01	0.03	0.15	0.37	#
8	Pred1	J	A	0.09	0.32	#	#	#
9	Pred1	A	B	0.00	0.00	0.01	0.05	0.04
10	Pred1	A	A	0.01	0.04	0.10	0.22	0.23

11	StBass	J	A	0.01	0.06	0.07	0.09	0.15
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.02	0.07	0.09	0.18
15	DSLth	J	A	0.00	0.02	0.00	0.00	0.00
16	DSLth	A	A	0.00	0.00	0.00	0.01	0.08
17	TpJS	J	A	0.00	0.02	0.05	0.00	0.00
18	EPJA	J	A	0.04	0.28	0.36	#	#
19	Secchi	A	B	0.01	0.06	0.24	#	#
20	Secchi	A	A	0.01	0.06	0.16	*	*
21	Jent	L	A	0.01	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.07	0.14	0.37	#
23	Pred2	L	B	0.34	0.10	0.11	0.13	0.19
24	Pred2	A	A	0.02	0.06	0.12	0.12	0.10

Table S3c. AICc weights for each step in the two factor analysis for the model with Ricker survival from juvenile to adult. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.01	0.03	0.18	#	#
2	TpAJ	L	B	0.39	0.91	#	#	#
3	TpAJ	A	A	0.01	0.04	0.08	0.13	0.26
4	TpJul	L	A	0.17	0.50	#	#	#
5	EPAJ	L	B	0.44	#	#	#	#
6	EPAJ	A	A	0.00	0.00	0.00	0.00	0.00
7	EPJul	L	A	0.01	0.02	0.11	0.24	#
8	Pred1	J	A	0.02	0.16	0.38	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.00
10	Pred1	A	A	0.00	0.00	0.00	0.00	0.00

11	StBass	J	A	0.01	0.03	0.09	0.00	0.00
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.02	0.11	0.17	0.27
15	DSLth	J	A	0.00	0.04	0.17	0.15	0.26
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00
17	TpJS	J	A	0.00	0.00	0.00	0.00	0.00
18	EPJA	J	A	0.53	#	#	#	#
19	Secchi	A	B	0.01	0.04	0.18	0.26	#
20	Secchi	A	A	0.01	0.04	0.18	0.26	*
21	Jent	L	A	0.01	0.01	0.00	0.00	0.00
22	Aent	A	B	0.01	0.02	0.08	0.14	0.30
23	Pred2	L	B	0.37	0.09	0.11	0.18	0.26
24	Pred2	A	A	0.00	0.01	0.04	0.00	0.00

Table S3d. AICc weights for each step in the two factor analysis for the model with Ricker survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th	6th	7th
1	SpDys	A	B	0.00	0.02	0.04	0.03	0.23	#	#
2	TpAJ	L	B	0.32	0.38	#	#	#	#	#
3	TpAJ	A	A	0.01	0.04	0.05	0.08	0.12	0.48	#
4	TpJul	L	A	0.04	0.09	0.61	#	#	#	#
5	EPAJ	L	B	0.78	#	#	#	#	#	#
6	EPAJ	A	A	0.03	0.02	0.07	0.19	0.18	0.00	0.00
7	EPJul	L	A	0.01	0.03	0.06	0.21	0.61	#	#
8	Pred1	J	A	0.01	0.13	0.30	#	#	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.06	0.00	
10	Pred1	A	A	0.01	0.00	0.04	0.11	0.10	0.00	

11	StBass	J	A	0.00	0.04	0.08	0.00	0.00	0.00	0.00
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00	0.17	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.00	0.02	0.08	0.12	0.23	#
15	DSLth	J	A	0.00	0.04	0.09	0.09	0.10	0.20	0.54
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00	0.17	0.00
17	TpJS	J	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18	EPJA	J	A	0.35	0.89	#	#	#	#	#
19	Secchi	A	B	0.01	0.09	0.17	0.37	#	#	#
20	Secchi	A	A	0.00	0.04	0.09	0.15	*	*	*
21	Jent	L	A	0.00	0.03	0.00	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.07	0.15	0.23	#	#	#
23	Pred2	L	B	0.39	#	#	#	#	#	#
24	Pred2	A	A	0.01	0.00	0.05	0.10	0.04	0.05	0.53

Table S4a. AICc values and covariates included for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

					test1		test2		test3		test4		test5	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	841.06	833.44	827.58	824.00	823.01	823.30	824.61	825.95	828.28	831.08
				Δ	18.05	10.43	4.57	0.99	0.00	0.28	1.60	2.94	5.27	8.07
Run	Name	Stage	B/A											
1	SpDys	A	B								y	y	#	#
2	TpAJ	L	B			Y	#	#	#	#	#	#	#	#
3	TpAJ	A	A											y
4	TpJul	L	A				y	y	#	#	#	#	#	#
5	EPAJ	L	B			Y	#	#	#	#	#	#	#	#
6	EPAJ	A	A											
7	EPJul	L	A									y	#	#
8	Pred1	J	A					y	#	#	#	#	#	#
9	Pred1	A	B											
10	Pred1	A	A											
11	StBass	J	A											
12	StBass	A	B											

13	StBass	A	A								
14	DSLth	L	A								
15	DSLth	J	A								
16	DSLth	A	A								
17	TpJS	J	A								
18	EPJA	J	A			y	y	#	#	#	#
19	Secchi	A	B				y	#	#	#	#
20	Secchi	A	A				*	*	*	*	*
21	Jent	L	A								
22	Aent	A	B							y	y
23	Pred2	L	B		y						
24	Pred2	A	A								

Table S4b. AICc values and covariates included for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. y = covariate included in the lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

				test1		test2		test3		test4		test5	
				covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
			AICc	832.46	824.68	818.25	815.18	813.92	814.32	814.17	811.85	812.33	814.75
			AICc-min(AICc)	20.60	12.83	6.40	3.33	2.06	2.46	2.32	0.00	0.48	2.90
Run	Name	Stage	B/A										
1	SpDys	A	B										y
2	TpAJ	L	B		y	#	#	#	#	#	#	#	#
3	TpAJ	A	A										y
4	TpJul	L	A			y	y	#	#	#	#	#	#
5	EPAJ	L	B	Y	y	#	#	#	#	#	#	#	#
6	EPAJ	A	A										
7	EPJul	L	A							y	y	#	#
8	Pred1	J	A				y	#	#	#	#	#	#
9	Pred1	A	B										
10	Pred1	A	A									y	
11	StBass	J	A										
12	StBass	A	B										
13	StBass	A	A										

14	DSLth	L	A						
15	DSLth	J	A						
16	DSLth	A	A						
17	TpJS	J	A						
18	EPJA	J	A	y	y	#	#	#	#
19	Secchi	A	B		y	#	#	#	#
20	Secchi	A	A			*	*	*	*
21	Jent	L	A						
22	Aent	A	B				y	#	#
23	Pred2	L	B						
24	Pred2	A	A						

Table S4c. AICc values and covariates included for each step in the two factor analysis for the model with Ricker survival from juvenile to adult. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

					test1		test2		test3		test4		test5	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	841.80	833.67	826.25	821.40	820.00	821.10	822.58	823.71	826.26	828.86
				Δ	21.81	13.68	6.25	1.40	0.00	1.11	2.58	3.72	6.26	8.86
Run	name	Stage	B/A											
1	SpDys	A	B							y	#	#	#	#
2	TpAJ	L	B				y	y	#	#	#	#	#	#
3	TpAJ	A	A											y
4	TpJul	L	A					y	#	#	#	#	#	#
5	EPAJ	L	B				#	#	#	#	#	#	#	#
6	EPAJ	A	A											
7	EPJul	L	A									y	#	#
8	Pred1	J	A						y	y	#	#	#	#
9	Pred1	A	B											
10	Pred1	A	A											
11	StBass	J	A											
12	StBass	A	B											

13	StBass	A	A										
14	DSLth	L	A										
15	DSLth	J	A										
16	DSLth	A	A										
17	TpJS	J	A										
18	EPJA	J	A		Y	#	#	#	#	#	#	#	#
19	Secchi	A	B							y	y	#	#
20	Secchi	A	A							*	*	*	*
21	Jent	L	A										
22	Aent	A	B									y	y
23	Pred2	L	B	y	Y								
24	Pred2	A	A										

Table S4d. AICc values and covariates included for each step in the two factor analysis for the model with Ricker survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate. Additional covariates increased the AICc by more than 4 units and are not shown.

					test1		test2		test3		test4		test5		test6		test7	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	833.16	824.93	817.96	814.72	811.60	810.20	810.72	810.38	808.47	809.23	810.86	813.39	817.03	820.83
				AICc-min(AICc)	24.68	16.46	9.49	6.25	3.12	1.73	2.25	1.91	0.00	0.75	2.38	4.92	8.55	12.36
Run	name	Stage	B/A															
1	SpDys	A	B											y	#	#	#	#
2	TpAJ	L	B			y		y	#	#	#	#	#	#	#	#	#	#
3	TpAJ	A	A												y	y	#	#
4	TpJul	L	A						y	y	#	#	#	#	#	#	#	#
5	EPAJ	L	B		Y	y	#	#	#	#	#	#	#	#	#	#	#	#
6	EPAJ	A	A															
7	EPJul	L	A										y	y	#	#	#	#
8	Pred1	J	A							y	#	#	#	#	#	#	#	#
9	Pred1	A	B															
10	Pred1	A	A															

11	StBass	J	A													
12	StBass	A	B													
13	StBass	A	A													
14	DSLth	L	A											y	#	#
15	DSLth	J	A												y	y
16	DSLth	A	A													
17	TpJS	J	A													
18	EPJA	J	A	y	y	#	#	#	#	#	#	#	#	#	#	#
19	Secchi	A	B					y	y	#	#	#	#	#	#	#
20	Secchi	A	A							*	*	*	*	*	*	*
21	Jent	L	A													
22	Aent	A	B						y	#	#	#	#	#	#	#
23	Pred2	L	B	#	#	#	#	#	#	#	#	#	#	#	#	#
24	Pred2	A	A													y

Table S5. Correlation matrix for the covariates used in the analysis. See table 2 for definitions.

	Year	SpDys	TpAJ	TpJul	EPAJ	EPJul	Preds1	StBass	DSLth	TpJS	EPJA	Secci	JEnt	AEnt	Preds2
Year	1.00														
SpDys	0.03	1.00													
TpAJ	0.28	-0.41	1.00												
TpJul	0.41	0.06	0.21	1.00											
EPAJ	-0.48	0.03	-0.04	-0.31	1.00										
EPJul	-0.47	0.01	-0.23	-0.02	0.38	1.00									
Preds1	0.87	-0.06	0.44	0.45	-0.51	-0.36	1.00								
StBass	0.44	0.01	0.40	0.08	-0.23	0.00	0.54	1.00							
DSLth	-0.67	0.03	-0.10	-0.08	0.03	0.01	-0.53	-0.40	1.00						
TpJS	0.36	0.01	0.08	0.73	-0.35	-0.14	0.40	0.04	-0.16	1.00					
EPJA	-0.42	-0.07	-0.15	-0.04	0.27	0.94	-0.31	0.00	0.02	-0.16	1.00				
Secci	0.04	-0.13	0.21	0.06	-0.03	0.28	0.17	0.30	0.15	-0.26	0.31	1.00			
JEnt	-0.13	-0.11	0.33	0.25	-0.05	0.38	0.03	0.19	0.32	-0.09	0.47	0.60	1.00		
AEnt	0.38	0.22	0.15	0.45	-0.38	0.03	0.40	0.23	-0.04	0.30	0.10	-0.04	0.35	1.00	
Preds2	0.90	0.00	0.41	0.41	-0.44	-0.49	0.93	0.40	-0.50	0.33	-0.46	0.12	-0.05	0.39	1.00

Table S6. Correlation matrix for the parameters estimated in the model for the lowest AICc model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship. Many parameters are estimated on the log scale. See table 2 for covariate definitions.

			Correlation																
Parameter	Value	SD	$\ln(a_L)$	$\ln(a_J)$	$Ln(b_J)$	$Ln(a_A)$	$Ln(b_A)$	$Ln(N_{init})$	$Ln(\sigma_L)$	$Ln(\sigma_J)$	$Ln(\sigma_A)$	TpAJ	TpJul	EPAJ	EPJul	Pred1	EPJA	Secchi	Aent
$\ln(a_L)$	6.12	0.09	1.00																
$\ln(a_J)$	-0.84	0.27	-0.02	1.00															
$Ln(b_J)$	-8.85	0.15	-0.03	0.74	1.00														
$Ln(a_A)$	-1.40	0.87	0.12	0.06	0.05	1.00													
$Ln(b_A)$	-3.95	1.01	0.19	0.06	0.06	0.98	1.00												
$Ln(N_{init})$	2.03	0.42	-0.55	0.01	-0.02	-0.14	-0.17	1.00											
$Ln(\sigma_L)$	-10.30	3891.30	0.00	0.00	0.00	0.00	0.00	0.00	1.00										
$Ln(\sigma_J)$	-0.74	0.16	-0.03	0.06	-0.12	-0.01	-0.02	-0.01	0.00	1.00									
$Ln(\sigma_A)$	-0.48	0.13	-0.03	0.03	0.03	0.08	0.02	0.07	0.00	-0.03	1.00								
TpAJ	-0.22	0.07	0.07	0.07	0.03	0.06	0.04	-0.38	0.00	0.03	-0.01	1.00							
TpJul	-0.32	0.09	-0.22	0.02	-0.02	-0.24	-0.27	-0.07	0.00	0.05	-0.08	0.16	1.00						
EPAJ	0.36	0.11	-0.05	-0.02	-0.06	-0.05	-0.03	-0.30	0.00	0.05	-0.08	0.14	0.46	1.00					
EPJul	0.33	0.13	0.51	0.02	0.00	0.19	0.20	-0.64	0.00	0.00	-0.02	0.44	-0.17	-0.35	1.00				
Pred1	-0.44	0.17	-0.01	-0.86	-0.53	-0.07	-0.07	-0.02	0.00	0.04	-0.01	-0.07	-0.03	0.03	-0.03	1.00			
EPJA	0.46	0.12	-0.01	0.22	0.42	0.04	0.04	0.15	0.00	-0.06	0.04	-0.02	-0.02	-0.04	-0.03	-0.06	1.00		
Secchi	-1.15	0.48	-0.27	-0.08	-0.06	-0.81	-0.80	0.25	0.00	0.01	-0.01	-0.13	0.25	0.10	-0.35	0.08	-0.04	1.00	
Aent	10.32	4.67	0.18	0.07	0.06	0.89	0.85	-0.17	0.00	-0.01	0.01	0.11	-0.15	-0.13	0.29	-0.07	0.04	-0.71	1.00

Table S7. Correlation matrix for the parameters estimated in the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model). Many parameters are estimated on the log scale. See table 2 for covariate definitions.

			Correlation													
Parameter	Value	SD	$\ln(a_L)$	$\ln(a_J)$	$Ln(b_J)$	$Ln(a_A)$	$Ln(b_A)$	$Ln(N_{init})$	$Ln(\sigma_L)$	$Ln(\sigma_J)$	$Ln(\sigma_A)$	TpAJ	TpJul	EPAJ	Pred1	EPJA
$\ln(a_L)$	6.02	0.09	1.00													
$\ln(a_J)$	-0.89	0.27	-0.08	1.00												
$Ln(b_J)$	-8.85	0.15	-0.07	0.74	1.00											
$Ln(a_A)$	-2.52	0.52	0.05	0.04	0.02	1.00										
$Ln(b_A)$	-5.25	0.83	0.19	0.03	0.02	0.95	1.00									
$Ln(N_{init})$	2.67	0.39	-0.45	0.07	0.00	-0.13	-0.20	1.00								
$Ln(\sigma_L)$	-2.32	1.50	0.35	-0.14	-0.11	0.11	0.16	-0.34	1.00							
$Ln(\sigma_J)$	-0.76	0.16	-0.03	0.05	-0.12	0.03	0.02	0.00	-0.02	1.00						
$Ln(\sigma_A)$	-0.34	0.13	-0.08	0.08	0.05	0.14	0.01	0.13	-0.18	0.00	1.00					
TpAJ	-0.31	0.07	-0.19	0.09	0.04	0.04	0.00	-0.11	-0.10	0.03	0.06	1.00				
TpJul	-0.30	0.10	-0.16	0.05	0.00	-0.16	-0.19	-0.20	-0.13	0.02	-0.05	0.27	1.00			
EPAJ	0.47	0.12	0.28	-0.04	-0.08	0.16	0.21	-0.76	0.27	0.03	-0.14	0.29	0.40	1.00		
Pred1	-0.40	0.17	0.04	-0.87	-0.54	-0.05	-0.03	-0.08	0.13	0.05	-0.06	-0.08	-0.07	0.05	1.00	
EPJA	0.46	0.12	-0.02	0.22	0.41	0.01	0.01	0.17	-0.06	-0.07	0.03	0.00	-0.01	-0.07	-0.07	1.00

Public Workshop (9/5-6/12)
Bay-Delta Workshop 1
Deadline: 8/17/12 by 12 noon

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FISH AND WILDLIFE SERVICE
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Sacramento, California 95814

August 17, 2012

Technical Staff Comments to the State Water Resources Control Board re: the Comprehensive (Phase 2) Review and Update to the Bay-Delta Plan

The U.S. Fish and Wildlife Service (Service) submits the following written comments in response to the questions posed by the State Water Resources Control Board (Board) for discussion at the low-salinity zone and pelagic fish workshops that support the Comprehensive (Phase 2) Review and Update to the Bay-Delta Plan. The following discussion contains additional scientific and technical information that was not addressed in the 2009 Staff Report or the 2010 Delta Flow Criteria Report. It also provides general background information related to delta smelt and ecosystem changes in the low salinity zone (LSZ). These comments also supplement the Department of Interior's April 25, 2012 comments to the Board regarding the Comprehensive Review and Update of the Bay-Delta Plan. Overall, we make the following key points to supplement our April 25th key points:

- We suggest that the Board model and evaluate a range of flow objectives that could be incorporated in the Water Quality Control Plan (WQCP). Our suggested evaluation should include flow objectives that are likely to improve habitat conditions for delta smelt, longfin smelt, and other native estuarine biota and put the ecosystem on a path toward recovery.
- For adult delta smelt, negative Old and Middle River (OMR) flows contribute to entrainment risk during spawning migrations.
- For age-0 delta smelt OMR flows are a suitable index of the hydrodynamic conditions that *drive* entrainment loss.
- The Service recognizes that multiple factors have contributed to the substantial long-term degradation of the LSZ. Nonetheless, Sacramento-San Joaquin Delta (Delta) outflow remains an extremely important aspect of LSZ habitat suitability for delta smelt, particularly during low flow periods.

Background

The Service uses the Department of Fish and Game's (DFG) Fall Midwater Trawl (FMWT) index as our primary indicator of delta smelt status. The FMWT indices date to 1967. The 1967 index for delta smelt was 414. Since that time, the indices have occasionally reached new record lows reflecting the delta smelt decline that has been reported previously (Moyle et al. 1992;

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Bennett 2005; Sommer et al. 2007), but the frequency of occurrence of new record lows increased notably in the last decade. The time series of new lows in the delta smelt FMWT indices is as follows: 1969 index = 315, 1983 index = 132, 1985 index = 110, 1994 index = 102, 2004 index = 74, 2005 index = 26, 2008 index = 23, and 2009 index = 17. The delta smelt is an estuarine-dependent species (Moyle et al. 1992; Bennett 2005). Estuaries are places where marine water meets and mixes with sources of freshwater. Central San Francisco Bay to the Golden Gate Bridge is the seaward boundary of the San Francisco Estuary (Kimmerer 2004). Here, the estuary's waters are highly contiguous with the Pacific Ocean and thus they are typically about the same salinity as the open Pacific coast. The Delta is the landward region of the San Francisco Estuary. Most of the Delta is maintained as a freshwater environment to support water diversions that serve numerous agricultural, industrial, and municipal uses. Ecologically, the estuary extends upstream to the limit of tidal influence in the Sacramento and San Joaquin watersheds. However, the upstream limit of tidal influence depends on the magnitude of river flow and the strength of individual tides. The Board has provided a legal boundary for the Delta. It extends from Chipps Island in the west to the City of Sacramento on the Sacramento River and to Vernalis on the San Joaquin River.

The Service's comments focus on delta smelt and their interactions with Delta flows, including south Delta flows and the LSZ. Therefore, these comments are relevant to both the Board's upcoming Low Salinity Zone and the Pelagic Fishes workshops. The function of the LSZ is extremely important to delta smelt. The LSZ is a constantly moving habitat that frequently transcends the Board's legal boundaries (i.e., the Delta or Suisun Marsh). The LSZ is the primary freshwater-seawater mixing zone in the San Francisco Estuary (Kimmerer 2004). It has been defined differently by different authors, but Kimmerer (2004) reported that the historical chlorophyll maxima in the upper estuary occurred over a salinity range of about 0.5 to 6.0 psu[1], which represents an approximate definition of the LSZ. It is important to note however that a definition of a lower salinity bound near 0.5 psu is not based on fish distributions. It is based on the ability to distinguish oceanic salt from salts in agricultural return water flowing into the Delta based on measurements of specific conductance. Delta smelt are fairly freshwater tolerant fishes (Swanson et al. 2000). They do not recognize 0.5 psu as a boundary, and can sometimes be collected to the limits of tidal excursion and at salinities down to circa 0.1 psu when other water quality attributes like turbidity and temperature are suitable (Feyrer et al. 2007; 2011; Kimmerer et al. 2009). The upper bound of salinity chosen to represent the LSZ has typically been based on collection of the organisms that were the target species of individual studies. Delta smelt are somewhat tolerant of brackish water, but rarely captured at salinities higher than 10 psu. Thus, delta smelt can be considered to complete its life cycle in the LSZ and some fresher water habitats that are *highly contiguous* with the 'official' freshwater boundary salinities that scientists have proposed for the LSZ. The following sections crosswalk the life cycle of delta smelt with Delta flows.

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1 psu is 'practical salinity units' which are equivalent to parts per thousand

Migrating and Spawning Adults (~ December through March)

Adult Entrainment

Adult delta smelt are entrained during spawning migrations (Grimaldo et al. 2009a; Sommer et al. 2011). Their spawning migrations occur during the winter when precipitation increases the freshwater flow and turbidity in the Delta. Salvage of adults has occurred mainly from late December through March (Kimmerer 2008; Grimaldo et al. 2009a). For migrating adults, the risk of entrainment is influenced by flow cues and turbidity in the south Delta.

The Distribution of Spawning Delta Smelt

Delta smelt probably spawn in shallow, sandy habitats (Bennett 2005). This hypothesis is supported by laboratory experiments and by delta smelt's close evolutionary relationship with the marine surf smelt, which spawns in the intertidal habitat of Pacific coast beaches and embayments. Shallow, sandy habitats occur throughout the Delta. Given suitable conditions, delta smelt can spawn successfully throughout the Delta, Suisun Marsh, and as far seaward as the Napa River, but this full range of potential spawning habitats is not available every year (Hobbs et al. 2005; 2007).

Snapshots of adult delta smelt distribution are available via the Spring Kodiak Trawl Survey (SKTS) (www.dfg.ca.gov/delta/; Figure 1). The survey is conducted once per month from January-May and has been occurring since 2002. During the first nine years of the SKTS, most delta smelt have been collected in Montezuma Slough (36%) and the Cache Slough region (32%); 6% have been collected in the Delta at trawl stations numbered 809 and higher, i.e., the San Joaquin River 'half' of the Delta (Figure 2)[2]. Thus, the Service notes that most adult delta smelt have not been collected from locations where they would be expected to have a high risk of entrainment (i.e., stations numbered 809 and higher). However, the Service also notes that adult delta smelt have been collected in the lower San Joaquin River at or upstream of station 809 every year that the SKTS has been conducted and that the ability of the survey to detect delta smelt appears to be dependent on population abundance (Figure 3). Note that both Kimmerer (2008; 2011) and Miller (2011) have assumed the SKTS is essentially 100% efficient for collecting delta smelt. This assumption is mainly for computational simplicity. However, this assumption of 100% gear efficiency is probably not strictly correct because (1) the ability to detect delta smelt in the San Joaquin River is contingent upon overall abundance, and (2) delta smelt are observed in salvage even when they are not observed in south Delta trawls (Figure 4).

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2 Percentages calculated from the data shown in Figure 2. The region of the Delta encompassed by trawl stations numbered 809 and higher is considered by the Service to represent a region of elevated risk of entrainment based on Kimmerer and Nobriga (2008).

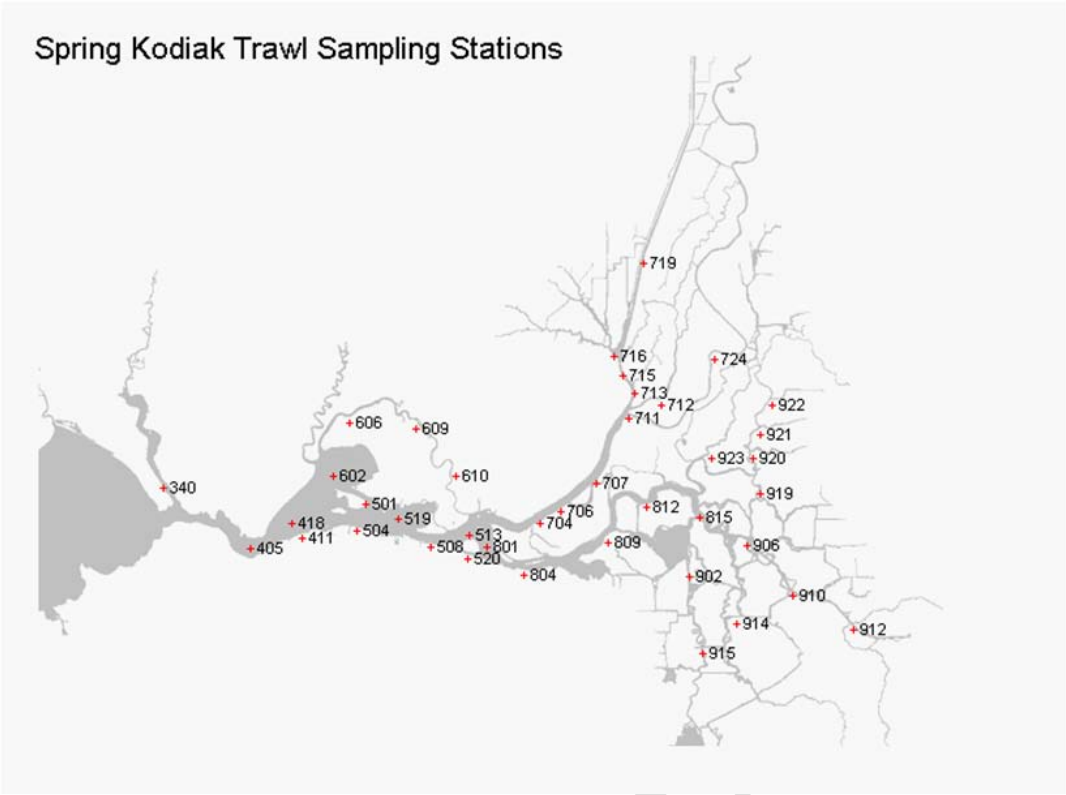

Figure 1. Map of the Department of Fish and Game's Spring Kodiak Trawl Survey sampling stations. Source: http://www.dfg.ca.gov/delta/data/skt/skt_stations.asp; August 30, 2011.

Sum of Catch	Column Labels																																							
Row Labels	340	405	411	418	501	504	508	513	519	520	602	606	609	610	704	705	706	707	711	712	713	715	716	719	724	725	801	804	809	812	815	902	906	910	912	914	915	919	920	921	922	923	Grand Total
2002	1	3	2	3	1	0	5	13	3	17	8	257	256	76	17		26	3	41	1	8	6	23			1	19	22	44	14	5	4	6	0	0	3	2	1	0	2	2	0	895
2003	0	0	5	14	8	5	13	12	17	0	21	42	13	24	13		23	54	2	13	39	125	173			7	8	1	28	4	2	0	3	0	0	1	0	0	0	0	2	9	681
2004	1	0	0	3	6	2	0	8	15	23	7	170	360	1	98		25	15	0	0	4	6	2			1	3	54	80	29	8	2	21	1	0	2	0	2	1	0	1	0	951
2005	3	0	1	3	18	4	4	2	11	0	1	92	128	10	34		34	4	1	0	6	20	51	42	1	0	1	0	2	4	2	2	1	0	0	0	0	0	2	0	0	0	484
2006	34	2	5	1	8	5	3	3	8	2	1	49	10	4	1		0	1	0	0	0	18	9	102	0		1	2	3	0	1	3	0	0	0	1	0	2	1	0	2	0	282
2007	0	0	0	0	0	0	1	8	21	0	1	53	29	3	40		16	3	1	0	1	13	12	187	0		0	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	398
2008	0	1	0	0	4	1	4	3	4	0	1	4	3	0	63	4	19	11	0	0	2	9	11	122	0		0	0	1	2	1	0	0	0	0	0	0	0	1	0	0	0	271
2009	0	0	0	0	0	0	1	2	13	0	0	64	34	3	35		99	19	0	0	0	0	3	459	0		0	0	11	0	1	0	0	0	0	0	0	0	0	0	1	0	745
2010	0	0	0	1	0	0	2	3	3	0	1	64	37	1	27		11	2	0	0	5	18	9	116	0		0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	303
Grand Total	39	6	13	25	45	17	33	54	95	42	41	795	870	122	328	4	253	112	45	14	65	215	293	1028	1	9	32	82	178	53	20	11	31	1	0	7	2	5	5	2	8	9	5010

Figure 2. Cross-tabular summary of adult delta smelt catch by survey station in the Spring Kodiak Trawl Survey, 2002-2010. The catch data were only summarized for surveys that sampled a full array of stations, i.e., no special surveys of only particular regions of the sampling grid. Empty cells show where no sampling occurred at a given station. Stations considered by the Service to potentially be within the typical hydrodynamic influence of the Projects' south Delta water diversions are shaded in light blue. See Figure 1 for locations of SKTS sampling stations.

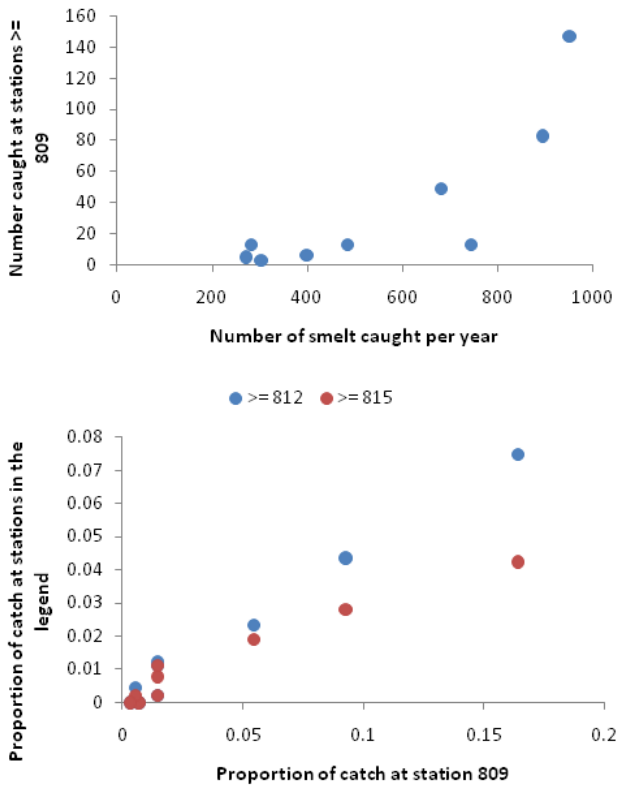

Figure 3. Top Panel: Scatterplot of number of delta smelt caught at all SKTS stations versus the number collected from stations numbered 809 and higher. Bottom panel: Scatterplot of the proportion of total SKTS catch collected from station 809 near Jersey Point on the San Joaquin River and the concurrent proportions collected at the next two stations located upstream, 812 (blue circles) and 815 (red circles). See Figure 1 for locations of sampling stations.

The entrainment of delta smelt into the State Water Project (SWP) and Central Valley Project (CVP) facilities is strongly influenced by Delta flows. Total entrainment is calculated based upon estimates of the number of fish salvaged[3] (Kimmerer 2008). However, these estimates are indices - most entrained fish are not observed (Table 1), so most of the fish are not salvaged and therefore do not survive. Many, if not most, of the delta smelt that do reach the fish facilities likely die due to predation and handling stress (Bennett 2005). Pre-screen loss (PSL) due to entrainment into the SWP and CVP facilities, is an additional cause of mortality for delta smelt. The PSL in Clifton Court Forebay was estimated to be up to 100 percent during recent studies that used captive bred fish (Castillo et al. 2010).

3 See Brown et al. (1996) for a description of fish salvage operations.

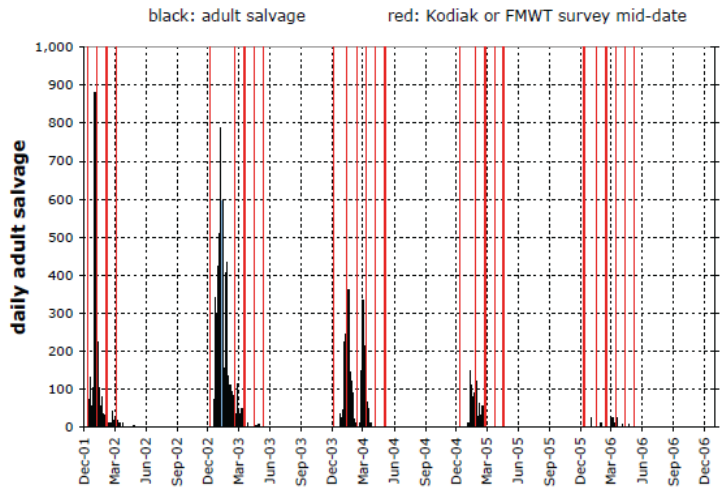

Figure 3 Daily adult salvage and mid-dates for Kodiak and Fall Midwater Trawl (FMWT) surveys

Figure 4. Copy of Figure 3 from Miller (2011). The vertical red lines denote dates of Spring Kodiak Trawl Surveys when very low numbers of delta smelt were collected from stations numbered 809 or higher (Figure 2). The black histogram data show the timing and magnitude of adult delta smelt salvage at the Projects' fish facilities as a continuous time series for December 2001-2006.

Old and Middle Rivers are distributary channels of the San Joaquin River. The export of water from the Delta can cause the tidally filtered, or "net" flows in these channels to move "upstream". This occurs because water removed by SWP's Banks Pumping Plant and CVP's Jones Pumping Plant is back-filled by tidal and river flows. This phenomenon is mathematically depicted as negative flow. Negative OMR flows are often associated with adult delta smelt entrainment (Kimmerer 2008; Grimaldo et al. 2009a), but there is no particular OMR flow that assures entrainment will or will not occur (Figure 5 to 8). The net OMR flows indicate how strongly the tidally averaged flows in these channels are moving toward Banks and Jones. Thus, it is possible the net flows themselves are the mechanism that increases entrainment risk for delta smelt. However, high exports can also lead to the loss of ebb tide flows in Old and Middle Rivers (Gartrell 2010), so altered tidal flows are a second, covarying mechanism that could increase delta smelt's risk of entrainment.

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Table 1. Factors affecting delta smelt entrainment and salvage.

	Adults	Larvae < 20 mm	Larvae > 20 mm and juveniles
Predation prior to encountering fish salvage facilities[a]	89.9-100%	unquantified	99.9%[b]
Fish facility efficiency (based on Kimmerer 2008)	Limited data indicate an efficiency of about 13 percent for the CVP facility; SWP efficiency averaged an estimated 50%, but actual efficiency was related to operating conditions (Castillo et al. in review)	~ 0 percent	Likely < 13 percent at any size; << 13 percent at less than 30 mm; estimated at 24% and 30% in two experiments in June 2009 (Castillo et al. in review)
Efficiency of collection screens	~ 100 percent	~ 0 percent	< 100 percent until at least 30 mm
Identification protocols	Identified from subsamples, then expanded in salvage estimates	Not identified	Identified from subsamples, then expanded in salvage estimates
Fish survival after Handling, trucking and release back into the Delta[c]	Controlled conditions trial (2005): 94% were recovered from the Skinner fish facility; 87% survived for 48 hrs in a holding tank after the experiment Empirical salvage trial (2006): 90% were recovered from the Skinner fish facility; 78% survived for 48 hrs in a holding tank after the experiment	0 percent	Controlled conditions trial (2005): 73% were recovered from the Skinner fish facility; 37% survived for 48 hrs in a holding tank after the experiment Empirical salvage trial (2006): 89% were recovered from the Skinner fish facility; 58% survived for 48 hrs in a holding tank after the experiment

[a]Pre-screen loss (Castillo et al. in review)
[b]Based on one release experiment (Castillo et al. in review)
[c]Unpublished report sent by Jerry Morinaka (CDFG) on July 13, 2011; numbers reported do not include predation at release sites

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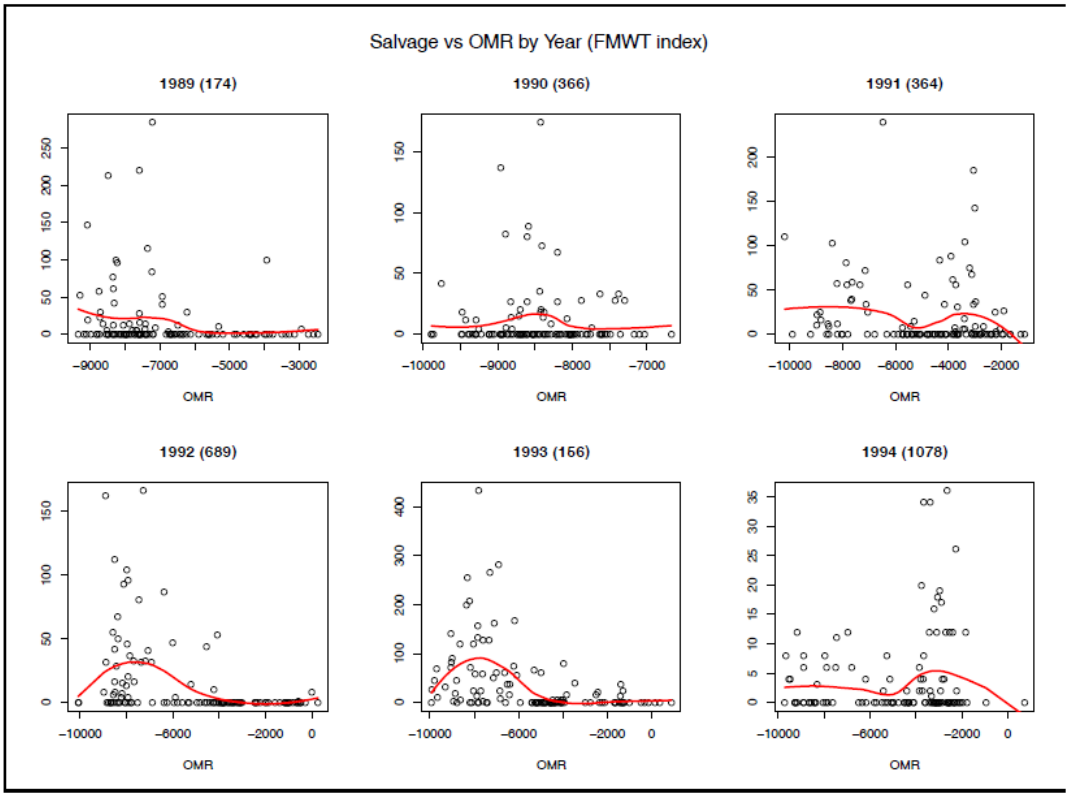

Figure 5.Scatterplots of net daily flow in Old and Middle rivers versus daily delta smelt salvage for the months December-March, 1989-1994 (December data are 1988-1993). The Fall Midwater Trawl (FMWT) abundance index for delta smelt that immediately precedes the salvage data in time is shown at the top of each panel in parentheses. The red lines are splines showing the empirical trend in the data. Source: Ken Newman (Stockton Fish and Wildlife Office)

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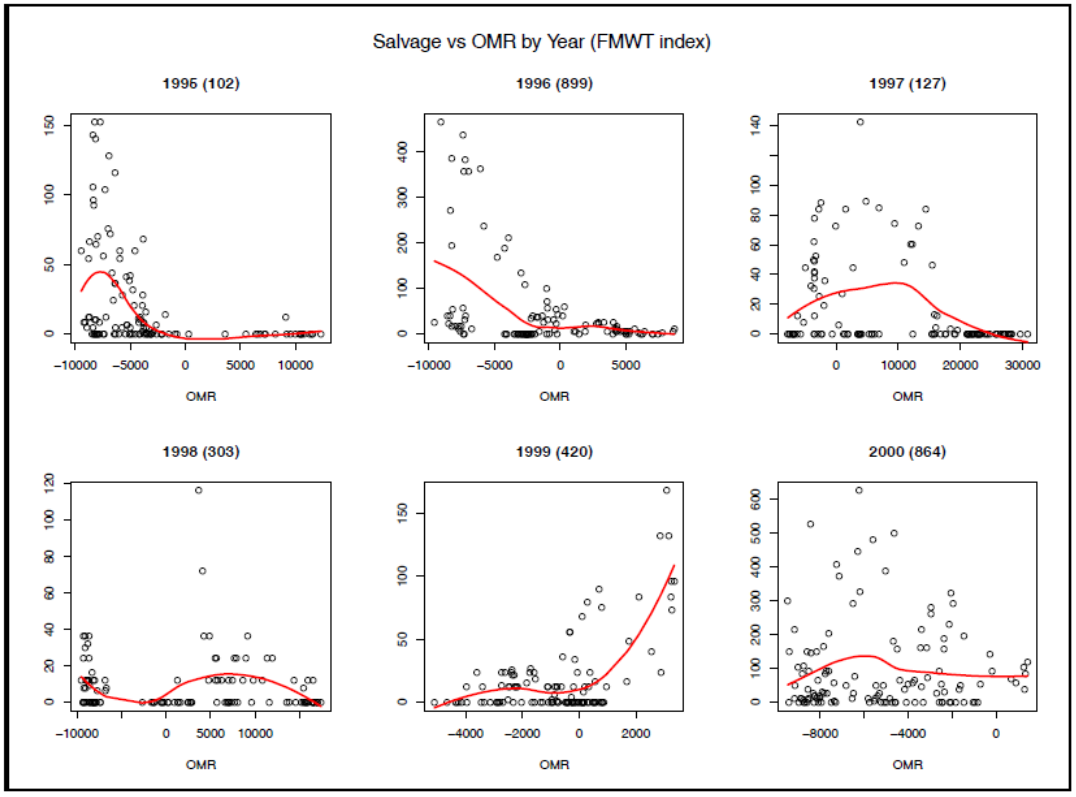

Figure 6. Scatterplots of net daily flow in Old and Middle rivers versus daily delta smelt salvage for the months December-March, 1995-2000 (December data are 1994-1999).The Fall Midwater Trawl (FMWT) abundance index for delta smelt that immediately precedes the salvage data in time is shown at the top of each panel in parentheses. The red lines are splines showing the empirical trend in the data. Source: Ken Newman (Stockton Fish and Wildlife Office)

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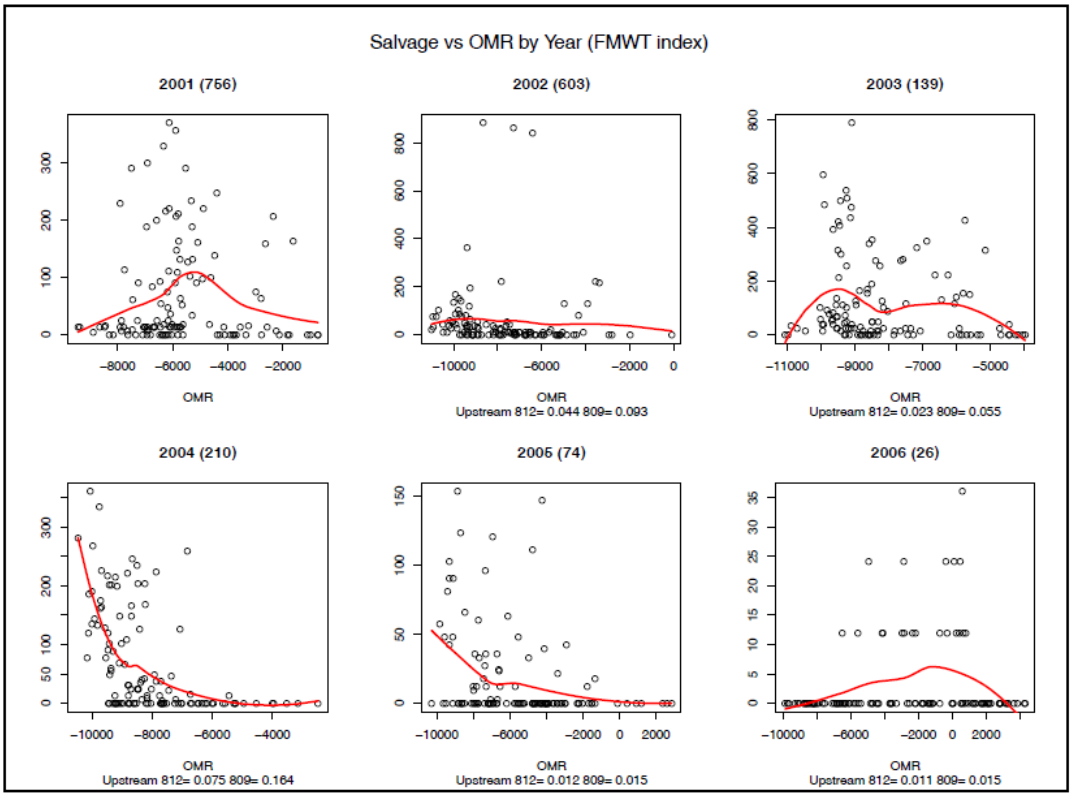

Figure 7. Scatterplots of net daily flow in Old and Middle rivers versus daily delta smelt salvage for the months December-March, 2001-2006 (December data are 2000-2005). The Fall Midwater Trawl (FMWT) abundance index for delta smelt that immediately precedes the salvage data in time is shown at the top of each panel in parentheses. The red lines are splines showing the empirical trend in the data. Source: Ken Newman (Stockton Fish and Wildlife Office)

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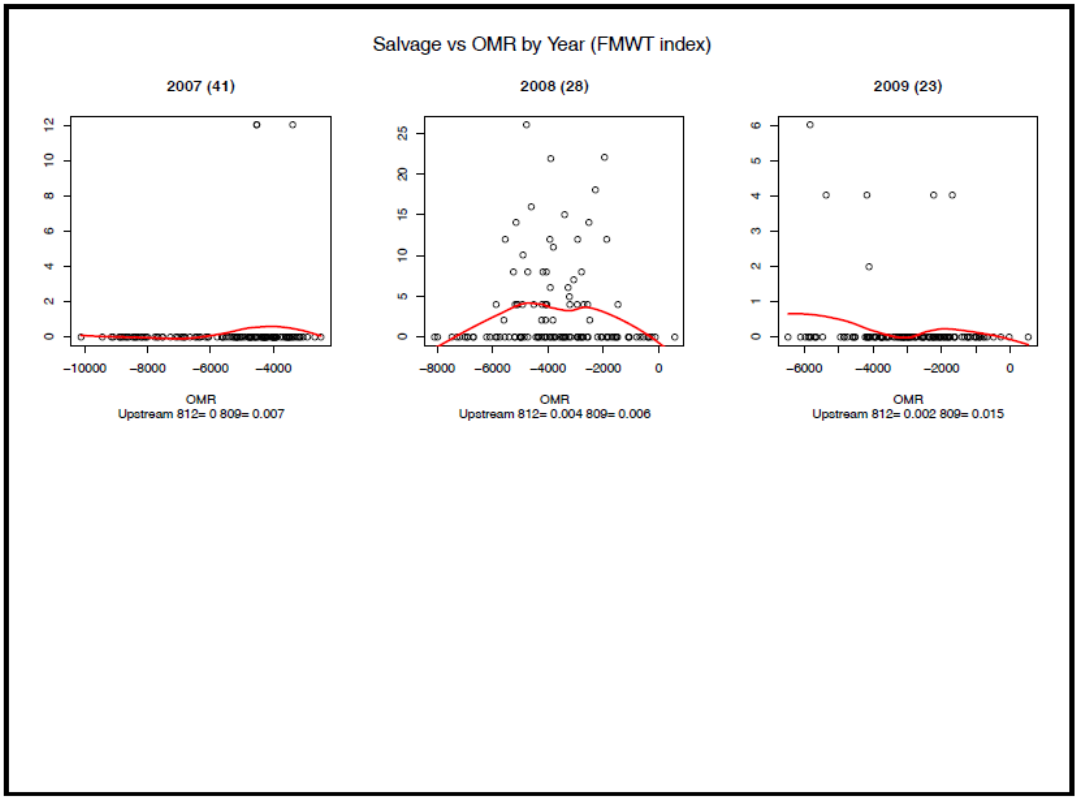

Figure 8. Scatterplots of net daily flow in Old and Middle rivers versus daily delta smelt salvage for the months December-March, 2007-2009 (December data are 2006-2008). The Fall Midwater Trawl (FMWT) abundance index for delta smelt that immediately precedes the salvage data in time is shown at the top of each panel in parentheses. The red lines are splines showing the empirical trend in the data. Source: Ken Newman (Stockton Fish and Wildlife Office)

The empirical shape of the associations between the geographic distribution of the 2 psu salinity isohaline (X2; Jassby et al. 1995), OMR, turbidity and adult delta smelt salvage normalized by the FMWT is shown in Figure 9. Normalized delta smelt salvage is correlated in a nonlinear way with X2. An interpretation of this is that the intermediate river flow or X2 conditions are associated with the highest salvage because flows are high enough to disperse turbidity around the Delta, but not so high that most delta smelt are distributed seaward of the Delta. At higher X2 (lower flows) the south Delta is infrequently turbid enough to attract delta smelt. Figure 9 shows that even when X2 and south Delta turbidity are accounted for, there is still no OMR flow that assures delta smelt entrainment will or will not occur. The predicted relationship is a smooth, accelerating function with increasing normalized salvage as OMR flow becomes more negative.

Full Model

```
*** Generalized Additive Model ***

Call: gam(formula = Sal.pfmwt ~ s(O.M.flow) + s(CCFNTU) + s(X2),
family = gaussian,
                data = biop, na.action = na.omit, control = list(epsilon =
0.001,
                bf.epsilon = 0.001, maxit = 50, bf.maxit = 10, trace = F))
Deviance Residuals:
     Min       1Q     Median       3Q     Max
 -0.6108443 -0.1510043 -0.05404843 0.0677257 4.971304

(Dispersion Parameter for Gaussian family taken to be 0.1261855 )

   Null Deviance: 355.2256 on 2060 degrees of freedom

Residual Deviance: 258.4277 on 2047.999 degrees of freedom

Number of Local Scoring Iterations: 1

DF for Terms and F-values for Nonparametric Effects

         Df Npar Df   Npar F        Pr(F)
(Intercept)  1
s(O.M.flow)  1      3 22.77489 1.698641e-014
 s(CCFNTU)  1      3 31.86953 0.000000e+000
    s(X2)  1      3 29.17776 0.000000e+000
```

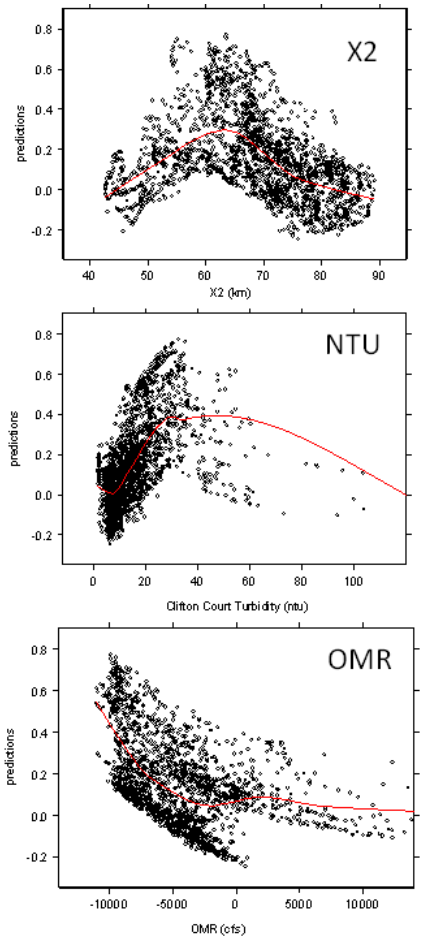

Figure 9. S-Plus output of a generalized additive model (GAM) testing for effects of X2, turbidity at Clifton Court Forebay (Nephelometric Turbidity Units; NTU), and net flow in Old and Middle rivers (OMR) on adult delta smelt salvage normalized by the preceding Fall Midwater Trawl abundance index. The text on the left shows the model code, the model fit is 1-(residual deviance/ null deviance). Thus, the model explains 1-(258/355) = 0.273 of the variation in normalized salvage. The column Pr(F) shows the probability of no trend in the data – these P-values are all much less than a standard 0.05 threshold due to the non-random trends in the data but also due somewhat to the very large sample size (> 2000 data points). The model predictions are shown in the panels on the right. The scatter in each panel is due to the interacting effects of the other two variables. The red lines are splines showing the empirical trends in the predictions. Source: Lenny Grimaldo (Reclamation Bay-Delta Office).

The entrainment risk of larval delta smelt has been estimated quantitatively with particle tracking models (PTMs), in particular, the Department of Water Resources' (DWR) DSM-2 PTM (Kimmerer and Nobriga 2008; Kimmerer 2008). The entrainment risk for adult delta smelt actively migrating into the lower San Joaquin River cannot be quantitatively summarized with current PTMs[4]. Even without a vetted quantitative modeling tool, PTM data provide the best available indication of the hydrodynamic influence on adult delta smelt entrainment risk given

4 DSM-2's particle tracking model can generate upstream particle movements when the particles are given simple tidal surfing behavior (Sommer et al. 2011). A PTM that may more accurately characterize delta smelt spawning migrations is being developed by RMA.

two conditions: (1) turbid water is present in Old and Middle rivers, and (2) adult delta smelt migrate into the San Joaquin River. This is likely true because the particle tracking modeling shows the extent of the Projects' hydrodynamic influence on the Delta and how that influence changes as river flows and exports vary (Kimmerer and Nobriga 2008).

Miller (2011) assumed that because migrating delta smelt actively swim, they would not be vulnerable to OMR flows and therefore scaling delta smelt loss to OMR flows would result in loss estimates that were persistently biased high. Kimmerer (2011) disagreed, noting that there were not automatically any environmental cues that would signal migrating delta smelt to stop swimming toward the pumps. The Service agrees with Kimmerer (2011) that Miller (2011) was confounding bias with statistical uncertainty. Bias occurs when an estimate is always too high or too low, whereas statistical uncertainty is variation around an estimate that is sometimes too high and sometimes too low.

Migrating delta smelt are actively swimming, likely using a combination of their own swimming behaviors and tidal currents to move upstream against the net Delta outflow (e.g., Sommer et al. 2011). If they encounter an adverse environmental cue in the south Delta, such as water that is not sufficiently turbid, they might adjust their behavior and stop short of being entrained. However, if they do not perceive such a cue, they may keep migrating and move south down Old and Middle rivers *faster or slower* than the net flow. Note that the occurrence of a spawning migration itself demonstrates that delta smelt can move faster than (and against) the net flow in the estuary. Thus, the link between adult delta smelt entrainment and OMR flows is more an issue of statistical uncertainty (sometimes their southward flux is slower than OMR flow and sometimes it is faster) than bias (always slower or higher).

OMR flows between -2000 and -5000 cfs minimize the Projects' hydrodynamic influence in the San Joaquin River (mainstem). Extending that hydrodynamic influence to the mainstem of the San Joaquin River decreases the likelihood that delta smelt can reproduce successfully in the expanses of shallow sandy habitats that occur from downstream of the City of Stockton to the City of Antioch.

The flow cues that contribute to adult delta smelt entrainment have increased over time. Winter exports first exceeded 400 thousand acre-feet (TAF)/month in March of 1972 (Figure 10). Since that time, monthly winter exports have seldom been less than that. Winter exports first exceeded 600 TAF/month in January 1978 and 700 TAF in January 1993. The frequency that monthly winter exports has exceeded 600-700 TAF has generally increased, though they were well below this level during the very wet middle of the 1990s and during the past few years, likely due to a combination of drought and export restrictions for fishery protection. Monthly winter exports have not dropped below 200 TAF since March of 1997.

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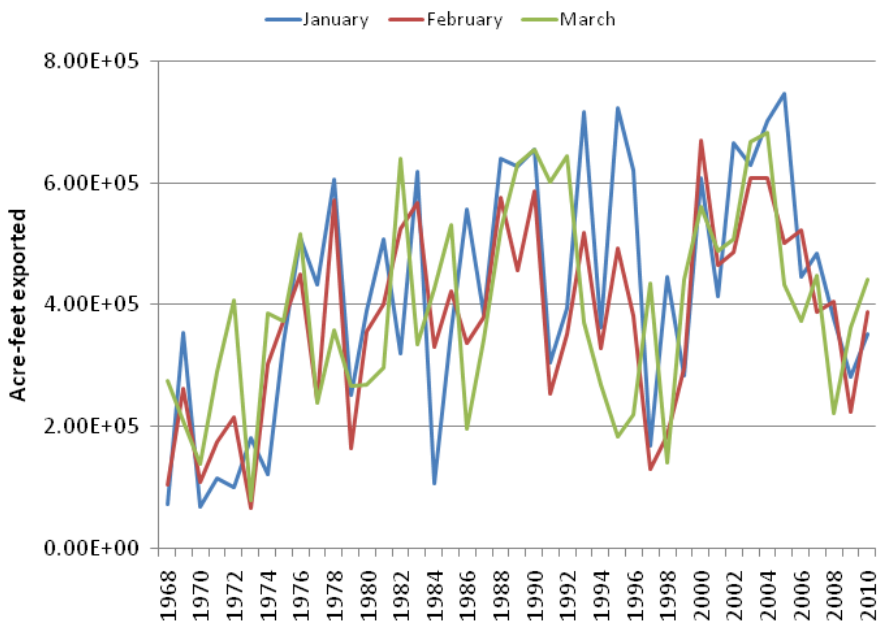

Figure 10. Time series of winter exports (CVP and SWP combined), 1968-2010. Source: DAYFLOW database

The population-level effects of winter exports via delta smelt entrainment vary; delta smelt entrainment can best be characterized as having a sporadically significant influence on population dynamics. Kimmerer (2008) estimated that annual entrainment of the adult delta smelt population ranged from approximately four percent to 50 percent per year from 2002-2006. He revised these estimates downward slightly (Kimmerer 2011) following a rebuttal by Miller (2011) (Table 2). Major population declines during the early 1980s (Moyle et al. 1992) and early 2000s (Sommer et al. 2007) were both associated with hydrodynamic conditions that increased delta smelt proportional entrainment losses. However, currently published analyses of long-term associations between delta smelt salvage and subsequent abundance do not support the hypothesis that entrainment is driving population dynamics year in and year out (Bennett 2005; Manly and Chotkowski 2006; Kimmerer 2008; Maunder and Deriso 2011).

Table 2. Estimates of the proportion of the adult delta smelt population entrained at Banks and Jones pumping plants.

Year	Kimmerer (2008) estimate	Kimmerer (2011) correction
1995	18	14
1996	3	2

1997	3	2
1998	1	0.76
1999	3	2
2000	5	4
2001	5	4
2002	16	12
2003	22	17
2004	19	14
2005	9	7
2006	3	2

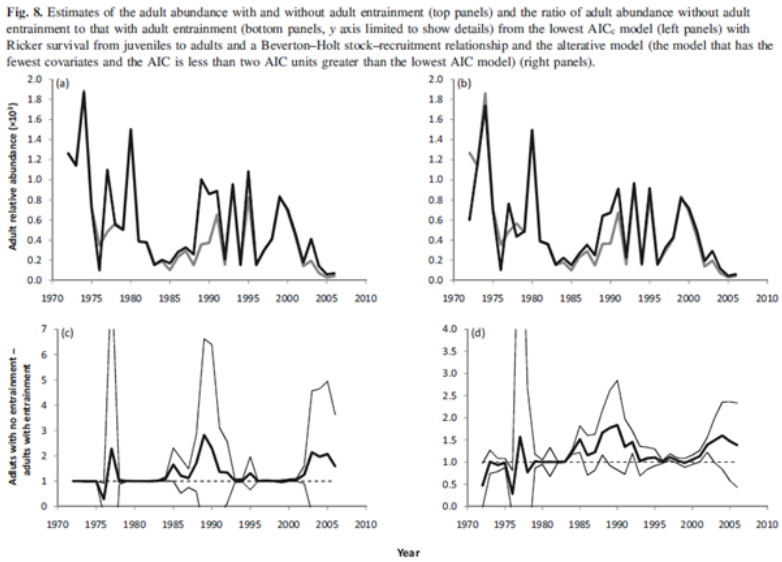

Figure 11. Copy of Figure 8 from Maunder and Deriso (2011). The top panels show predicted time series of delta smelt abundance based on two variations of life cycle models developed by the authors; black lines are predicted abundance without adult entrainment, gray lines are predicted abundance with adult entrainment.

The bottom panels depict the same data as relative deviations. "AIC_c" in the authors' caption refers to the Akaike Information Criterion, an indicator of the relative fit of alternative statistical models.

The evidence for a negative effect of adult entrainment on delta smelt population dynamics is supported by Maunder and Deriso's (2011) Figure 8, reproduced here as Figure 11 and Kimmerer's (2011) Figure 3, reproduced here as Figure 12. In the Maunder and Deriso simulations, adult entrainment had the sporadically significant effect mentioned above. Entrainment did not drive the delta smelt decline in their simulations, but it sometimes exacerbated it (Figure 11). Kimmerer developed a simulation model which showed that, given delta smelt's present-day, essentially density-independent population dynamics, an average entrainment loss of 10% would cause a 10-fold reduction in abundance and it would probably not be discernable using correlation-based statistics (Figure 12). In conclusion, the scientific evidence available to the Service is inconclusive about the *long-term* population-level importance of adult entrainment. However, there is new evidence based on model simulations that in years with comparatively negative OMR flows, adult entrainment can cause the population to decline (Kimmerer 2011; Maunder and Deriso 2011).

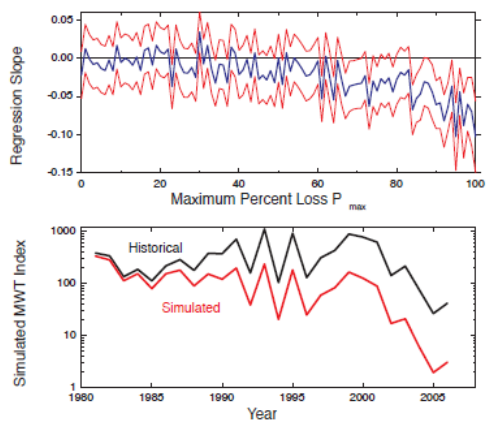

Figure 3 Results of simulation of ability to detect export loss through regression analysis. Upper panel: individual simulation results giving the slope (thick blue line) and 95% confidence limits (thin red lines) for regressions of the stock-recruit index on southward OMR flow. Lower panel: trajectory of the fall midwater trawl index (upper line) and the same index with a 20% P_{max} value imposed for the entire time series (mean P_L ~10%). This is for illustration only (see text), and does not imply anything about the cause of the decline in delta smelt.

Figure 12. Copy of Figure 3 from Kimmerer (2011). In the author's caption, P_{max} refers to a maximum proportion of the delta smelt population assumed to be entrained by the Projects and P_L refers to an average proportional entrainment loss of 10% of the population. The bottom panel shows how much this level of entrainment loss would cause the delta smelt population to decline in the absence of density-dependence. Note (1) the log-scale on the y-axis of the bottom panel; (2) the author made the case, similar to the Service, that compensatory density-dependence is unlikely to be an important regulator of delta smelt population growth rate due to its very low abundance. The top panel shows that a standard regression analysis searching for an entrainment effect on delta smelt abundance would be unlikely to find one unless the entrainment loss was exceptionally high (> 60% of the entire population).

Adult entrainment and south Delta turbidity

Adult delta smelt are strongly associated with turbid water (Feyrer et al. 2007; 2010; Miller 2011; Figure 13). Thus, if turbid water is present in the south Delta then delta smelt are more likely to inhabit that water and be more vulnerable to entrainment. Miller (2011) noted that south Delta waterways often are less turbid than regions to the north and west, a conclusion which had been reported several times in prior studies, albeit for different times of year (Nobriga et al. 2005; Feyrer et al. 2007; Nobriga et al. 2008).

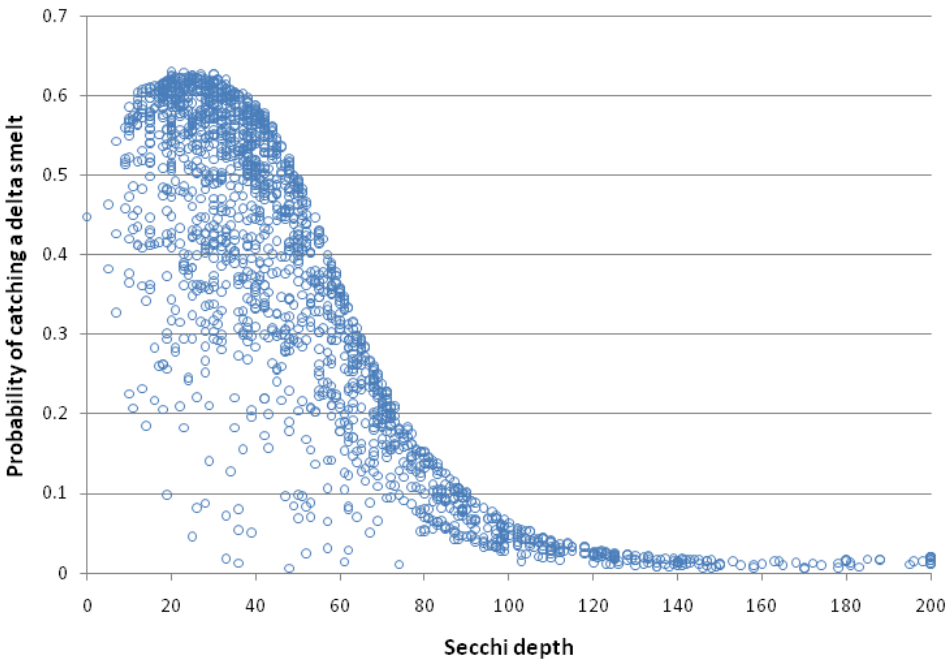

Figure 13. Scatterplot showing the predicted probability of capturing a delta smelt in the Spring Kodiak Trawl Survey relative to water transparency measured as Secchi disk depth in cm. The predictions are based on a binomial generalized additive model as was previously done by Feyrer et al. (2007) for the Fall Midwater Trawl and Nobriga et al. (2008) for the Summer Townet Survey. The scatter shows the variation in predictions caused by the interaction of two other variables (specific conductance and water temperature). In other words, probability of capture can be low in turbid water if salinity or temperature are too high, but probability of capture will never be high where turbidity is low, regardless of the other variables.

Despite the generality that the water in the south Delta is often comparatively clear, turbid conditions can occur there – particularly during winter storms (Grimaldo et al. 2009a). The longest running turbidity sensor in the south Delta is at the intakes of Clifton Court Forebay (CCF). The data from this sensor were used by Deriso (2011) to develop an OMR flow + turbidity model to predict adult delta smelt entrainment events. Figure 14 shows the trend in CCF turbidity for the winter (December-March, 1988-2009). This time period is coincident with the time period of our adult delta smelt salvage analysis, presented below, which was done to expand on that of Deriso (2011). The turbidity at CCF declined during the 1987-1992 drought, then increased to a peak in 1997. The turbidity declined after 1997, but generally remained elevated relative to 1987-1996 levels, during 1998-2006. Turbidity was low in 2007 and 2009,

but was fairly high again in 2008. Thus, there has not been a long-term unidirectional trend in turbidity at CCF during the winter. This indicates that comparably turbid conditions can be expected to keep occurring into the future. This contrasts with the south Delta regionally, which has been shown to have trended toward higher water transparency in the summer-fall (Feyrer et al. 2007; Nobriga et al. 2008). The trends in south Delta water transparency for the spring have not been reported in the literature, but they are presented in the larval-juvenile entrainment section of these comments.

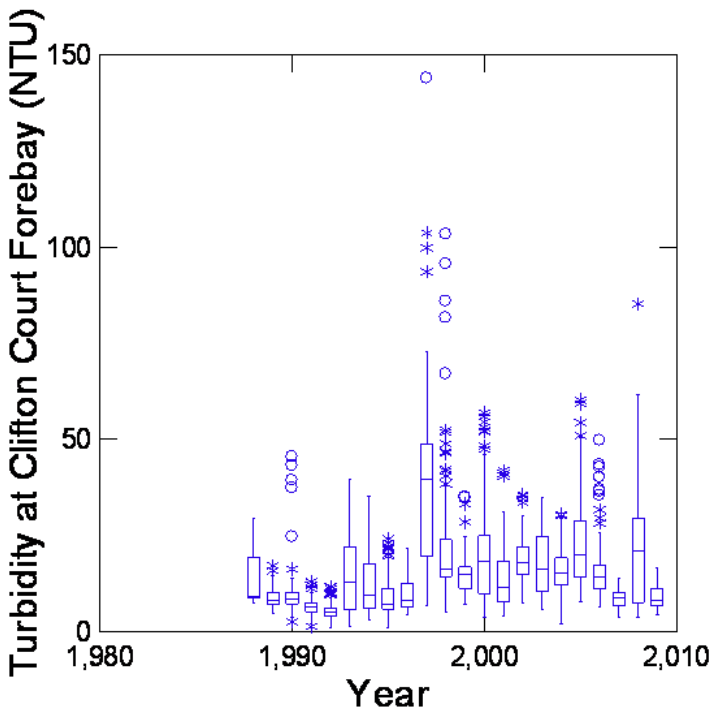

Figure 14. Time series of turbidity measurements at Clifton Court Forebay for the months of December-March (beginning December 1988 and ending March 2009). NTU = nephelometric turbidity units. The box plots are as follows: rectangular box = interquartile range of observations; horizontal line in the box = median; vertical lines = 95% confidence intervals; open circles and asterisks = individual data points the Systat software program determined were "outliers".

Deriso (2011) proposed a statistical model to guide Project operations during winter. The model was developed to predict the combinations of OMR flow and CCF turbidity that resulted in large delta smelt salvage events. The model was developed using daily OMR flow and an average turbidity for the three days prior to the OMR flow estimate (Figure 15). The model predicts the median adult delta smelt salvage normalized to the prior FMWT abundance index.

The Service compiled a dataset based on historical salvage normalized to the prior FMWT, OMR flow and CCF turbidity and explored it using several alternative time scales. The purpose of this analysis was to determine how consistent turbidity and OMR thresholds like those proposed by Deriso (2011) were across time scales.

- daily – mimics Deriso's analysis
- 7-day – a typical management time scale, e.g., the Water Operations Management Team meets weekly to review fishery and operations data
- 14-day – the OMR flow averaging period used in the Service's December 2008 OCAP Biological Opinion
- 24-day – the estimated average migration time for delta smelt to migrate from Chipps Island to Banks (Sommer et al. 2011)
- 30 or 31-day – another time scale included in some previous OMR-salvage relationships including those submitted by DWR during the 2008 consultations with the Service and National Marine Fisheries Service (NMFS)

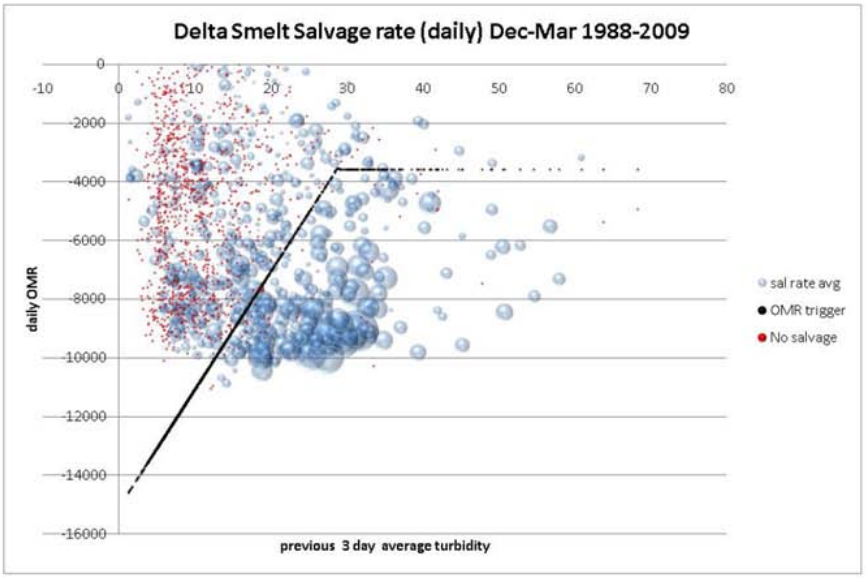

Figure 15. Copy of Figure 3 from Deriso (2011; January 28, 2011 Declaration in support of Plaintiffs' request for injunctive relief in the delta smelt consolidated cases; court document # 772). Bubble plot of average turbidity (NTU at Clifton Court Forebay) for three days prior to a daily net flow in Old and Middle rivers (OMR). The blue data points are sized to reflect the co-occurring adult delta smelt salvage normalized to the Fall Midwater Trawl abundance index immediately preceding fall. Red data = no salvage on that day. The black line is a prediction line generated by the author and proposed as a guide to developing Project operating rules based on combinations of turbidity and OMR. December-March data for December 1988 through March 2009.

Deriso's model showed the general trend in the data is for the highest normalized salvage to occur at combinations of high turbidity and highly negative OMR flows (Figure 15). This trend is generally maintained across each time scale the Service analyzed (Table 3). Other general trends the Service found when analyzing the data over increasingly long time scales, were that the longer the averaging period for the data, (1) the higher the turbidity needed to be to affect the OMR flow that would envelope the data points reflecting more than 5% of the historical maximum normalized salvage, and (2) the more negative the OMR flow could be after the turbidity threshold had changed that would keep normalized salvage lower than 5% of its

historical maximum at that time scale (Table 3). The starting point OMR flow or "low turbidity" OMR flow threshold varied inconsistently across averaging periods, but was always between negative 5200 cfs and negative 3000 cfs.

Table 3. Summary information of the combinations of turbidity and OMR flow that corresponded with normalized salvage of at least 5.1% of the historical maximum normalized salvage when OMR flow was less than -1000 cfs.

Time step (days)	Starting OMR (cfs)		Turbidity threshold (NTU)		Alternative OMR
1	-3000	Until	13	Then	-1900
7	-5200	Until	23	Then	-1900
14	-3300	Until	25	Then	-2500
24	-4600	Until	29	Then	-3600
28-31	-4200	Until	No threshold	Then	-4200

The Service also calculated the daily residual mean square (RMS) tide height at Antioch for December-March, of water years 1989-2009. This variable indexes whether the tides are causing a net 'filling' or 'draining' of the Delta. We generated annual time series plots of (1) turbidity at CCF, or (2) adult delta smelt salvaged normalized to the prior FMWT versus RMS tide height. No consistent influence of this tidal variable was evident on either turbidity or salvage. Thus, the Service does not recommend adding this variable into potential OMR flow rules.

The year to year variability in the OMR-salvage relationships (Figure 5 to Figure 8) is evidence that delta smelt spawning migrations and the distribution changes that result from those migrations also influence their risk of entrainment. The Service recognizes that the upstream migration path of some individuals leads them into Old and Middle rivers regardless of south Delta exports because adult delta smelt salvage has occurred at all OMR flows less than 0 cfs and has even occasionally occurred when OMR was positive.

Larvae (~ March-June)

Delta smelt are "larvae" from the time they hatch and enter the estuary's planktonic community until they reach lengths of 23-25 mm (Mager et al. 2004). However, we term age-0[5] delta smelt as "larvae" during the period they are vulnerable to SWP and CVP water diversions even though many individuals are morphologically "juveniles" by the end of May. This is done only for organizational convenience. The period of entrainment vulnerability extends from larval emergence through the end of June or the first week of July each year (Kimmerer 2008).
Delta smelt can hatch into pelagic larvae from February-June, but peak hatching usually occurs in April. The distribution of delta smelt larvae initially follows that of the spawners because larvae

5 The term 'age-0' refers to fish that are less than a year old. It is synonymous with terms like 'young-of-the-year' and 'larval-juvenile'.

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emerge near where they were spawned. Thus, larvae are distributed more widely during high outflow periods because the spawning range extends further west when Delta outflows are high (Hobbs et al. 2007). The survival of delta smelt larvae is probably driven mainly by the interaction of their bioenergetic environment[6] and entrainment, but only mortality rates associated with the latter have been estimated (Kimmerer 2008).

The distribution of larval delta smelt

Delta smelt larvae are generally open-water and planktonic, but they can and do swim (Bennett et al. 2002; Baskerville-Bridges et al. 2004; Mager et al. 2004). They also generally manage to maintain positions within favorable habitats (Bennett et al. 2002; Hobbs et al. 2006). The distribution of age-0 delta smelt collected in the Department of Fish and Game's 20-mm Survey has been analyzed relative to concurrent water quality conditions using the generalized additive modeling framework described by Feyrer et al. (2007) (Figure 16). The analysis shows that larvae tend to be distributed in fresher water than juveniles. This is consistent with the findings of Dege and Brown (2004). These authors noted that delta smelt larvae (< 20 mm) were centered 5-20 km upstream of X2; delta smelt > 20 mm were distributed closer to X2 and later stage juveniles are likewise centered very near X2 (Sweetnam 1999; Nobriga et al. 2008; Sommer et al. 2011). Delta smelt larvae are less sensitive to water transparency than juveniles. Miller (2011) showed that the influence of water transparency on proportional catch increases as the larvae grow larger. Thus, as the larvae transition to the juvenile stage, they tend to occupy more brackish water and limit their distribution more strongly to the most turbid waters available. The distribution of larvae relative to water temperature is similar to juveniles, with a peak probability of capture near 20°C. There is also a tendency for larval capture probabilities to be highest where prey densities are highest.

It has recently been documented that substantial numbers of delta smelt spawn in Liberty Island and the immediately adjacent region including the Sacramento Deep Water Shipping Channel (http://www.dfg.ca.gov/delta/data/skt/DisplayMaps.asp). Subsequent catches of larvae in this region have also been high at times (http://www.dfg.ca.gov/delta/data/20mm/CPUE_map.asp) and have comprised an increasing proportion of total larval catch over time (Kimmerer 2011). The permanent flooding of Liberty Island in the latter 1990s changed north Delta hydrodynamics (Lehman et al. 2010a) and opened up a large area of shallow and turbid open-water habitat that is used by spawning delta smelt and their progeny (Figure 17). Turbidity is the most likely explanation for a shift in delta smelt distribution to the north (Feyrer et al. 2007; Miller 2011; Kimmerer 2011). Water transparency, an index of turbidity (Shoup and Wahl 2009[7]), is lower in the north Delta than the south Delta (Figure 18). Further, water transparency has trended upward in the south, but not in the north.

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6 The bioenergetic environment refers to the interaction of food quality/quantity and water temperature. The interaction occurs because delta smelt, like most fishes, require higher amounts of food to maintain any given growth rate at higher temperatures.

7 These authors provided a statistical translation between Secchi disk depth (water transparency in cm) and turbidity: NTU = 1761 · (Secchi depth$^{-1.514}$); r^2 = 0.99.

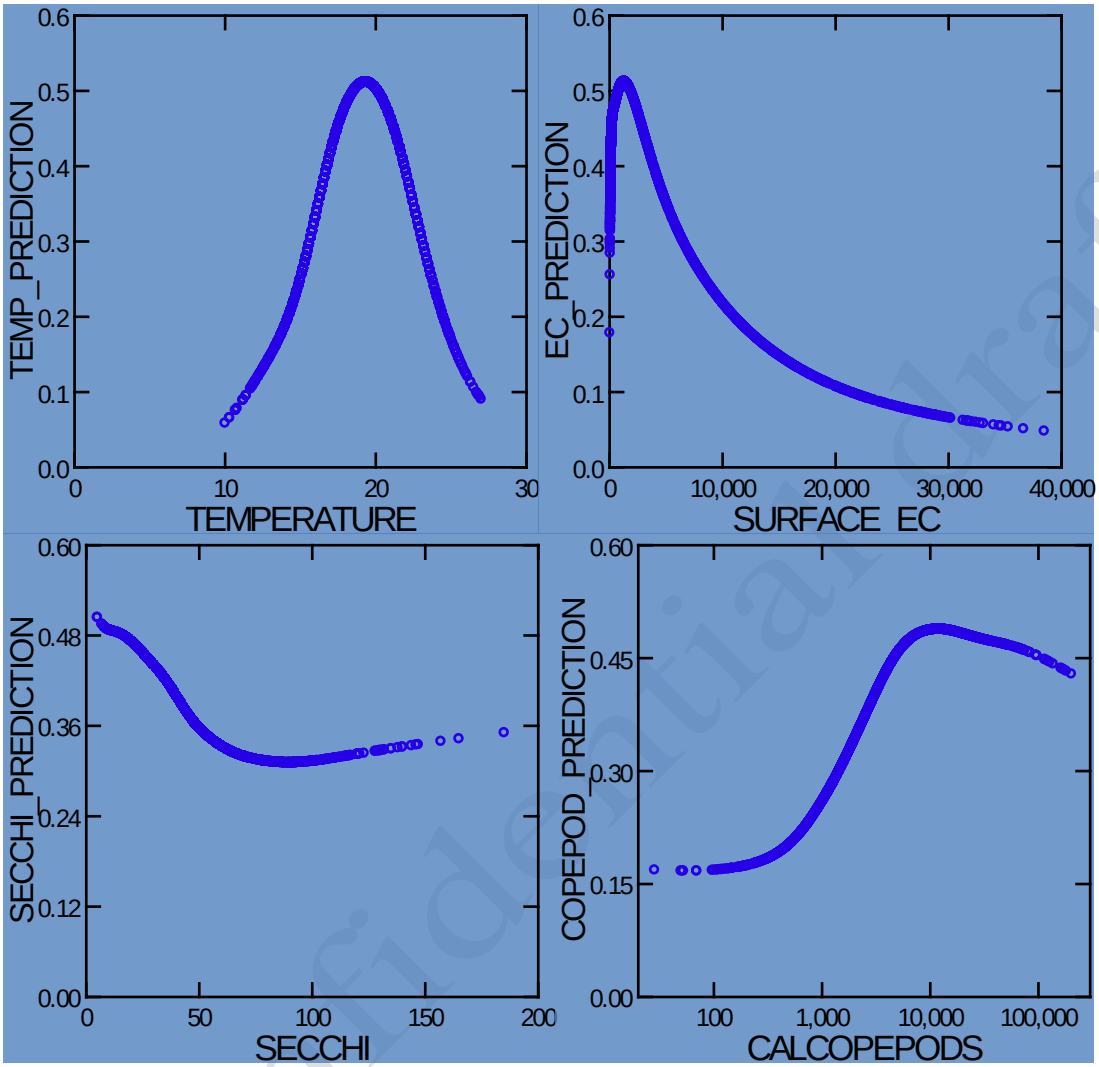

Figure 16. Larval delta smelt capture probabilities based on binomial generalized additive modeling of the 20-mm Survey data. Capture probabilities are shown for individual predicted responses to water temperature in C°, specific conductance at the water surface in µS/cm, water transparency as cm Secchi disk depth, and an index of prey density, average number of calanoid copepods per cubic meter sampled.

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The south Delta is also warmer than the north Delta (Figure 19). However, the median difference has tended to be only about 1°C in any given year, with most of that difference occurring in June-July. In contrast to Secchi depth, the 20-mm Survey data does not show evidence of a time trend in water temperature in either region.

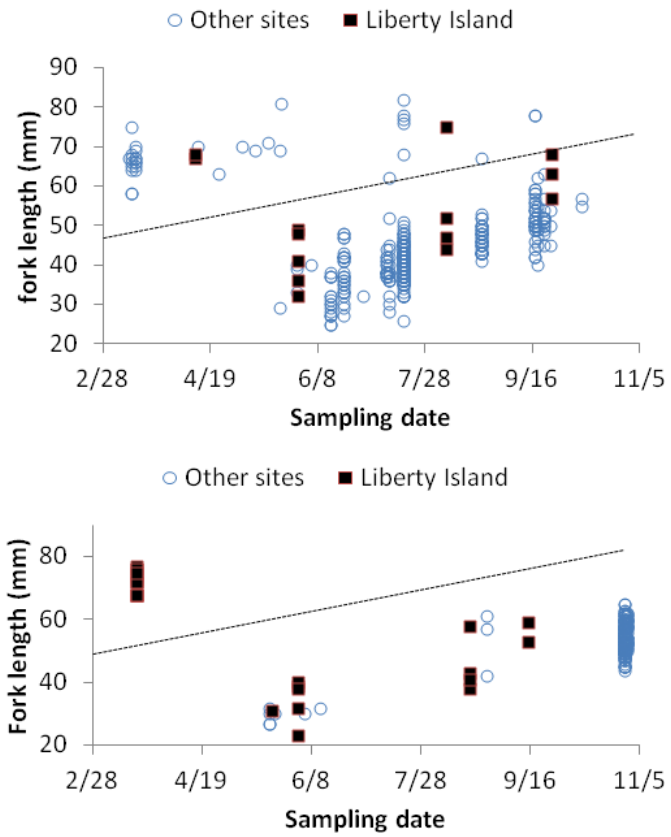

Figure 17. Scatterplots showing the sizes of delta smelt collected in beach seine sampling during 2001 (top graph) and 2003 (bottom graph) (see Nobriga et al. 2005 for details). The dashed lines separate delta smelt year classes; older fish occur above the lines. Thus, the data above the line in the top graph are year class 2000 and below the line they are the age-0 fish born in 2001. Similarly in the bottom plot, fish above the line are year class 2002 and below the line they are the age-0 fish born in 2003. Note that all four cohorts were collected in Liberty Island. Catches were much lower in 2003 than 2001 consistent with previous descriptions of the "Pelagic Organism Decline" (Sommer et al. 2007).

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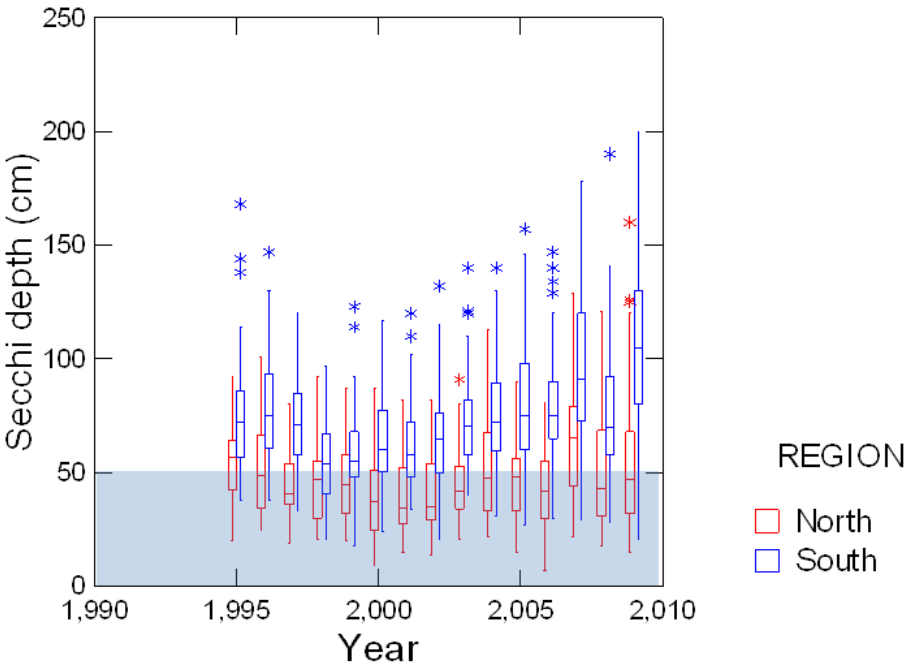

Figure 18. Box plot time series of Secchi disk depth measurements in the California Department of Fish and Game's 20-mm Survey, 1995-2009. The red boxes are for 'north' Delta stations, which are the stations numbered from 704-799 in the 20-mm Survey (http://www.dfg.ca.gov/delta/data/20mm/stations.asp). The blue boxes are for 'south' Delta stations, which are the stations numbered 809-919 in the 20-mm Survey (Figure 1). The box plots are as follows: rectangular box = interquartile range of observations; horizontal line in the box = median; vertical lines = 95% confidence intervals; asterisks = individual data points the Systat software program determined were "outliers". The blue shaded box denotes the region of Secchi disk depths ≤ 50 cm. This is an approximate level of Secchi disk depth below which delta smelt capture probability is somewhat higher based on analysis of the 20-mm Survey data set (see Figure 16).

The freshwater flows that enter the Delta as inflow and pass through it as outflow influence habitat volume for delta smelt during the spring (Kimmerer et al. 2009). They also influence proportional entrainment of the larval delta smelt population (Kimmerer and Nobriga 2008). The combined CVP and SWP water systems began diverting water year-around from the Delta in 1968. Thus, the following analysis considers historical flow conditions based on summaries of the DAYFLOW database for the period 1968-2010. Delta inflows vary among years due largely to interannual differences in precipitation[8] (Kimmerer 2004; Figure 20). Inflows are thus highly correlated among months in the springtime, but typically decline with each successive month as snowmelt and runoff recede. The Projects can have considerable control over Delta inflows during spring, though they tend to have greater control over inflows by early summer (e.g., June) than in the winter and spring.

8 However, the Service reiterates its April 25, 2012 comment that spring inflows and outflows have changed considerably over the longer term due to the cumulative development of freshwater supplies in California.

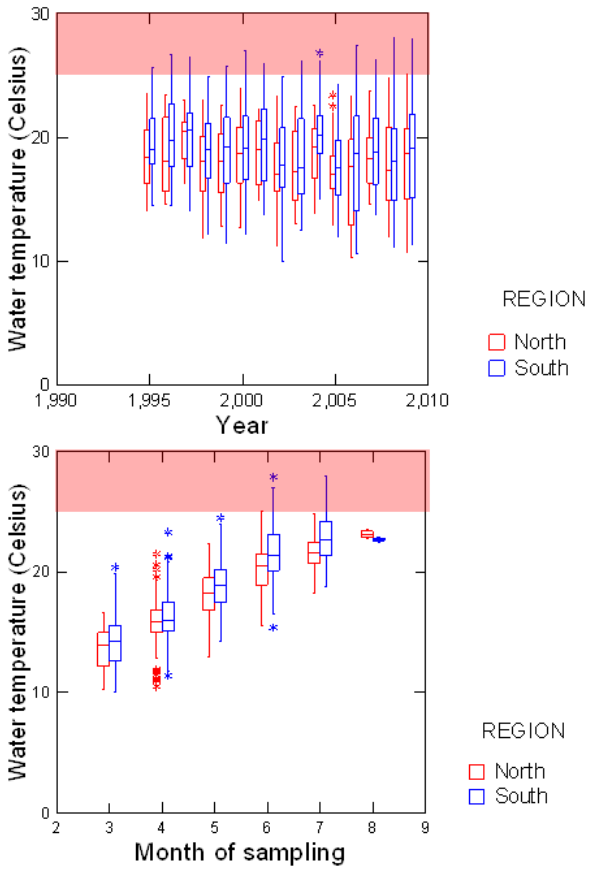

Figure 19. Box plot time series of water temperature measurements in the California Department of Fish and Game's 20-mm Survey, 1995-2009. The red boxes are for 'north' Delta stations, which are the stations numbered from 704-799 in the 20-mm Survey (http://www.dfg.ca.gov/delta/data/20mm/stations.asp). The blue boxes are for 'south' Delta stations, which are the stations numbered 809-919 in the 20-mm Survey. The box plots are as follows: rectangular box = interquartile range of observations; horizontal line in the box = median; vertical lines = 95% confidence intervals; asterisks = individual data points the Systat software program determined were "outliers". The shaded red box in each panel denotes water temperatures ≥ 25ºC. This is an approximate upper lethal water temperature limit for young delta smelt (Swanson et al. 2000).

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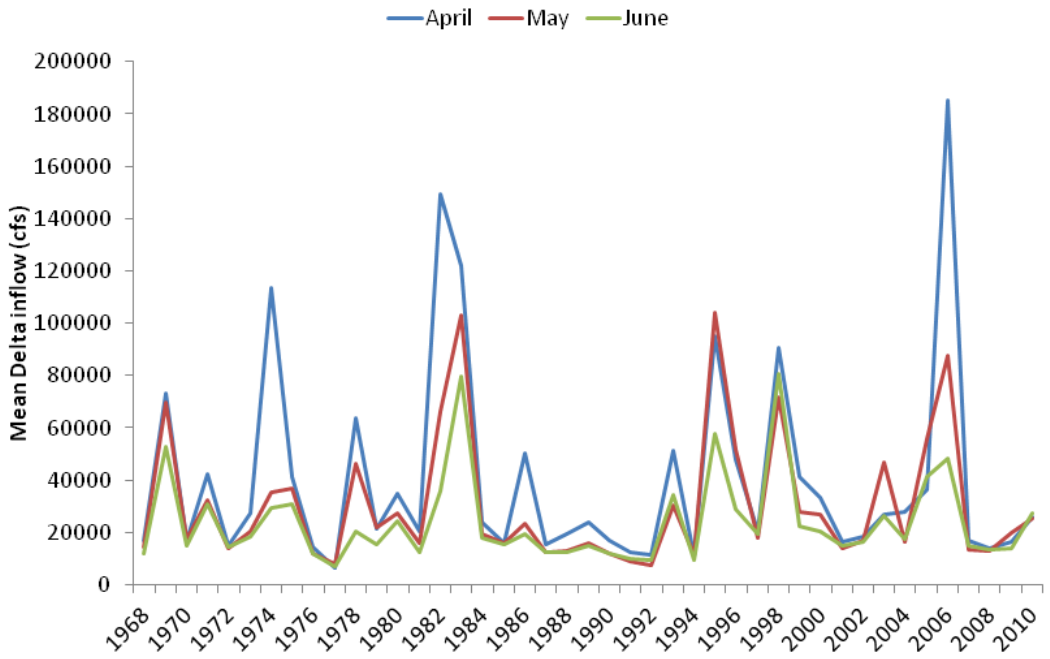

Figure 20. Time series of total Delta inflow for April-June, 1968-2010. Source: DAYFLOW database

April-May exports underwent a step-decline starting in the early 1990s (Figure 21). This was initially due to several years of successive drought but the lower export levels have continued because the Board implemented the X2 standard and the Vernalis Adaptive Management Plan (VAMP) experiment. Project exports frequently exceeded 300 TAF during April-May 1968-1988, but they have only infrequently exceeded that threshold since. Project exports are higher in June, sometimes exceeding 400 TAF per month, but there is no evidence of a long-term trend, except that they first exceeded 600 TAF in 2003. Overall, Project exports are usually lower during April-June than other times of year. The trends in the E:I ratio for the spring months mirror the export trend; step-declines in April-May and no trend in June (Figure 22). The State of California's X2 standard has also shifted the upstream limit of X2 further to the west during April-June (Figure 23).

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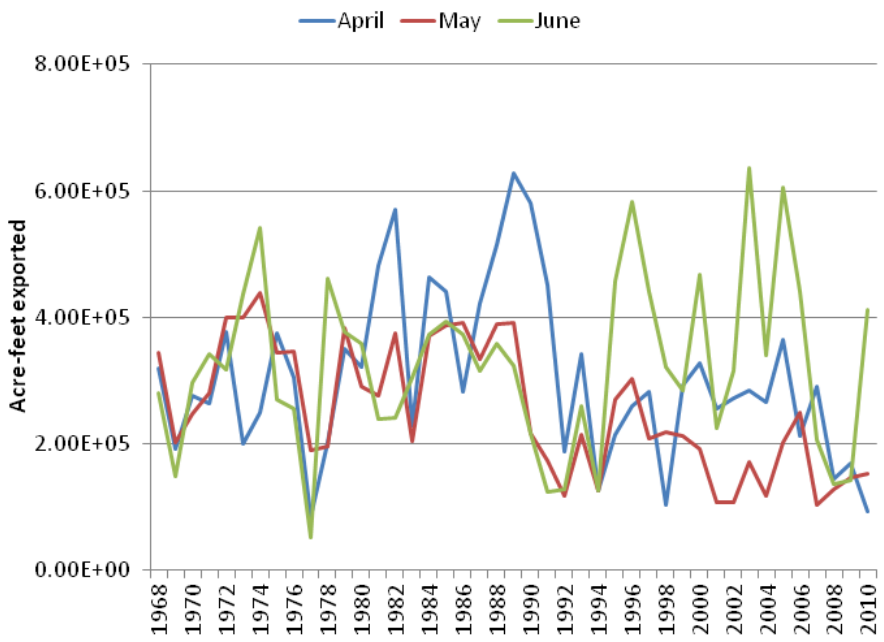

Figure 21. Time series of monthly SWP and CVP exports for April-June, 1968-2010. Source: DAYFLOW database

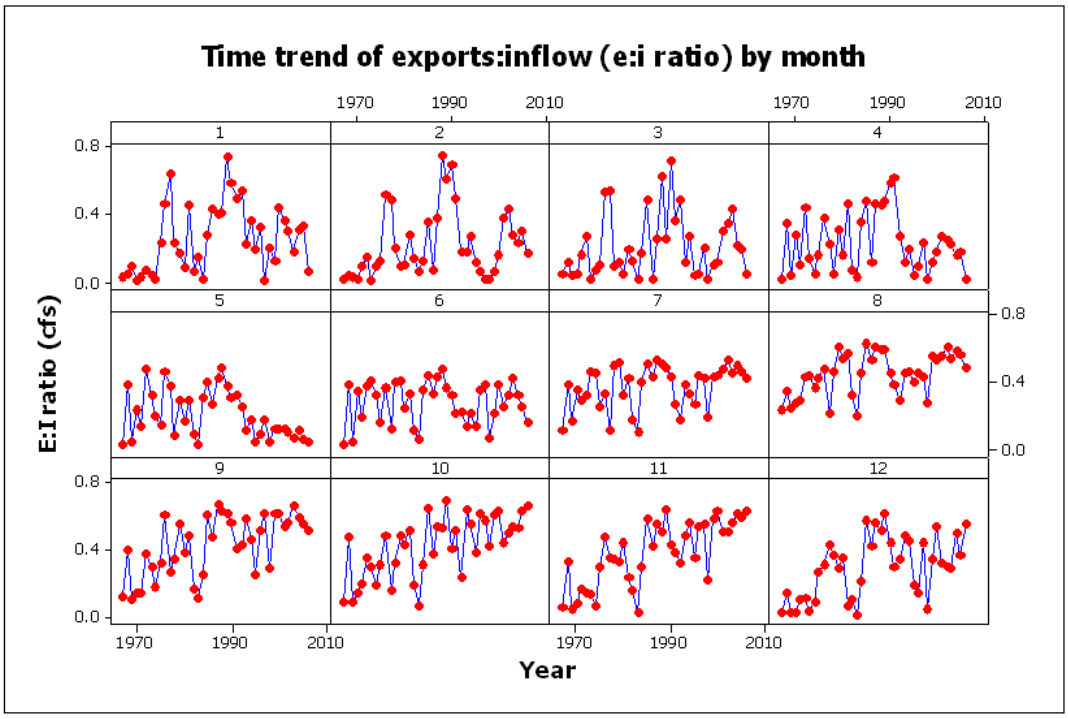

Figure 22. Time series of the monthly mean Export to Inflow ratio, January-December, 1968-2006. Source: DAYFLOW database

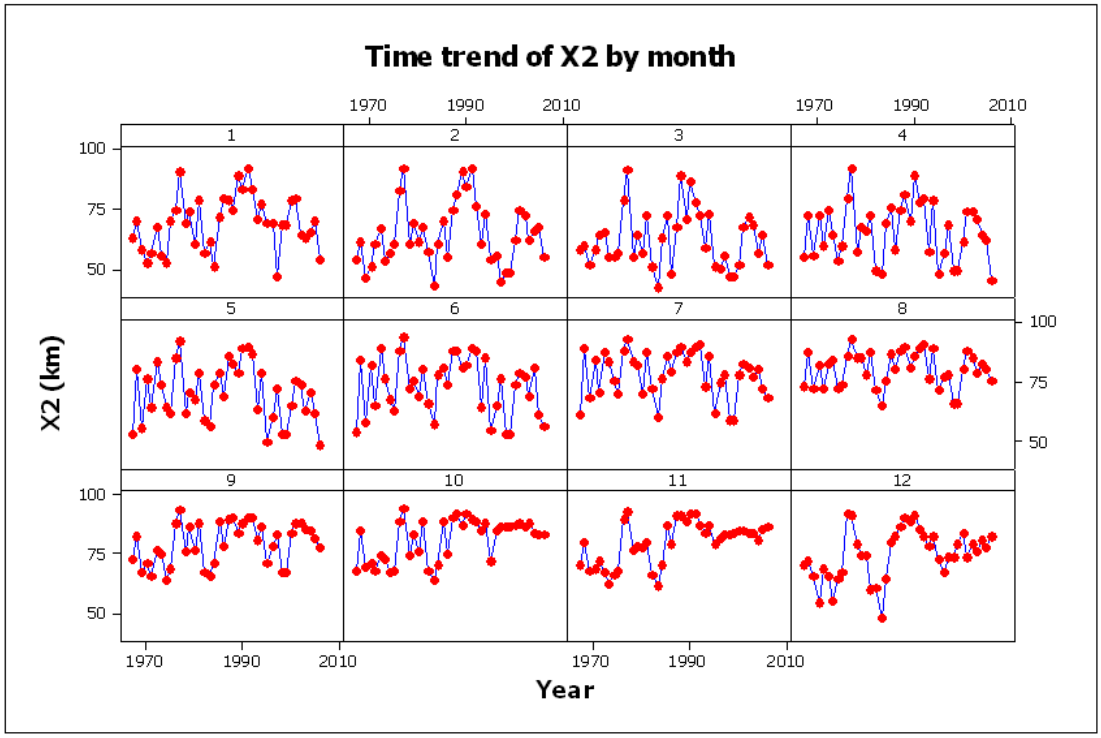

Figure 23. Time series of X2 January-December, 1967-2008. Source: DAYFLOW database

Conceptual background for south Delta entrainment risk

Most age-0 delta smelt *entrainment* at Banks and Jones happens during the true larval stage and is not observed and counted (Kimmerer 2008). The *salvage* of age-0 delta smelt reflects the tail end of the entrainment of age-0 cohorts that started before the fish were large enough to be observed in the fish salvage facilities. Delta smelt are not counted in fish salvage until they reach a minimum length of 20 mm. Age-0 delta smelt are not salvaged efficiently (Table 1). Kimmerer (2008) showed that delta smelt salvage was inefficient, even by delta smelt standards, until the fish were 30 mm long (by which time they are morphologically juveniles; Mager et al. 2004). They typically reach 20-30 mm in May and June. Thus, April is typically the month of highest Project entrainment of age-0 delta smelt, while May-June are the months of highest salvage (Kimmerer 2008).

Previously, the Service (2008) translated Kimmerer's (2008) data-intensive age-0 delta smelt entrainment estimates into a multiple linear regression equation using multi-month averages of X2 and OMR flow as predictor variables. This allowed the Service to hind cast and forecast proportional entrainment (Figure 24). The regression was a quantitative representation of the following conceptual model: (1) the geographic distribution of the population is strongly associated with Delta outflow (or its surrogate, X2; Dege and Brown 2004). Thus, Delta outflow determines how much of the age-0 delta smelt population rears in the Delta during the spring and early summer where it is potentially vulnerable to entrainment, and (2) OMR flow reflects the hydrodynamic influence of the water projects' diversions on the southern half of the Delta and

thus the degree of entrainment risk for fishes in that region (Kimmerer 2008; Grimaldo et al. 2009a; Figure 25). The long-term declines in April-May exports and E:I ratio, and April-June X2 location are all indications that the proportional entrainment of age-0 delta smelt has declined. In addition, proportional entrainment may be continuing to decline due to a general shift in delta smelt spawning distribution toward the north Delta (Miller 2011; Kimmerer 2011).

This conceptual model remains valid. The Service notes that Kimmerer's (2008) estimates have recently been criticized on numerous grounds (Miller 2011). However, the Service believes most of Miller's criticisms are unfounded, incorrectly cast, or beyond the scope of currently available data sets to address (Kimmerer 2011). The Service recognizes that the shift in delta smelt distribution toward the north affects the accuracy of the translation of hydrodynamic conditions into specific predictions of proportional entrainment (Miller 2011; Kimmerer 2011).

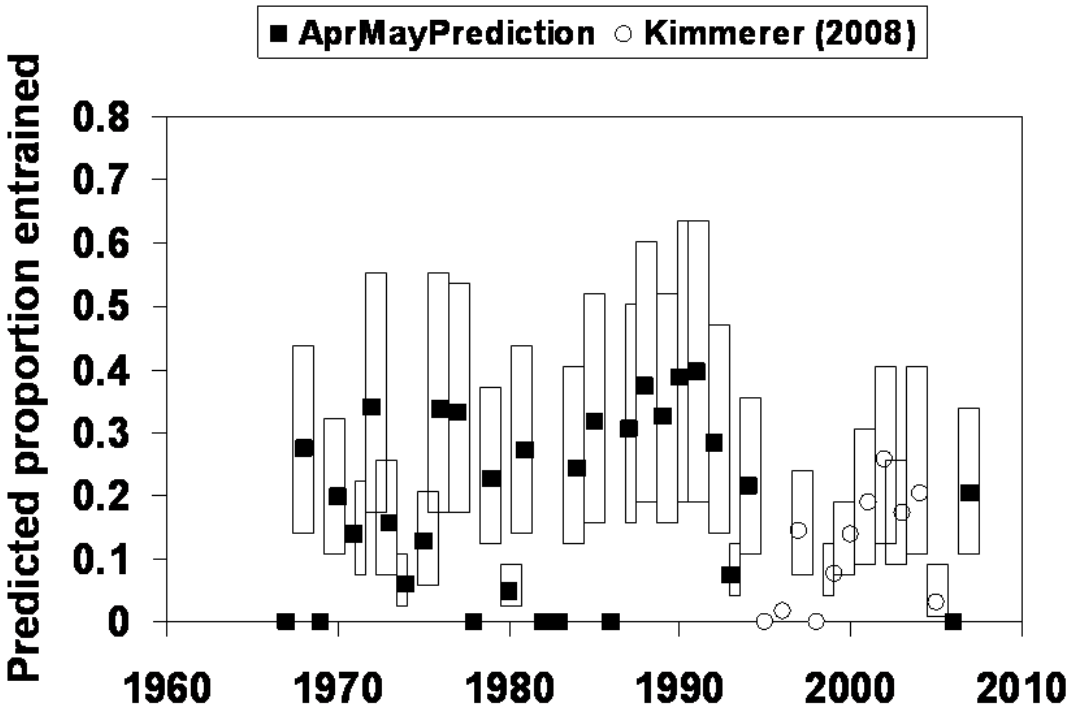

Figure 24. Copy of Figure E-16 from Service (2008). Time series of estimated proportion of the age-0 delta smelt population entrained at Banks and Jones. Open symbols are the empirical estimates made by Kimmerer (2008). Solid symbols were estimated using the linear regression equation developed by the Service (2008). The rectangles depict the approximate 95% confidence intervals on the estimates.

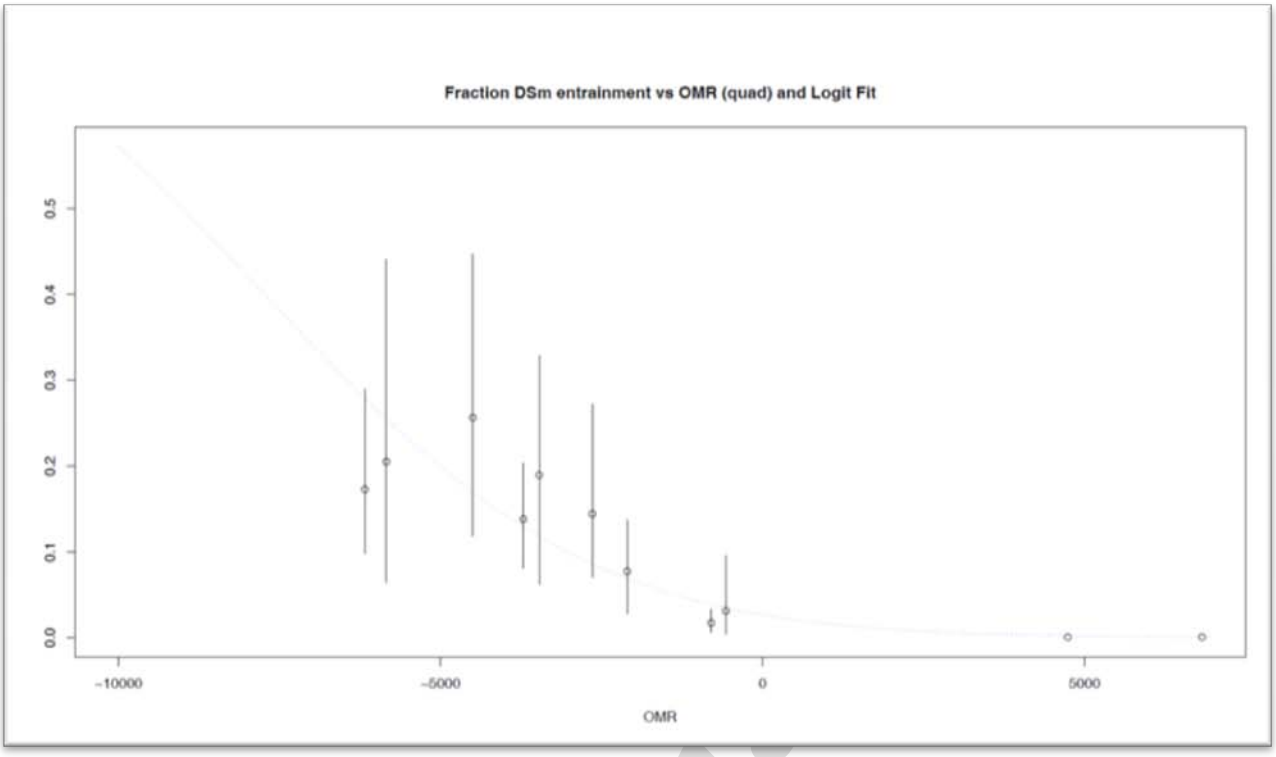

Figure 25. Relationship between Old and Middle river (OMR) flow and the proportional entrainment of age-0 delta smelt (proportional entrainment data provided by W. Kimmerer; plot provided by K. Newman).

The potential for entrainment of fishes rearing in the lower San Joaquin River can be visualized with PTM results based on neutrally buoyant particles. The Service understands that these results reflect predictions about water movement in the Delta rather than fish movement per se. However, the water movement data provide the best available indication of entrainment risk. In fact, Kimmerer (2008) showed that the entrainment estimates he derived from empirical flow and 20-mm data matched predictions of entrainment based on PTM simulations very well[9] (Figure 26). Thus, PTM provides a reliable estimate of entrainment for fish inhabiting the San Joaquin River and south Delta. It has been shown that larval fishes in the San Francisco Estuary can maintain positions in favorable habitats by swimming in concert with the tide (Bennett et al. 2002). Thus, delta smelt larvae have some capacity to avoid "going with the flow". This ability increases as the fish grow. However, a pelagic fish is only likely to avoid going in a particular direction in a tidal environment if it has a cue to avoid the conditions it is exposed to on either the ebbing or flooding tide. Thus, the close association between predictions based on neutrally buoyant particle movement and empirical fish distributions from the 20-mm Survey imply that delta smelt larvae do not perceive a habitat "problem" while they are tidally transported around the south Delta even though they are swimming to find and capture prey, avoid predators, etc. The young fish that have not been entrained do migrate out of the south Delta in the early summer to avoid warm water temperatures (Kimmerer 2008).

9 Note that the ptm results were not used to develop the proportional entrainment estimates. Thus, the data shown in Figure 26 are not depicting a circular argument.

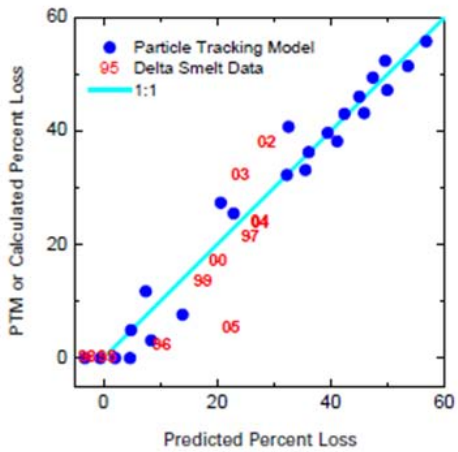

Figure 16. Larval/juvenile delta smelt. Predicted percent loss to the population by regression using log of Delta inflow and log of export flow as predictors (with interaction), and particle-tracking model results as the dependent variable (circles), with the line indicating a 1:1 relationship. The regression is: log (y) = 4.29 – (0.36 ± 0.17) log(inflow) – (0.90 ± 0.11) log(export flow) + (0.10 ± 0.03) log(inflow) × log(export flow), parameters with 95% confidence limits. Estimates of delta smelt losses from Figure 15 with no natural mortality (to match the particle tracking model results) are plotted against predictions from the above statistical model using mean flow conditions during the hatch period; numbers indicate years.

Figure 26. Copy of Figure 16 from Kimmerer (2008). The Figure compares the empirically derived age-0 delta smelt entrainment estimates for Banks and Jones (combined) against estimates of neutrally buoyant particle entrainment into those facilities based on DSM2 particle tracking modeling.

Based on existing summaries of PTM results, it appears that delta smelt cannot be protected from entrainment once they enter Old or Middle rivers (Figure 27). Particle fluxes into Old and Middle rivers are proportional to predicted entrainment into Banks and Jones pumping plants, the SWP and CVP diversions in the south Delta. The relationship deviates from the one to one line when loss to agricultural irrigation diversions is high. Thus, PTM indicates that almost all particles, and by extension larval fishes, that enter Old and Middle rivers will eventually be entrained somewhere; larval fishes will be entrained either at Banks, Jones, or one of numerous smaller agricultural irrigation diversions en route to Banks and Jones. Thus, currently available scientific evidence indicates that OMR flow limits cannot be used to 'help' larval fish migrate out of Old and Middle rivers if they are already there. Rather, OMR flow limits would be most effective if they minimized the hydrodynamic conditions that entrain young delta smelt into Old and Middle Rivers from the mainstem San Joaquin River.

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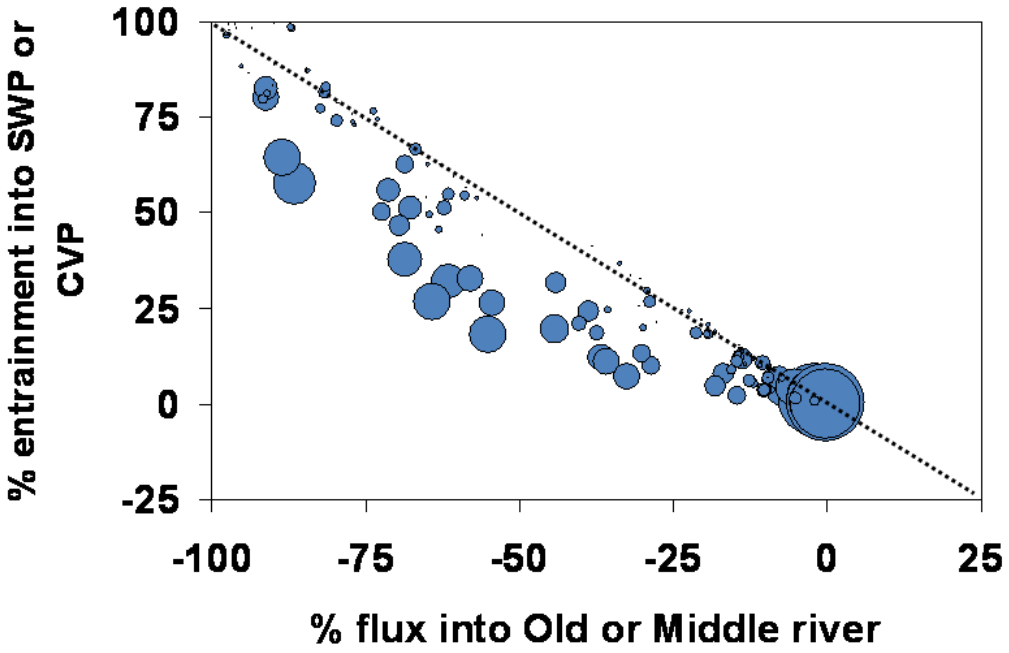

Figure 27. Scatterplot showing the relationship between flux into Old and Middle rivers and entrainment based on simulations using the DSM-2 particle tracking model. The plot demonstrates that particle flux into Old and Middle rivers is strongly linked to entrainment risk. Note that DSM-2 codes fluxes into Old and Middle rivers from elsewhere as negative percentages. The individual data points are sized according to their predicted entrainment into agricultural irrigation diversions. The dotted line is an approximate 1:1 line. Note that large bubbles at Old and Middle river fluxes ranging from about 25% to 90% are often associated with deviations from the 1:1 line. This occurs because particles can be lost to agricultural irrigation diversions in Old and Middle rivers before being transported all the way to Banks and Jones Pumping Plants. Data source: particle tracking model runs done to support the State Water Project's California Endangered Species Act (CESA) Incidental Take authorization for longfin smelt (DFG 2009).

Monitoring the south Delta for evidence of spawning and then applying OMR limits is unlikely to be effective because (1) there are no available data on the distribution of delta smelt eggs; (2) the net efficiency of the 20-mm Survey is very low for hatch sized larvae (Kimmerer 2008); and (3) PTM simulations show that the ultimate entrainment of particles is closely tied to OMR flows during particle release (Figure 28),. In other words, if larvae get into Old and Middle rivers, the PTM indicates it is too late to get them out by changing OMR flows.

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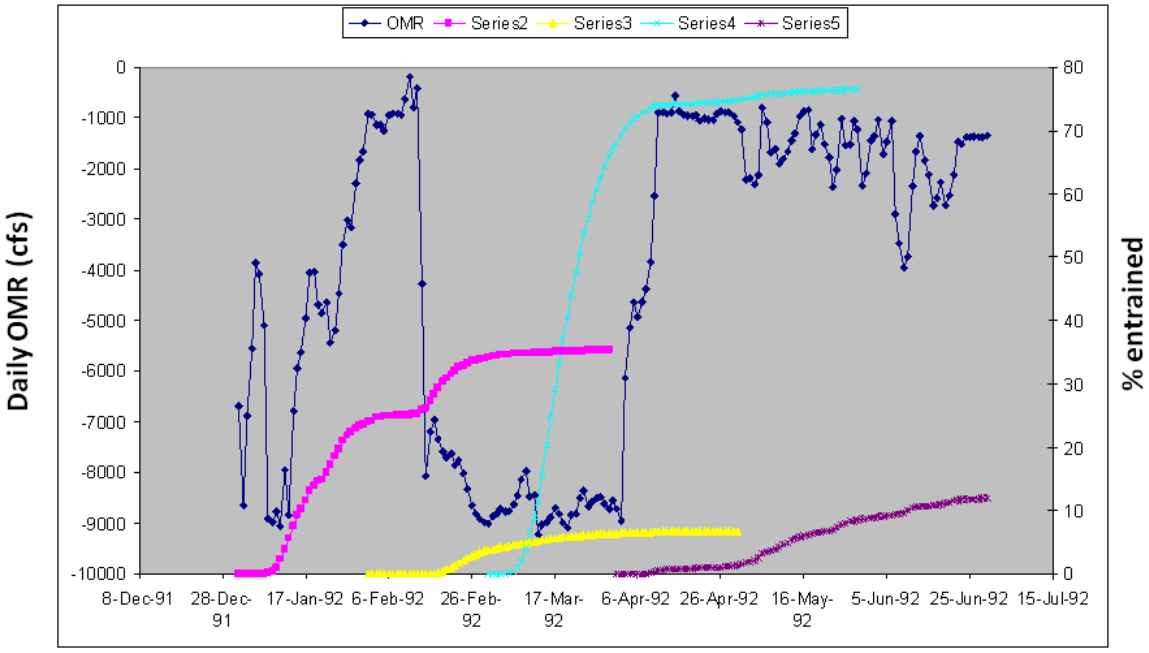

Figure 28. Time series plots of daily particle fate predicted from the DSM-2 particle tracking model for four different particle releases at trawl station 812 (see Figure 1 for location). The simulations used the actual hydrology from winter-spring, 1992, a dry year with a lot of variation in OMR flows. Particles were released on January 1 (Series 2), February 1 (Series 3), March 1 (Series 4), and April 1 (Series 5) and each of the four simulations was run for a total of 90 days. The dark blue line shows the daily mean OMR flow. The other lines show the accumulation of particles entrained at Banks and Jones. Note that the general magnitude of final particle loss was apparent in much less than 90 days and was closely associated with OMR flow at or very near the time of initial particle release. Data source: particle tracking model runs done to support the State Water Project's CESA Incidental Take authorization for longfin smelt (DFG 2009).

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The risk of delta smelt entrainment into smaller agricultural irrigation diversions used mainly to irrigate crops within the Delta is also related to flow conditions. These in-Delta irrigation diversions generally have mean flow rates less than 1 cubic meter per second (Nobriga et al. 2004). The lower the Delta outflow, the higher the proportion of the young delta smelt population that overlaps the array of irrigation diversions in the Delta (Kimmerer and Nobriga 2008). However, the irrigation diversions are not currently considered to represent a substantial source of mortality because (1) they individually draw small quantities of water relative to channel volumes, and (2) densities of entrained fishes are circa 1-2 orders of magnitude lower than densities of fish from in-channel sampling (Nobriga et al. 2004).

In Suisun Marsh, water diversions are largely made to support waterfowl production. Based on hydrodynamic simulations, proximity to water diversions in the marsh is expected to correlate strongly with entrainment (Culberson et al. 2004), and substantial losses of delta smelt were reported for Roaring River before it was screened (Pickard 1982). Entrainment risk for delta smelt at Morrow Island in western Suisun Marsh, which is unscreened, is considered low because the habitat surrounding the diversions is often too saline (Enos et al. 2007).

Juveniles (~ July-December)

Conceptual background for juvenile rearing

Delta smelt larvae are present in the estuary in July. However, by this time most individuals are morphologically juveniles (Table 4). These juveniles are pelagic with a spatial distribution that varies with salinity, turbidity, water temperature, and possibly other habitat features (Moyle et al. 1992; Sweetnam 1999; Bennett 2005; Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009; Sommer et al. 2011). Most of them will be 60-70 mm long by December. They are still considered juveniles at that time because their reproductive organs are not functional, but the delta smelt collected in the fall are often referred to as "adults" or "sub-adults". The center of the juvenile delta smelt population during summer and fall is typically very near X2 (Moyle et al. 1992; Sweetnam 1999; Dege and Brown 2004; Sommer et al. 2011). However, some individuals continue to rear in fresher water in the Liberty Island- Sacramento River Deep Water Shipping Channel area (Sommer et al. 2011). This is probably due in large part to the comparatively turbid water in this region (Nobriga et al. 2005). A few individuals are also collected at salinities higher than 6 psu but these are low probability events (Feyrer et al. 2007; Nobriga et al. 2008). It is not known how long individual delta smelt occupy waters seaward of the low-salinity zone. However, delta smelt can tolerate salinities up to about 19 psu for short periods (Swanson et al. 2000), so it is not surprising that their spatial distribution relative to salinity has some variability around it in a tidally dispersive environment like the LSZ.

Table 4. Summary of mean delta smelt lengths in the 20 mm Survey for the sampling dates nearest to July 1, 1995-2011. Note that no July sampling occurred 2000-2002. Delta smelt are beyond the larval stage by the time they reach about 23-25 mm in length (Mager et al. 2004). Data source: http://www.dfg.ca.gov/delta

Year	Survey Number	Sampling dates	Mean Length (mm)
1995	6	July 3-10	30.5
1996	7	July 8-13	30.4
1997	8	July 8-13	36.9
1998	7	June 28-July 3	33.0
1999	7	July 6-10	25.7
2000	8	June 26-30	25.9
2001	8	June 25-30	30.0
2002	8	June 24-29	38.5
2003	8	June 30-July 3	29.7
2004	8	July 6-10	36.5
2005	9	July 5-9	37.1
2006	8	June 26-July 1	28.1
2007	9	July 2-7	41.2
2008	9	July 7-11	41.7
2009	9	June 29-July 2	31.8
2010	9	July 6-9	26.0
2011	9	July 5-8	24.9
2012	9	July 9-12	37.6

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Delta smelt's juvenile rearing habitat has undergone profound changes which have led to increasingly degraded habitat conditions over time.

Alterations to LSZ bathymetry have changed the amount of freshwater flow needed to place the LSZ over structurally complex landscapes (~ 1850-present):

The first major change in the LSZ was the conversion of the landscape over which tides oscillate and river flows vary (Nichols et al. 1986). The ancestral Delta was a large tidal marsh-floodplain habitat totaling approximately 700,000 acres. Most of the wetlands were diked and reclaimed for agriculture or other human use by the 1920s. In the 1930s to 1960s, shipping channels were dredged deeper (~12 m) to accommodate shipping traffic from the Pacific Ocean and San Francisco Bay to ports in Sacramento and Stockton. These changes due to land reclamation and channel dredging left Suisun Bay/Marsh and the Sacramento-San Joaquin river confluence region as the largest and most bathymetrically variable places in the LSZ. This region remained a highly productive ecological nursery for many decades (Stevens and Miller 1983; Moyle et al. 1992; Jassby et al. 1995). However, the deeper landscape created to support shipping and flood control requires more freshwater outflow to maintain the LSZ in this large Suisun Bay/river confluence region than was once required (Gartrell 2010). Further, low outflows due to combinations and drought and water demand may have contributed to some of the food web changes discussed below (Winder et al. 2011). Presently, seasonal salinity intrusion reduces the temporal overlap of the LSZ (indexed by X2) with the Suisun Bay region, especially in the fall (Feyrer et al. 2007). Based on model forecasts of climate change and water demand, this trend is expected to continue (Feyrer et al. 2011).

Fish species introductions may have changed predator-prey dynamics (1879 to present)

Nothing is known about the historical role of predation on the population dynamics of delta smelt or longfin smelt. Fish eggs and larvae can be opportunistically preyed upon by many invertebrate and vertebrate animals so there has always been a very long list of potential predators of these species' eggs and larvae. Potential native predators of juvenile and adult delta and longfin smelt would also have included numerous bird and fish species.

The introduction of striped bass into the San Francisco Estuary in 1879 added a permanently resident, large piscivorous fish to the LSZ, a habitat that is not known to have had an equivalent predator prior to the establishment of striped bass (Moyle 2002). This likely changed predation rates on delta smelt and longfin smelt, but there are no data available to confirm this hypothesis. For many decades the estuary supported higher numbers of all three species than it does currently. This is evidence that the smelts are able to successfully coexist with striped bass. Further, striped bass recruitment is influenced by flow variation and the supporting food web in a manner similar to the smelts (Kimmerer et al. 2000; 2001; Loboschefsky et al. 2012). Thus, although it lives longer than the smelts and can reproduce more than once, it is likewise not expected to thrive under conditions that do not support a healthy LSZ ecosystem.
Predation is a common source of density-dependent mortality in fish populations (Walters and Juanes 1993; Rose et al. 2001). Thus, it is possible that predation was a mechanism that historically generated the density-dependence observed in delta smelt population dynamics

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(Bennett 2005; Maunder and Deriso 2011). Because it is generally true for fishes, the vulnerability of delta smelt to predators is probably influenced by habitat conditions. Turbidity may be a key mediator of delta smelt's vulnerability to predators (Nobriga et al. 2005; 2008). Growth rates, which are an interactive outcome of feeding success and water temperature, are also well known to affect fishes' cumulative vulnerability to predation (Sogard 1997). Thus, if predation rate is best characterized as an aspect food web function and abiotic habitat suitability, it may be unrelated to striped bass abundance. This conclusion is supported by several recent studies that did not find evidence for a link between striped bass abundance estimates and population dynamics of delta smelt (Mac Nally et al. 2010; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012) and longfin smelt (Mac Nally et al. 2010; Thomson et al. 2010). Several of these studies did find inverse correlations between largemouth bass abundance (or variables that included largemouth bass abundance) and delta smelt population dynamics. This might be evidence for a predatory effect of largemouth bass on delta smelt, but it also may simply reflect the greatly changing habitats in the Delta toward conditions that support largemouth bass and similar fishes and away from conditions that support delta smelt and other LSZ fishes (Nobriga et al. 2005; Moyle and Bennett 2008). This change is discussed below in the section on submerged aquatic vegetation.

Entrainment into water export diversions has increased the total mortality experienced by LSZ fish populations (1951 to present)

The amount of water diverted from the estuary has generally increased over time (Figure 29), and most of the increase during the 1950s and 1960s was due to CVP exports and since the latter 1960s, State Water Project (SWP) exports. There are two basic potential fishery impacts that result from water diversion from the Delta: ecosystem impacts and direct entrainment. From the ecosystem perspective, water diversions are unnatural 'predators' because they 'consume' organisms at every trophic level in the ecosystem from phytoplankton (Jassby et al. 2002) to fish (Kimmerer 2008). Unlike natural predators which typically shift their prey use over time in association with changes in prey fish density (Nobriga and Feyrer 2008), fractional entrainment losses of fishes to diversions are functions of water demand (e.g., Grimaldo et al. 2009a). Thus, water diversions not only elevate 'predation' mortality in an aquatic system, but they can do so in an atypical, density-independent manner. Additionally, the Project diversions and fish collection facilities in the south Delta are very large structures which attract large aggregations of actual predatory fish that prey on smaller species like delta smelt before they reach the fish salvage facilities and within these facilities (Gingras 1997). As discussed above, this gauntlet of predators may bias the salvage data that often are used to link the Project operations with entrainment (Castillo et al. 2010).

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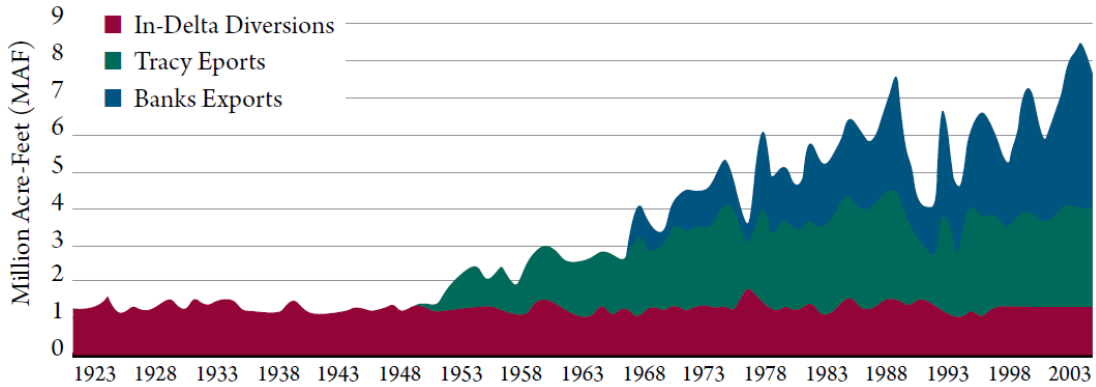

Figure 2.8. Delta Water Diversions and Exports. Delta diversions and exports have grown over time. In-Delta diversions for irrigation have been about the same since the early 1900s. Federal exports (Tracy) began in the early 1950s, and state exports (Banks) began in the late 1960s. (Source: URS Corporation 2007)

Figure 29. Source CALFED Science Program State of Science Report, 2008

Food web alterations attributable to the overbite clam have decreased the production of zooplankton that most efficiently support LSZ pelagic fish production (1987-present)

Major changes to the estuarine food web followed the invasion of the overbite clam. The overbite clam was first detected in 1986 and from 1987-1990 its influence on the ecosystem became evident. The first responses were step-declines in phytoplankton (especially diatom) biomass (Alpine and Cloern 1992; Jassby et al. 2002) and the density of two historically important zooplankton prey, *Eurytemora affinis* and *Neomysis mercedis* (Kimmerer et al. 1994; Kimmerer and Orsi 1996; Orsi and Mecum 1996). The grazing pressure applied by the overbite clam rippled through the historical zooplankton community that fueled fishery production in the LSZ (Kimmerer et al. 1996; Orsi and Mecum 1996; Kimmerer 2002a; Feyrer et al. 2003). This major change in the way energy moved through the ecosystem has likely facilitated the numerous subsequent invasions of the estuary by suppressing the production of historically dominant zooplankton, which increases the opportunity for invasion by other species that are less dependent on high densities of LSZ diatoms (Winder and Jassby 2011).

Longfin smelt abundance per unit of outflow has steadily declined following the overbite clam invasion. Delta smelt size at the end of their first calendar year of life also declined shortly after the overbite clam invasion. These trends provide circumstantial evidence for food limitation (Kimmerer 2002a; Bennett 2005).

The Projects entrain some food web production (about 4.5% on a daily average basis was attributed to all Project and non-project water diversion in the Delta; Jassby et al. 2002). However, diatom standing stocks and zooplankton densities have been most strongly affected by clam grazing and the species invasions it facilitated (Kimmerer et al. 1994; Jassby et al. 2002; Winder and Jassby 2011). Urban wastewater input impairs diatom bloom production (Wilkerson

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et al. 2006; Dugdale et al. 2007; Parker et al. 2012a,b). At times, *Microcystis* blooms and pesticides also impair the production of zooplankton eaten by delta and longfin smelt or their prey (Ger et al. 2009; Werner et al. 2010).

Proliferation of Submerged Aquatic Vegetation is a second food web alteration that has changed turbidity and nearshore fish assemblages (1980s to present)

For many decades, the Delta's waterways were turbid and the growth of submerged plants was apparently unremarkable. That began to change in the mid-1980s, when the non-native Brazilian waterweed *Egeria densa*, a fast-growing aquarium plant took hold in many shallow habitats (Brown and Michnuik 2007; Hestir 2010). *Egeria densa* and other non-native species of submerged aquatic vegetation (SAV) grow most rapidly in the summer and late fall when water temperatures are warm (> 20°C) and outflow is relatively low (Hestir 2010). The large canopies formed by these plants have physical and biological consequences for the ecosystem (Kimmerer et al. 2008). First, dense SAV promotes higher water transparency. Increased water transparency leads to a loss of habitat for delta smelt (Feyrer et al. 2007; Nobriga et al. 2008). Second, dense SAV canopies provide habitat for a suite of non-native fishes, including largemouth bass, which now dominate many shallow habitats of the Delta and displace native fishes (Nobriga et al. 2005; Brown and Michniuk 2007). Finally, SAV colonization over the last three decades has led to a shift in the dominant freshwater food web pathways that fuel fish production (Grimaldo et al. 2009b). It is noteworthy that SAV-dominated habitats are comparatively productive (Nobriga et al. 2005; Grimaldo et al. 2009b), but most of the productivity they generate remains in the nearshore environment and therefore does not contribute much to the production of pelagic fishes like delta smelt and longfin smelt (Grimaldo et al. 2009b).

Reduced turbidity has decreased LSZ habitat suitability for delta smelt (1999-present)

The next major change was a change in estuarine turbidity that culminated in an estuary-wide step-decline in 1999 (Schoellhamer 2011). For decades, the turbidity of the modified estuary had been sustained by very large sediment deposits resulting mainly from gold mining in the latter 19th century. The sediments continued to accumulate into the mid-20th century, keeping the water relatively turbid even as sediment loads from the Sacramento River basin declined due to dam and levee construction (Wright and Schoellhamer 2004). The flushing of the sediment deposits may also have made the estuary deeper overall (Schroeter 2008) and thus a less suitable nursery from the 'static' bathymetric perspective. Delta smelt larvae require turbidity to initiate feeding (Baskerville-Bridges et al. 2004), and as explained above, older fish are thought to use turbidity as cover from predators. Thus, turbidity is a necessary water quality aspect of delta smelt habitat.

Predictions of warmer water temperature are likely to be very stressful to delta smelt and longfin smelt (present through long-term climate forecasts)

Delta smelt is already subjected to thermally stressful temperatures every summer. Water temperatures are presently above 20°C for most of the summer in core habitat areas (Figure 30), sometimes even exceeding delta smelt's nominal lethal limit of 25°C (Swanson et al. 2000) for

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short periods. Note that coldwater fishes begin to have behavioral impairments (Marine and Cech 2004) and lose competitive abilities (Taniguchi et al. 1998) prior to reaching their thermal tolerance limits. Thus, the estuary can already be considered thermally stressful to delta smelt and can only become more so if temperatures warm in the coming decades.

All available regional climate change projections predict central California will be warmer still in the coming decades (Dettinger 2005). The Service expects that warmer estuary temperatures will be yet another significant conservation challenge. Higher water temperatures will limit abiotic habitat suitability further than indicated by flow-based projections (e.g., Feyrer et al. 2011; Wagner et al. 2011). In addition, warmer water temperatures mean that higher prey densities will be required just to maintain present-day growth rates, which are already lower than they once were (Sweetnam 1999; Bennett 2005).

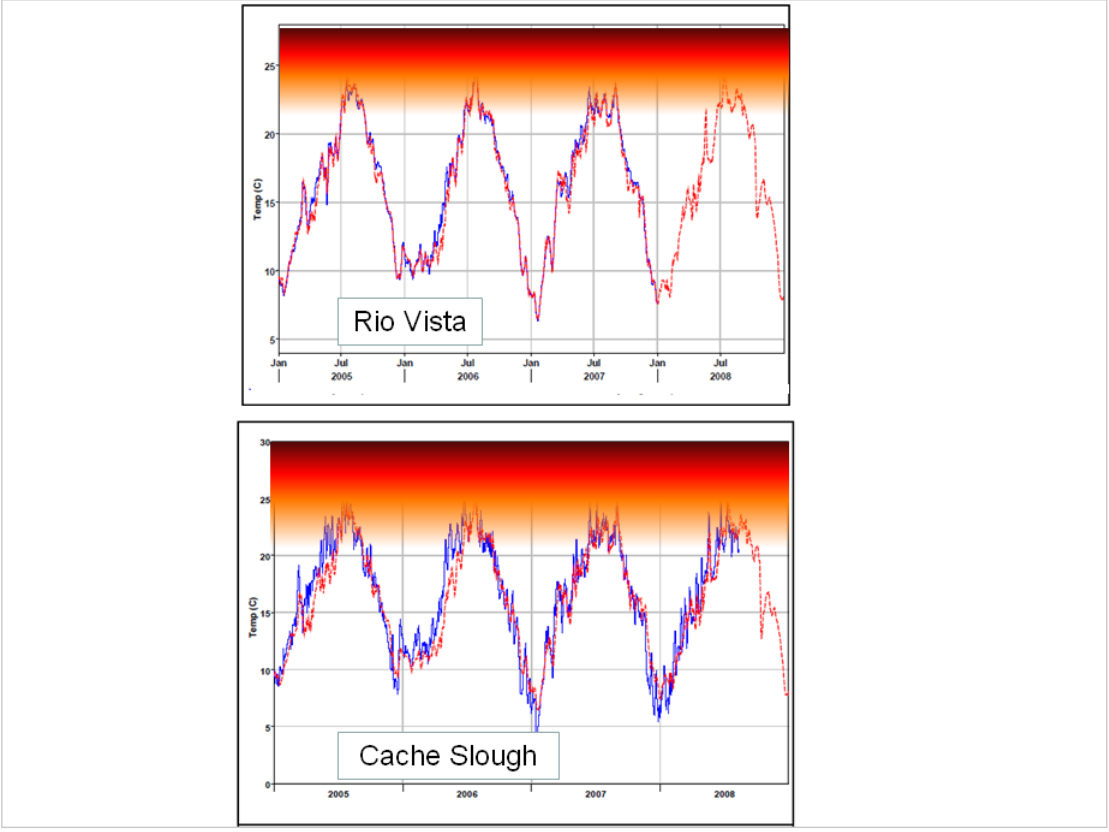

Figure 30. Source: Bay-Delta Conservation Plan, Chapter 5 Technical Appendix E. The red gradients were added by Service staff to show the temperatures where delta smelt health and survival can be impaired.

Contaminant exposures chronically impair food web production and fish health (ongoing)

Delta smelt's spawning migration coincides with early winter rains (Sommer et al. 2011). This 'first-flush' of inflow to the Delta brings sediment-bound pesticides with it (Bergamaschi et al. 2001), and peak densities of larvae and juveniles can co-occur with numerous pesticides (Kuivila

and Moon 2004). Bennett (2005) reported that about 10% of the delta smelt analyzed for histopathological anomalies in 1999-2000 showed evidence of deleterious contaminant exposure, but this was low compared to the 30%-60% of these fish that appeared to be food-limited. Delta smelt can also be exposed to other toxic substances. Recent toxicological research has provided dose-response curves for several contaminants (Connon et al. 2009; 2011a,b). This research has also shown that gene expression changes and impairment of delta smelt swimming performance occur at contaminant concentrations lower than levels that cause mortality. Climatic scale flow variation (e.g., flood versus drought scale variation) affects the amount of methyl mercury entering the ecosystem and may have some influence on the meaningful dilution of ammonium from urban wastewater inputs. However, the Service is not aware of evidence that the amount of flow variation that can be sustainably provided by Project operations substantively influences contaminant dynamics in the estuary.

Invasive species may also affect contaminant dynamics. For instance, *Microcystis* blooms generate toxic compounds that can kill delta smelt prey (Ger et al. 2009) and accumulate in the estuarine food web (Lehman et al. 2010b). A second example is the biomagnification of selenium in the food web by *Corbula* (Stewart et al. 2004). This has been considered a potential issue for the clam's predators – namely sturgeon, splittail, and diving ducks (Richman and Lovvorn 2004; Stewart et al. 2004). However, it is not known whether this change in selenium dynamics negatively affects delta smelt, longfin smelt, or other fishes that do not directly prey on the clams.

Habitat suitability

Summer-fall hydrodynamics

The freshwater flows that enter the Delta as inflow and pass through it as outflow influence habitat suitability for delta smelt (Kimmerer et al. 2009; Feyrer et al. 2011). The combined CVP and SWP water systems began diverting water year-around from the Delta in 1968. Thus, the following analysis considers historical flow conditions based on summaries of the DAYFLOW database for the period 1968-2009/2010[10]. Delta inflows vary among years due largely to interannual differences in precipitation (Kimmerer 2004). However, the Projects often have considerable control over Delta inflows during most of delta smelt's juvenile life stage – particularly July-October, which are the 'base flow' months in the watershed (Kimmerer 2002b; 2004). Inflows have been variable during July-August, but with consistently higher minima since the mid-1990s (Figure 31). In contrast, inflows during September-December have been lower since the mid-1980s than they were prior. This is particularly apparent in November-December because peak flows are so much larger than low flows in these months due to occasional large autumn storms.

10 At the time this section was written, official DAYFLOW data were available through water year 2010 (i.e., September 2010).

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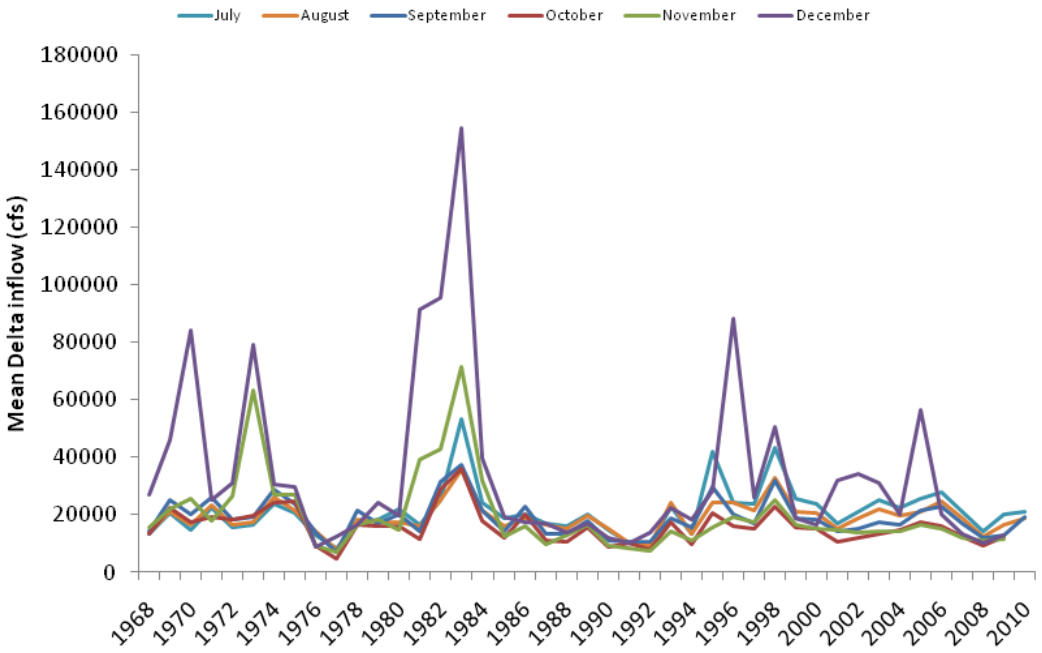

Figure 31. Time series of total Delta inflow for July-September, 1968-2010 and October-December, 1968-2009. Source: DAYFLOW database

As was the case for the winter months of January-March, Project exports have generally increased during July-December (Figure 32). Monthly exports first reached 400 TAF in July 1971. They first reached 500 and 600 TAF in July and August 1974. September exports specifically, first reached 500 and 600 TAF in 1976 and 1985. July-December exports have often ranged between 400-600 TAF per month since 1980. Monthly exports exceeded 700 TAF a few times during the mid-2000s. Summer-fall exports are typically less than 400-600 TAF per month during droughts (1976-1977; 1990-1992; 2007-2009).

The net effect of these inflow and export trends is clearer when plotted as the export to inflow ratio (E:I; Figure 33). The E:I is highly variable among months and years because both exports and inflows vary considerably. Nonetheless, with the possible exception of December, summer-fall E:I has generally been higher since the mid-1980s than it was prior. Since 2000, it has only dropped below 0.40 once during the months of July-November. These trends are very different than what has occurred during other times of the year (Figure 22). During January-March, E:I has not had any trend except to increase temporarily during droughts (1976-1977, 1987-1992). The E:I has decreased during April-May because of the VAMP, and it has shown no obvious long-term trend during June.

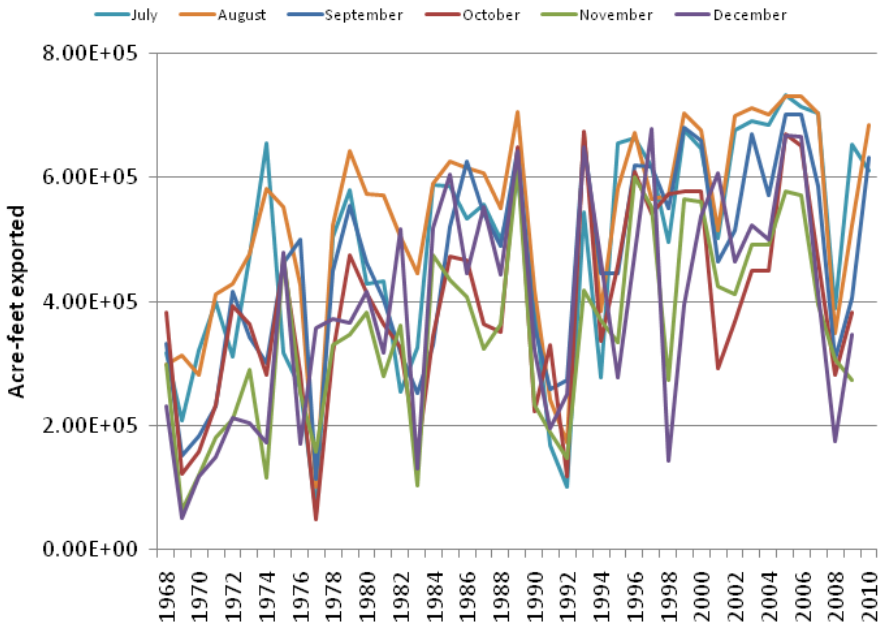

Figure 32. Time series of combined Project exports for July-September, 1968-2010 and October-December, 1968-2009. Source: converted from cfs data in DAYFLOW database

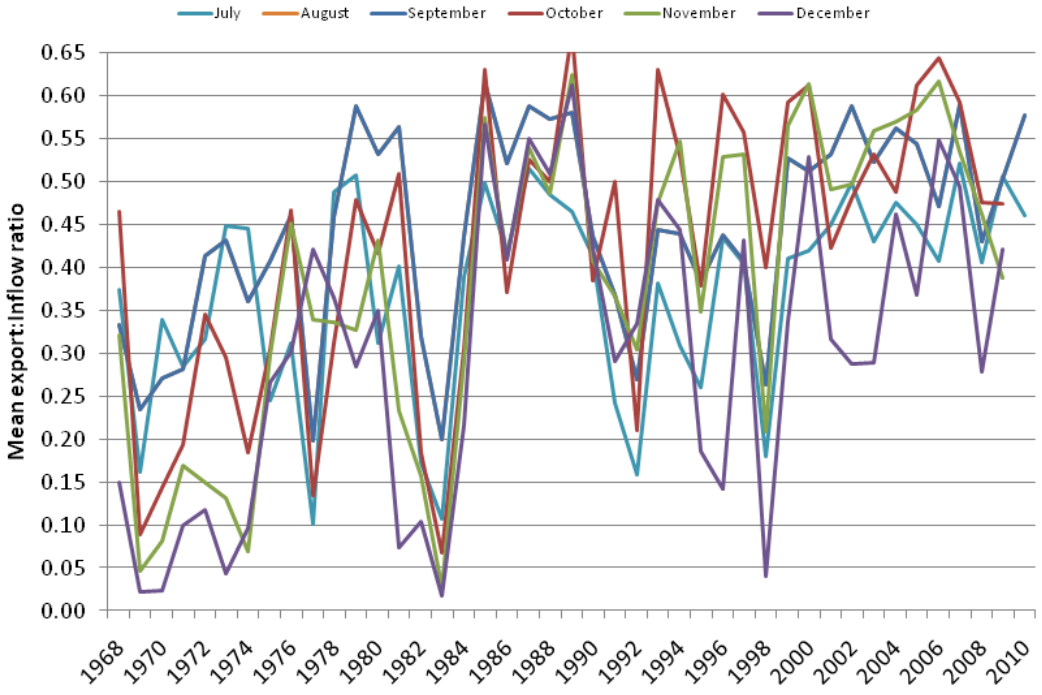

Figure 33. Time series of the monthly mean Export to Inflow ratio for July-September, 1968-2010 and October-December, 1968-2009. The upper limit of the y-axis (0.65) is the upper limit for this ratio set by the State Water Resources Control Board. Source: DAYFLOW database

The increased export flows relative to inflows translate into lower Delta outflow (Kimmerer 2004). This in turn allows the estuarine salinity distribution to move upstream. The salinity distribution of the San Francisco Estuary is often indexed using X2 (Jassby et al. 1995). The Board enacted a salinity standard that can be met using X2 location during February-June (SWRCB 1995). The Projects began operating to the standard in the mid-1990s. This can be seen in monthly time series of X2 (Figure 23). Since the mid-1990s, X2 has not migrated as far upstream as it did prior during February-June[11]. This is also true of January and July even though the salinity standard does not apply in these months. This is likely due to inertia in the location of X2; its average location does not move as quickly as Delta outflow changes (Jassby et al. 1995). It takes more Delta outflow to move X2 from a starting location to a downstream location than it takes to maintain it at the downstream location once it is there. Thus, the Projects may sometimes need to start moving X2 downstream in January to meet the February standard if precipitation is not sufficient to provide the needed outflow. The inertia also works in reverse, but the landward encroachment is even slower. If Delta outflow decreases in July, a month in which the Projects usually have a substantial influence on Delta outflow, then X2 will not immediately move upstream. Project influence is probably why upstream limits of July X2 have remained seaward of historical locations even though the Projects are not required to meet an X2 standard in July. By August, present-day X2 locations are more comparable to what they were prior to the mid-1990s (Figure 23). In contrast, September-December X2 locations have recently been persistently skewed toward the upstream end of where they occurred in the early years of combined Project pumping. This trend is particularly pronounced during October-December, during which the historical interannual variability in fall X2 location had largely disappeared by the mid-1980s. The trend toward increasing exports with decreasing inflows shown in Figure 31 to Figure 33 is a proximal cause of this change in X2 and is thus at least somewhat attributable to Delta flows.

The linkage of fall hydrodynamics to delta smelt habitat suitability

The Department of Fish and Game collects data on three water quality variables along with its trawl surveys: specific conductance, which is a surrogate for salinity; Secchi disk depth, which is a measure of water transparency, and water temperature. Feyrer et al. (2007) showed that the FMWT had most frequently collected delta smelt in water that had very low transparency and specific conductance that ranged from fresh water to about 10,000 microseimens per centimeter or about 6 psu. The approximate conversion between these salinity units is provided in Table 5. Feyrer et al. (2007) showed the water quality conditions that were historically associated with the highest chances of catching delta smelt were occurring at progressively fewer locations over time in the FMWT. This decline in the mixture of water quality conditions that provided the best chances of catching a delta smelt had occurred because the water transparency had been generally increasing, particularly in the south Delta, and because specific conductance had been generally increasing in Suisun Bay. The former was due mostly to changes in sediment inputs and outputs over time (Wright and Schoellhamer 2004; Schoellhamer 2011) and the proliferation of submerged aquatic vegetation (Hestir 2010). The latter was due to the hydrodynamic changes discussed above.

11 Note that downstream limits of X2 during winter and spring are driven by flood flows and are thus not under substantive control of the Projects.

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Table 5. Approximate translation of specific conductance into oceanic salinity based on Obrebski et al. 1992. Note that a full conversion requires a correction for water temperature.

Specific conductance (μS/cm)	Approximately salinity (psu or parts per thousand)
187	0.105
910	0.5
1750	1.0
3400	2.0
5075	3.0
6750	4.0
8400	5.0
10,000	6.0

The correspondence of declining delta smelt capture probabilities and changing water quality is an indicator of declining habitat suitability. This linkage was made more explicit by Feyrer et al. (2011). Feyrer et al. (2011) showed how the predicted probability of capturing a delta smelt in the FMWT varied for each year of the survey (1967-2008; Figure 34). The cluster of lines with the higher probabilities of delta smelt occurrence represent years of relatively high FMWT indices; the cluster with lower probabilities are years of relatively low FMWT indices. This analysis showed that historical capture probabilities reached about 0.5 or 50 percent at a specific conductance between 3 and 3.5 on a $\log_{10}$ scale. This is about 1000-3200 microseimens per centimeter or about 0.5 to 2 psu. During years of lower abundance, there is less evidence of a peak in catch relative to salinity, but there is a slight increase in capture probability at $\log_{10}$ specific conductance between 3.5 and 4.0, or 3200 to 10,000 microseimens per centimeter; about 2-6 psu. The chances of catching a delta smelt decrease rapidly at specific conductance corresponding to more than about 6 psu.

Probabilities of delta smelt occurrence are also highest where the Secchi disk depths are lowest (Figure 34). This is most pronounced in high abundance years, but still apparent in most low abundance years as well. As with specific conductance, the high and low abundance years converged on near zero chance of delta smelt detection where Secchi depths approach 1 meter (0 on a log scale). The basic reason for these combined trends is that water transparency has increased the most at the freshwater sampling stations (Feyrer et al. 2007), though water clarity has increased somewhat throughout the estuary (Schoellhamer 2011).

Next, Feyrer et al. (2011) developed a unit less delta smelt habitat suitability index based on the FMWT. This was an improvement over the Feyrer et al. (2007) version which did not factor geography into the index. Each year's index is the predicted chance of catching a delta smelt based on specific conductance and Secchi depth at each of 73 FMWT sampling stations multiplied by a corresponding areal estimate represented by each station. These areas can be seen as polygons in Figure 35. The Figure provides an example of how much predicted habitat suitability for delta smelt improves in Suisun Bay when X2 is downstream of the Sacramento-San Joaquin river confluence.

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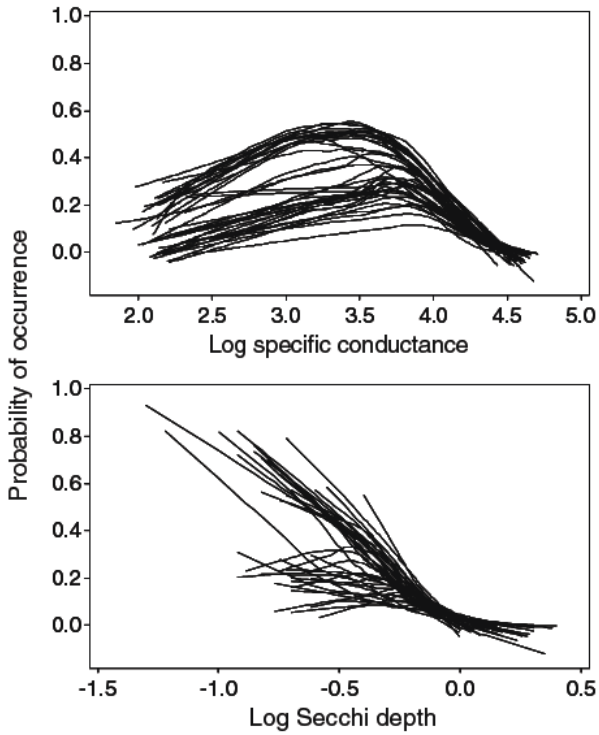

Fig. 1 Plot of the GAM response predictions (probability of occurrence) against specific conductance and Secchi depth. Individual lines are LOESS smooths drawn through the points for individual years

Figure 34. Source: Feyrer et al. (2011); GAM refers to generalized additive modeling of the Fall Midwater Trawl data for delta smelt, 1967-2008.

The fall habitat suitability index showed evidence of a step-decline in the mid-1980s (Figure 36; top panel "A"). This corresponded in time with the hydrodynamic changes discussed above (Figure 31 to Figure 33). The habitat index reflects long-term trends in both salinity and water transparency. Feyrer et al. (2011) plotted their habitat index versus average September-December X2 as a means of determining how strongly Delta flow conditions can influence delta smelt habitat suitability (Figure 36; middle panel "B"). The rationale was that because the Projects can control X2 location during periods of low Delta outflow (SWRCB 1995), this would test how well the Projects could control abiotic habitat suitability for delta smelt. The habitat index is related to fall X2, but in a nonlinear way. Generally speaking, the habitat index is low whenever X2 is upstream of 80 km (near Broad Slough at the confluence of the Sacramento and San Joaquin rivers). The habitat index increases when X2 is downstream of 80 km, but the rate of increase per km of X2 appears to slow down considerably once X2 move seaward of about 75 km (Chipps Island).

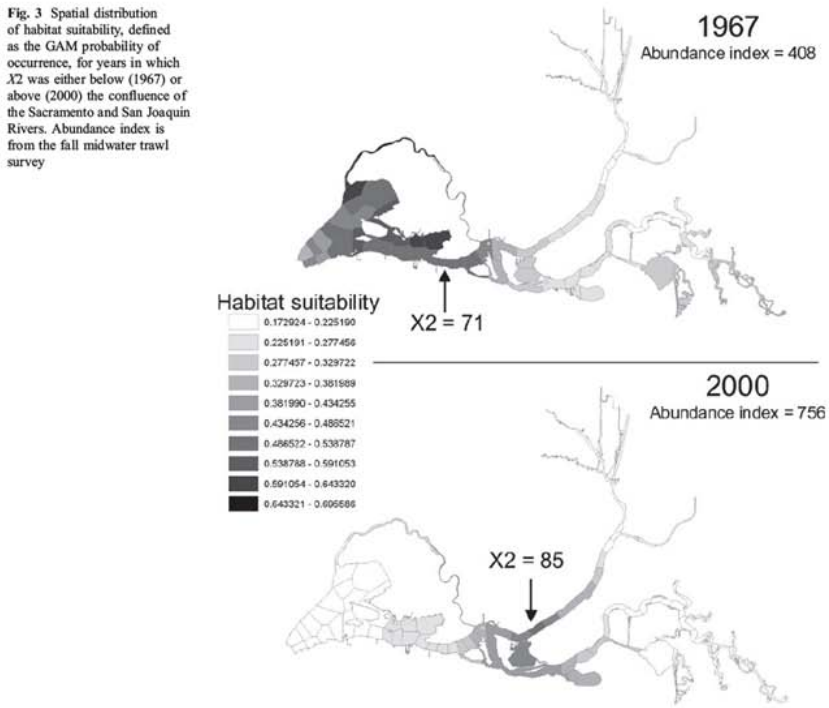

Figure 35. Maps showing the spatial distribution of estimated delta smelt habitat suitability for two example years in the Department of Fish and Game's Fall Midwater Trawl Survey. 1967 was a high outflow fall with an average fall X2 location of 71 km; 2000 was a low outflow fall with an average X2 location of 85 km.

The GAM analyses performed by Feyrer et al. (2007; 2011) and others (e.g., Nobriga et al. 2008; Kimmerer et al. 2009) are reporting concurrent associations of fish catches and water quality. Thus, they show that some of the variation in delta smelt catch is explained by environmental conditions that occurred during the sampling. Feyrer et al. (2011) showed that despite being based on presence or absence of delta smelt, their resultant habitat index was correlated with the FMWT abundance index (Pearson r = 0.51; P = 0.001; Figure 36; bottom panel "C"). However, this is an expected outcome because delta smelt abundance and presence-absence are correlated. The point in showing this association was to demonstrate that although the linkage is variable and inherently based on a circular argument (because catch was used to define habitat suitability), there is nonetheless a correlation between the FMWT indices and the habitat indices, which are nonlinearly related to fall X2. The FMWT index is one of the best available predictors of the next year's 20-mm and Summer Townet indices (Maunder and Deriso 2011; Miller et al. 2012). This suggests that fall habitat conditions may have some influence on egg supply available to produce the next generation of smelt. Note that some authors have tried to use fall specific conductance or X2 as a covariate to explain additional variation in the relationship between successive delta smelt abundance indices (Feyrer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010; Miller et al. 2012). However, it is not necessary to make this second analytical step to link fall habitat to delta smelt population dynamics. Fall habitat conditions influence the FMWT index itself. Thus, when a FMWT index is plotted against an index of the following generation's abundance, the fall habitat effect is already built into the relationship. In fall of 2011, X2

remained downstream of 79 km for much of the season. The 2011 delta smelt FMWT index was 343, the highest index since 2001. The 2011 FMWT index was 11.8 times higher than the 2010 index, even though the 2011 20mm Survey (spring relative abundance) and STNS (summer relative abundance) indices for delta smelt were only about twice as high in 2011 as they were in 2010.

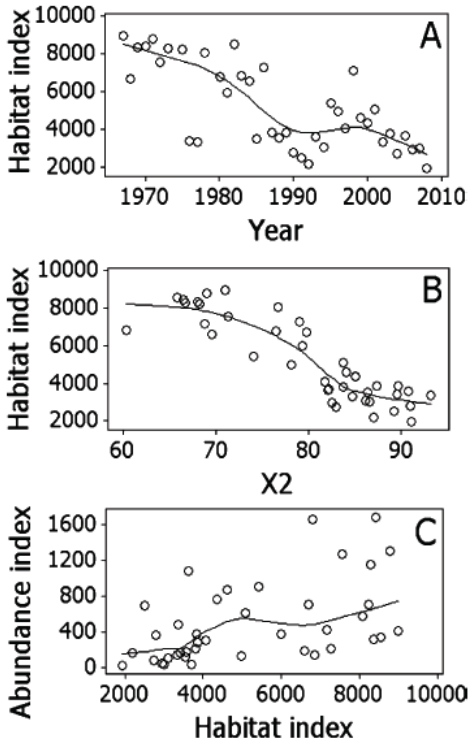

Fig. 2 Plots of the habitat index time series (**a**), relationship between *X*2 (km) and the habitat index (**b**), and relationship between the habitat index and delta smelt abundance measured as the fall midwater trawl index. Curves are LOESS smooths

Figure 36. Time series of a delta smelt habitat index based on the Department of Fish and Game's Fall Midwater Trawl (FMWT) Survey, 1967-2008, and relationships of the index with the geographic location of the 2 psu salinity isohaline (X2) and and FMWT abundance index for delta smelt. Figure copied from Feyrer et al. (2011).

Feyrer et al. (2011) showed that the hydrologic modeling done to support this consultation provides an imperfect representation of present-day hydrodynamic conditions. Nonetheless, the modeling shows that the combination of a 2030 level of development and the sea-level rise that is predicted to occur by 2030 due to climate change, decrease predicted habitat suitability for delta smelt in all but critical water years (Figure 37). The comparison between Scenarios A and B isolates the influence of Delta flows on delta smelt's habitat index because it compares the Projects' modeled baseline to a predicted 2030 operation without including the climate changes explored in Scenarios C-G. Note that Feyrer et al. (2011) estimated future values of the index by using the predicted X2 locations output by the CALSIM II model and predicting the habitat index

from X2 using the relationship shown in Figure 36 panel “B”.

The comparison of Scenarios A and B shows that outflow-induced changes in X2 cause most of the predicted change in the habitat index. In wet years, the median habitat index in Scenario B is just over 4000, which is about half the value of the median in Scenario A (just under 8000). In above-normal, below-normal, and dry water year types, not only do predicted median habitat indices decline, but the variability that occurs in Scenario A is greatly reduced in Scenario B.

Fig. 5 Box plots of the habitat index values for each scenario across water year types. The *box plots* show medians and first and third quartiles. *Whiskers* show the highest or lowest values in the upper or lower limits, respectively. Table 1 provides details on the modeled outflow scenarios

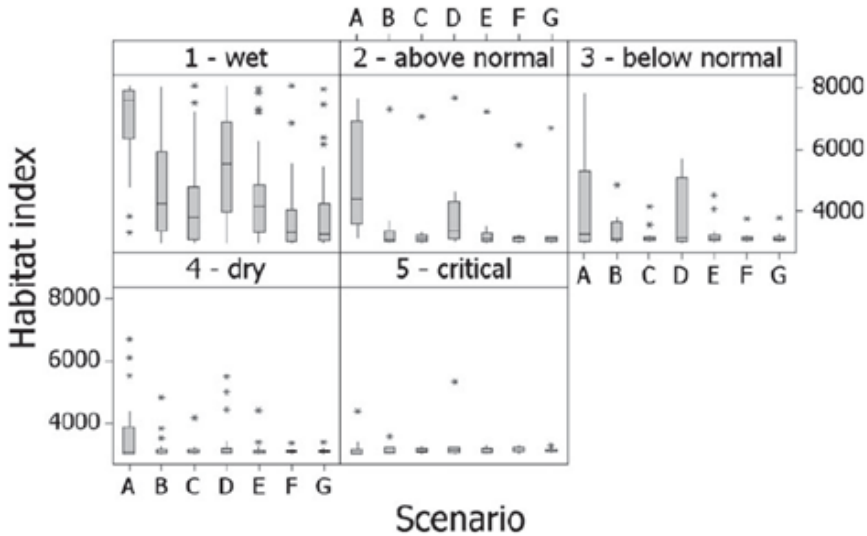

Figure 37. Comparisons of the hydrologic simulation model CALSIM II results for delta smelt fall habitat index by water year type from Feyrer et al. (2011). Scenario A = 2005 level of development, current sea level; Scenario B = 2030 level of development, current sea level; Scenario C = 2030 level of development, 0.33 m increase in sea level and 10% increase in tidal range; Scenarios D-G, same as Scenario C except, Scenario D = higher mean precipitation and somewhat warmer weather than present; Scenario E = higher mean precipitation and warmer weather than Scenario D; Scenario F = lower mean precipitation and temperatures equivalent to Scenario D; Scenario G = lower mean precipitation and temperatures equivalent to Scenario E.

Limitations of the habitat index

The delta smelt habitat index discussed above is based on two abiotic habitat characteristics (salinity and water transparency). Two other abiotic habitat attributes have been evaluated in the generalized additive modeling framework. Water temperature is an important aspect of delta smelt habitat suitability in the summer (Nobriga et al. 2008), but not in the fall (Feyrer et al. 2007). This is likely because lethal temperatures do not often occur in the estuary during September-December so there is little opportunity for temperature to constrain delta smelt distribution. Additionally, water depth is not an important aspect of delta smelt’s summer habitat (Kimmerer et al. 2009). However, including it did improve the fit of Kimmerer et al.’s (2009) fall habitat model. The caveat to this statement is that Kimmerer’s FMWT analysis explained less than or equal to 4 percent of the variability in delta smelt catch. When so little variance is

explained, any increment of variability makes a difference. Note that the Feyrer et al. (2007; 2009) analyses of the same data explain up to 25 percent of the variance. The Service does not know why this discrepancy exists between these two analyses of the FMWT data.

Delta smelt habitat suitability is also influenced by biotic variables (food supply, predation, and possibly disease). The degree to which biotic habitat attributes might confound conclusions based on the abiotic habitat index is unknown. The reason that Feyrer et al. (2007; 2011) did not explicitly include any biotic variables in their analyses is simple and was acknowledged by the authors – biotic variables like zooplankton prey data have not historically been taken concurrently with the FMWT. Further, there are no existing data that can be used to quantify predation rates or disease trends during summer-fall, though some scientists have made speculative attempts to quantify prey and predator abundances using data from other times of year or other imperfectly matched sampling programs (Mac Nally et al. 2010; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012). However, it should be noted that biotic and abiotic habitat attributes cannot always be easily separated. For instance, the prey density needed for delta smelt to grow at a given rate is affected by water temperature (e.g., Lantry and Stewart 1993). As a second example, the predation rates on delta smelt are hypothesized to be influenced by both water temperature and water transparency based on studies of salmonid fishes (e.g., Gregory and Levings 1998; Marine and Cech 2004).

Life Cycle Models for Delta Smelt

Density dependence in the Delta Smelt Population

Several statistical life cycle models for delta smelt have been published over the past several years (Mac Nally et al. 2010; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012). These models are all correlation-based, but they have each employed different statistical approaches and have not tested the same suites of variables (usually called covariates in the cited papers). Thus, there is not a lot of concurrence in the conclusions drawn using these tools (Table 6). Overall, the collective results of these four papers show that results depend (1) on what variables get tested, and (2) what assumptions are made about density dependence.

Table 6. Summary of delta smelt life cycle model results published between 2010 and 2012. Covariates are general descriptions of the variables that the authors attempted to correlate with delta smelt abundance or survival. Different authors often used different forms of covariates that are listed under the same name in this table so the variables are nominally similar, but not necessarily equivalent. Note that Miller et al. (2012) in particular often tested multiple versions of covariates that are given one name in this table (e.g., summer temperature or spring copepods). Question marks denote covariates where the description in the paper is not adequate to determine if the variable was tested; the entrainment terms in Maunder and Deriso (2011) may be highly congruous with OMR flows. Miller et al. (2012) used proportional entrainment estimates as adjusted by Miller (2011). Like Kimmerer's (2008) entrainment estimates, the estimates reported in Miller et al. (2012) are highly congruous with OMR flows – particularly in the spring, though the relationship is not linear. Dark green shading depicts covariates that were strongly correlated with delta smelt survival over some life cycle interval. Mac Nally et al. and Thomson et al. defined this as an odds ratio > 3; for Maunder and Deriso, support was considered strong (by the Service) if the covariate was retained in more than 3 of their top 6 models using different density dependence assumptions; strong support in the Miller et al. models were those factors retained in the best-fitting models. Note that summer copepods was originally included in

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their best-fitting models, but then fall copepods was added and the authors reported that variable worked better. Both are shown as strongly supported here because they likely are highly correlated. Light green shading is used to depict covariates that had weaker statistical support as described by Mac Nally et al. and Thomson et al. (odds ratios between about 1 and 3) and covariates that were retained in 1-3 of Maunder and Deriso's top 6 models. Miller et al. did not report their data in a way that would allow a clear determination of variables with lesser support. Note that PDO is the acronym for the ocean index known as the Pacific Decadal Oscillation.

Covariate	Mac Nally et al. (2010)[a]	Thomson et al. (2010) [a]	Maunder and Deriso (2011)[b]	Miller et al. (2012) [a]	Miller et al. (2012 v2)[c]
Prior abundance (density dependence)	FMWT-FMWT	FMWT-FMWT	FMWT-20mm-TNS-FMWT	FMWT-FMWT-FMWT	FMWT-FMWT-TNS-FMWT
WINTER					
Winter copepods[prey]	Not tested	Not tested	Not tested		
Adult entrainment[entr]	Not tested	Not tested		Not tested	Not tested
Winter exports[entr]			Not tested	Not tested	Not tested
Winter Limnoithona[prey, comp]	Not tested	Not tested	Not tested		
Winter OMR flow[entr]	Not tested	Not tested	???		Not tested
Winter PDO[hab]			Not tested	Not tested	Not tested
Winter Secchi depth[hab]	Not tested				Not tested
SPRING					
Spawning days (~ spring) [hab]					
Spring chlorophyll[hab]			Not tested	Not tested	Not tested
Spring copepods[prey]					
Spring entrainment[entr]	Not tested	Not tested		Not tested	Not tested
Spring exports[entr]			Not tested	Not tested	Not tested
Spring Limnoithona[prey, comp]	Not tested	Not tested	Not tested		
Spring nonnatives[pred]	Not tested	Not tested			
Spring OMR flow[entr]	Not tested	Not tested	???		Not tested
Sprng other zooplankton[prey]			Not tested	Not tested	Not tested
Spring Secchi depth[hab]	Not tested	Not tested	Not tested		
Spring temperature[hab]	Not tested	Not tested			
Spring X2[hab, entr]			Not tested	Not tested	Not tested
SUMMER					
Summer anchovies[comp]			Not tested	Not tested	Not tested
Summer copepods[prey]					
Summer lrgmouth bass[pred]			Not tested	Not tested	Not tested

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Summer Limnoithna[prey, comp]			Not tested		
Summer mysid shrimp[prey]			Not tested		
Summer PDO[hab]	Not tested		Not tested	Not tested	Not tested
Summer silverside[pred, comp]			Not tested	Not tested	Not tested
Summer temperature[hab]					
Maximum summer temp[hab]	Not tested	Not tested			
FALL					
Fall copepods[prey]	Not tested	Not tested	Not tested		
Fall delta smelt fork length	Not tested	Not tested			
Fall Limnoithona[prey, comp]	Not tested	Not tested	Not tested		
Fall nonnatives[pred]	Not tested	Not tested			
Fall Secchi depth[hab]			Not tested		Not tested
Fall X2[hab]			Not tested		Not tested
MULTIPLE SEASON					
Adjusted entrainment[entr]	Not tested	Not tested	???		
Adult striped bass[pred]					
Overbite clam[comp]			Not tested		Not tested

[a]Results based on a one year time step (fall to fall)
[b]Results based on a 0.33 year time step (fall to spring to summer to fall)
[c]Results based on a 0.5 year time step (fall to summer to fall)
[prey]Delta smelt prey item
[pred]Delta smelt predator
[comp]Delta smelt competitor
[hab]Delta smelt habitat component other than predator or prey
[entr]Source or index of entrainment loss

The concept of density-dependence and how it has affected the delta smelt is important because it gets erroneously used as a reason not to protect particular life stages from sources of mortality (Kimmerer 2011). Density dependence refers to situations in which vital rates like growth and reproduction change with the abundance of an organism (Rose et al. 2001). Density dependence is not always obvious in abundance data, but it is likely a universal aspect of population ecology because no organism can increase to infinite abundance. Typically (i.e., absent Allee effects), growth and reproductive rates speed up as abundance decreases and slow down or even decline as abundance increases. The basic reason is that crowding leads to faster disease transmission, higher rates of cannibalism and resource limitation, and greater attraction of predators. However, fish do not need to be abundant to have population dynamics that reflect density dependence (Walters and Juanes 1993). Fish have to balance getting enough to eat with the risk of becoming food themselves. The numbers of fish that can be supported in a system are therefore context-dependent; the optimal balance between eating and getting eaten depends on what fish species, what life stage, what the prey and predator densities are, what condition the habitat is in, etc.

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Statistically speaking, evidence for density dependence is provided by any of several nonlinear correlations between abundance at one point in time and abundance at a future point in time. In contrast, evidence for density independent population dynamics is provided by a linear relationship (when data are not transformed in any way) between abundance at one point in time and abundance at a future point in time. It is unclear whether density-dependence has occurred between delta smelt generations because statistical assessments of the relationship between the adult stock and the next generation of recruits (juveniles) result in similar fits for linear (density-independent) and nonlinear (density-dependent) relationships (Bennett 2005; Maunder and Deriso 2011; Figure 38). One reason for this is that delta smelt population dynamics may have changed over time. Previous papers have reported a delta smelt step-decline during 1981-1982 (Moyle et al. 1992; Thomson et al. 2010). Prior to this decline, the stock-recruit data are consistent with "Ricker" type density-dependence where increasing adult abundance resulted in *decreased* juvenile abundance (Figure 38). Since the decline, recruitment has been positively and essentially linearly related to prior adult abundance, suggesting that reproduction has been basically density-independent for the past 30 years. This means that since the early 1980s, more adults translates into more juveniles and fewer adults translates into fewer juveniles without being 'compensated for' by density-dependence between generations. This interpretation of the data contrasts the conclusions of Maunder and Deriso (2011) and Miller et al. (2012).

In contrast to the transition among generations, the scientific evidence supports the hypothesis that, at least over the history of Interagency Ecological Program (IEP) fish monitoring, delta smelt has experienced density-dependence during the juvenile stage of its life cycle, i.e., between the summer and fall (Bennett 2005; Maunder and Deriso 2011; Figure 38). From a species conservation perspective, the most relevant aspect of this juvenile density dependence is that the carrying capacity of the estuary for delta smelt has declined (Bennett 2005).

Thus, the Service believes that the delta smelt decline has occurred for two basic reasons. First, the compensatory density-dependence that historically enabled juvenile abundance to rebound from low adult numbers stopped happening. This change had occurred by the early 1980s as described above. The reason is still not known, but the consequence of the change is that for the past several decades, adult abundance drives juvenile production in a largely density-independent manner. Thus, if adult numbers or adult fecundity decline, juvenile production will also (Kimmerer 2011). Second, because juvenile carrying capacity has declined, so juvenile production hits a 'ceiling' at a lower abundance than it once did. This limits adult abundance and possibly per capita fecundity, which cycles around and limits the abundance of the next generation of juveniles. The mechanism causing carrying capacity to decline is likely due to the long-term accumulation of deleterious habitat changes – both physical and biological – during the summer-fall (i.e., associated with the kinds of covariates listed in Table 6).

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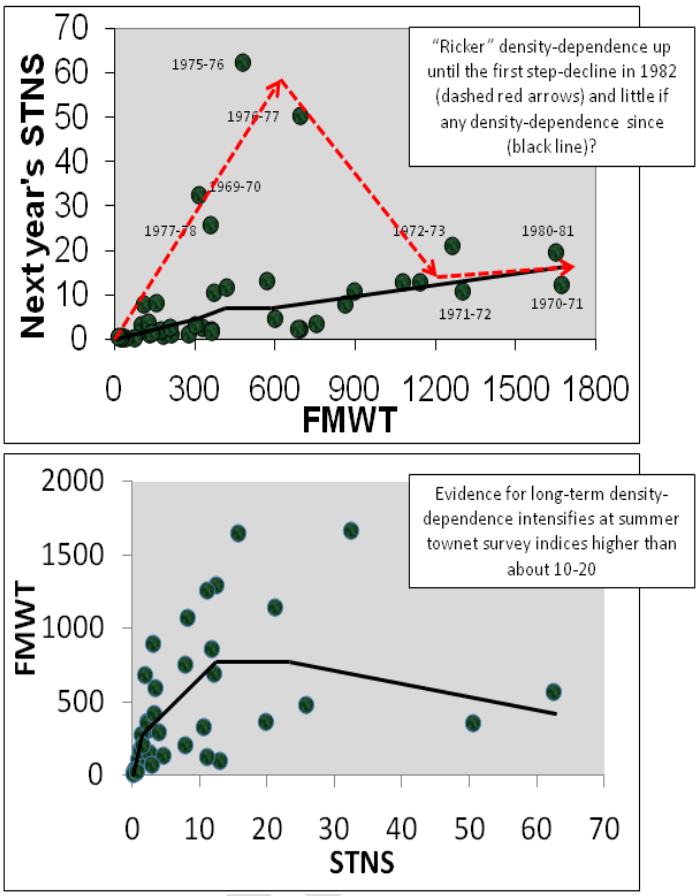

Figure 38. Upper Panel: plot of the FMWT index for delta smelt vs. the following year's summer townet survey (STNS) index. The "pre-decline" years based on Kimmerer (2002a) are individually labeled. The red arrows reflect the Service's hypothesis that a "Ricker" type curve would best fit the data through 1981. The black line is a trace of the LOWESS spline that the Systat software program fit to the data. Lower Panel: plot of the STNS index for delta smelt vs. the FMWT index determined a few months later in the same calendar year. The black line is a trace of the LOWESS spline fit to the data.

Conclusions

- In conclusion, we suggest that the Board model and evaluate a range of flow objectives that could be incorporated in the WQCP. Our suggested evaluation should include flow objectives that are likely to improve habitat conditions for delta smelt, longfin smelt, and other native estuarine biota and put the Bay-Delta ecosystem on a path toward recovery.

- For adult delta smelt, negative Old and Middle River (OMR) flows contribute to entrainment risk during spawning migrations.

- For age-0 delta smelt OMR flows are a suitable index of the hydrodynamic conditions that *drive* entrainment loss.

- The Service recognizes that multiple factors have contributed to the substantial long-term degradation of the low-salinity zone (LSZ). Nonetheless, Delta outflow remains an extremely important aspect of LSZ habitat suitability for delta smelt, particularly during low flow periods.

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Title:
Losses of Sacramento River Chinook Salmon and Delta Smelt to Entrainment in Water Diversions in the Sacramento-San Joaquin Delta

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Abstract:
Pumping at the water export facilities in the southern Sacramento-San Joaquin Delta kills fish at and near the associated fish-salvage facilities. Correlative analyses of salvage counts with population indices have failed to provide quantitative estimates of the magnitude of this mortality. I estimated the proportional losses of Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*) and delta smelt (*Hypomesus transpacificus*) to place these losses in a population context. The estimate for salmon was based on recoveries of tagged smolts released in the upper Sacramento River basin, and recovered at the fish-salvage facilities in the south Delta and in a trawling program in the western Delta. The proportion of fish salvaged increased with export flow, with a mean value around 10% at the highest export flows recorded. Mortality was around 10% if pre-salvage losses were about 80%, but this value is nearly unconstrained. Losses of adult delta smelt in winter and young delta smelt in spring were estimated from salvage data (adults) corrected for estimated pre-salvage survival, or from trawl data in the southern Delta (young). These losses were divided by population size and accumulated over the respective seasons. Losses of adult delta smelt were 1–50% (median 15%) although the highest value may have been biased upward.

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Daily losses of larvae and juveniles were 0–8%, and seasonal losses accumulated were 0–25% (median 13%). The effect of these losses on population abundance was obscured by subsequent 50-fold variability in survival from summer to fall.

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Losses of Sacramento River Chinook Salmon and Delta Smelt to Entrainment in Water Diversions in the Sacramento-San Joaquin Delta

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ABSTRACT

Pumping at the water export facilities in the southern Sacramento-San Joaquin Delta kills fish at and near the associated fish-salvage facilities. Correlative analyses of salvage counts with population indices have failed to provide quantitative estimates of the magnitude of this mortality. I estimated the proportional losses of Sacramento River Chinook salmon *(Oncorhynchus tshawytscha)* and delta smelt *(Hypomesus transpacificus)* to place these losses in a population context. The estimate for salmon was based on recoveries of tagged smolts released in the upper Sacramento River basin, and recovered at the fish-salvage facilities in the south Delta and in a trawling program in the western Delta. The proportion of fish salvaged increased with export flow, with a mean value around 10% at the highest export flows recorded. Mortality was around 10% if pre-salvage losses were about 80%, but this value is nearly unconstrained. Losses of adult delta smelt in winter and young delta smelt in spring were estimated from salvage data (adults) corrected for estimated pre-salvage survival, or from trawl data in the southern Delta (young). These losses were divided by population size and accumulated over the respective seasons. Losses of adult delta smelt were 1–50% (median 15%), although the highest value may have been biased upward. Daily losses of larvae and juveniles were 0–8%, and seasonal losses accumulated were 0–25% (median 13%). The effect of these losses on population abundance was obscured by subsequent 50-fold variability in survival from summer to fall.

KEYWORDS

Chinook salmon *Oncorhynchus tshawytscha*, delta smelt *Hypomesus transpacificus*, diversions, population ecology

SUGGESTED CITATION

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INTRODUCTION

One of the greatest challenges facing resource managers is assessing the effectiveness of their actions in influencing ecosystems or biological populations. This difficulty arises from three sources: 1) weak or

inaccurate understanding of the causal links between actions and responses; 2) inability to control for other sources of variability; and 3) inherent inaccuracy in monitoring causal and response variables. Yet, managers are held accountable for successes and failures, as we have witnessed recently with the decline of pelagic organisms in the upper San Francisco Estuary (Sommer et al. 2008). Thus, the challenge for the scientific community is how to detect and quantify effects of management actions in the absence of strong correlative relationships between these actions and the response variables. This requires an analysis of mechanisms rather than one based on correlative relationships alone.

The San Francisco Estuary is a highly altered and managed system (Nichols et al. 1986) in which conflicts over resources are particularly strong. Perhaps the greatest conflict is due to the diversion and export of substantial quantities of freshwater from the tidal freshwater reach in the Sacramento-San Joaquin Delta. Losses of fish to mortality associated with export pumping have been blamed in part for declines of numerous species including striped bass (Stevens et al. 1985), Chinook salmon (Kjelson and Brandes 1989), and delta smelt (Bennett 2005). Nevertheless, no quantitative estimates have been made of the population-level consequences of losses to the export facilities of any fish species. Kimmerer et al. (2001) concluded that large proportional losses to the export facilities were a minor contributor to variability in the striped bass population of the Estuary. Jassby et al. (2002) conducted a mass balance of chlorophyll concentration in the Delta and concluded that losses of phytoplankton to export pumping must be large, but were masked in correlative analyses by other sources of variation. Similar calculations have not been made for other taxonomic groups, and there have been no published reports of correlations between any measure of export losses and subsequent population size.

Despite the lack of evidence for population-level effects, a strong influence of the south Delta export facilities on populations of estuarine and anadromous fish has been assumed for several reasons. First, large numbers of fish are entrained in the fish facilities (Brown et al. 1996). Second, it is reasonable to expect a large effect on some fish because of the large quantities of water exported, at times more than half of the inflow to the Delta (Kimmerer 2004). Third, manipulations of flow patterns in the Delta provide the only apparent tool for managing some fish populations such as delta smelt.

In this paper I estimate the effects of export pumping in terms of proportional losses of two fish species. Chinook salmon *(Oncorhynchus tshawytscha)* and the threatened delta smelt *(Hypomesus transpacificus)* are target taxa for restoration and management in the Delta. Data for several races of Chinook salmon are available to estimate the losses of these fish to direct effects of entrainment. I focus on winter Chinook because it has been the target of considerable restoration effort, although data for other races are used to provide greater resolution. Two life stages of delta smelt are examined: adults in late winter, and larvae and juveniles in spring. Effects of export pumping are estimated mechanistically, rather than through correlative analyses with the respective population abundances.

The conceptual framework for these calculations differs for the two species. Young Chinook salmon are exposed to export effects during movement through the Delta. Data on length distributions at the export facilities and in field studies suggest that juvenile Chinook generally are exposed to entrainment only during movement, and are rarely entrained while rearing. Young Chinook rear in or migrate through the Delta at various times of year but are most abundant in the Delta from March through June (Williams 2006). Although most of the migrating fish are small fall-run Chinook, winter Chinook and other runs form a substantial pulse of fish larger than the fall run in February–March (Williams 2006). Chinook smolts may take any of several pathways that lead them through the Delta either to the export facilities or through the western margin of the Delta at Chipps Island, and then to sea (Figure 1). When control gates in the Delta Cross-Channel (Figure 1) are open, the smolts may enter the central Delta further upstream, and this could increase their probability of entrainment in the export facilities.

Delta smelt are considered to be resident fish but are actually weakly anadromous, spending most of their

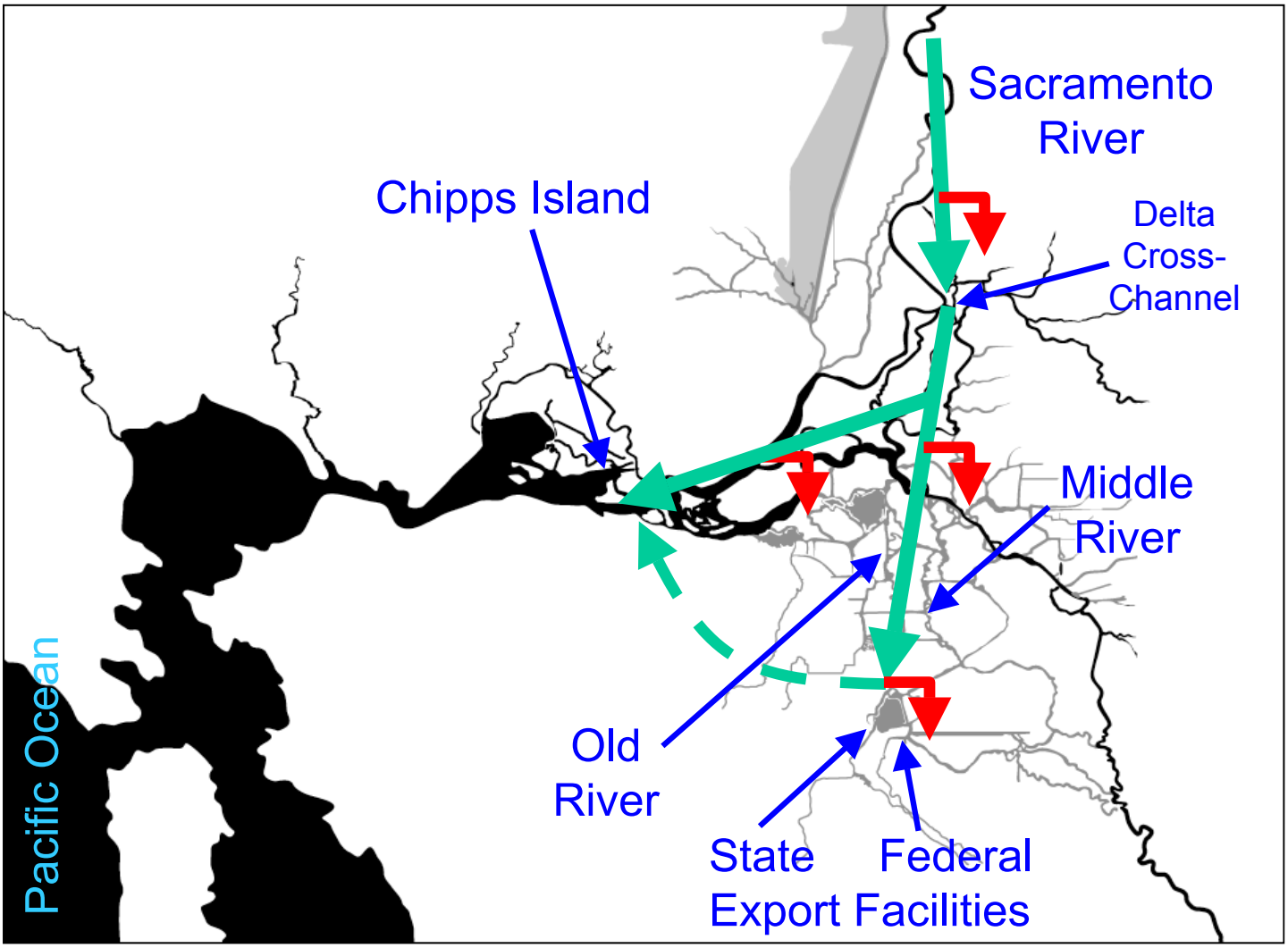

Figure 1. Map of the San Francisco Estuary showing locations mentioned in the text. Green arrows indicate general movement pathways for winter Chinook salmon; the dashed arrow represents movement of salvaged fish by truck. Red arrows indicate mortality losses; only those occurring at the export facilities are accounted for here.

lives in brackish water where they are not exposed to export entrainment (Bennett 2005). The adults spawn in freshwater in late winter, and those in the southern Delta are then vulnerable to entrainment at the export facilities. Eggs are demersal and therefore invulnerable to entrainment, but the pelagic larvae and juveniles in the southern Delta are vulnerable from the time they hatch until they move seaward into brackish water. Thus, export pumping causes a continuous mortality that acts on the population over time during two life stages.

Fish Facility Operations

Fish facilities associated with the state and federal water export facilities (Figure 1) are designed to salvage fish from the water and return them to the Estuary (Brown et al. 1996; Haefner and Bowen 2002). These facilities use two sets of louvers to concentrate the fish behaviorally, but this process is not very efficient. For example, many salmon and other fish are lost to predation in the waterways leading to the fish facilities (Gingras 1997). The efficiency with which the louvers concentrate the fish can be << 100% (Bowen et al. 2004). In addition, few delta smelt probably survive the salvage process (Bennett 2005).

The salvage facilities accumulate fish in holding tanks during sampling periods that are most often 2 hours but have ranged from 10 minutes to 9 hours during 1995–2006. During each sampling period, a sub-sample may be taken over a shorter time-period, nominally 20 minutes (state facility) or 10 minutes (federal facility) although it may be longer or shorter. Karp et al. (1997) compared the sub-sampling procedure for the federal facility with complete analysis of the salvaged fish, validating this procedure. All fish > 20 mm in a sub-sample are counted and identified, and salmon marked with clipped adipose fins are inspected for coded-wire tags and, if present, the tags are read.

It is helpful to define terms (see Table 1 for symbols). Daily *salvage* is the number of fish of given characteristics (species, stage, length) estimated to have entered a fish facility in a day. Daily *entrainment* is the estimated net number of fish that arrived at the entrance to the fish facility per day, i.e., those that arrived and did not leave the area except via the fish facilities. Entrainment exceeds salvage because of mortality in the waterways, leading to the export facilities and losses through the louvers. Daily *loss* is the estimated number entrained that were not subsequently salvaged and returned alive to the Estuary, which includes losses both before and after the salvage process; these are also termed "direct" losses because they are directly attributable to pumping operations.

Losses of fish due to altered hydrodynamic conditions or migration cues in the Delta are called "indirect" losses. Although export pumping has substantial impacts on flow patterns in the Delta, the extent to which such alterations affect survival of fish is much less clear. Indirect losses may be important (NMFS 2004), but they remain hypothetical and unquantified, and are not calculated in this paper.

METHODS

Daily salvage (see Table 1 for all symbols used in this paper) is calculated from the counts taken during each sampling period as:

$$\hat{N}_{di} = \sum_{p=1}^{P_{di}} \frac{N_{dpi} M_{dpi}}{m_{dpi}} \qquad (1)$$

where hats indicate estimated quantities. For tagged Chinook salmon (see below), salvage counts were available only for the entire day, so Equation 1 was simplified by summing over all time-periods within each day:

$$\hat{N}_{di} = \frac{\sum_{p=1}^{P_d} N_{dpi} \sum_{p=1}^{P_d} M_{dpi}}{\sum_{p=1}^{P_d} m_{dpi}} \qquad (2)$$

Equations 1 and 2 were compared using salvage data for total Chinook salmon from 1995–2006. The mean ratio of estimates from Equation 2 to those from Equation 1 for all samples with total daily counts > 100 was 0.98 ± 0.017 (95% CL, N = 219), so these equations were considered equivalent for tagged

Table 1. Definition of terms used in the models for Chinook salmon (C) and delta smelt (D). Terms are unitless unless stated. Subscripts may be added to indicate export facilities (i, state = 1, federal = 2, combined = x), cohorts (j), surveys (s), sampling time-periods for calculating salvage (p), or calendar time-periods (d, mo).

Term	Species	Definition
A	D	Total abundance of fish = Ds V
$A_{L,t}$	D	Abundance of fish of length L at time t
D	CD	Duration of the sampling period (days)
D_s	D	Mean density over all samples (m^{-3})
E_i	CD	Louver efficiency of facility i
E_k	D	Efficiency of Kodiak trawl
E_L	D	Relative efficiency of the 20-mm net as a logistic function of length of fish
g	D	Growth rate (mm d^{-1})
H	D	Number of fish hatching per day
L	D	Length of fish (mm)
m	D	Daily mortality rate (d^{-1})
m_n	D	Daily natural mortality rate (i.e., not due to direct export effects) (d^{-1})
M_{dpi}	CD	Duration of fish salvage period p (min) on day d
m_{dpi}	CD	Duration of subsampling during salvage period p (min) on day d
N_{dpc}	C	Number of fish counted during Chipps Island trawl p on day d
N_{dpi}	CD	Number of fish counted at facility i during period p on day d
N_{di}	CD	Daily salvage for facility i (d^{-1})
N_i	CD	Total salvage for facility i
N_{Ri}	C	Daily number of fish successfully released from fish facility i (d^{-1})
N_{SD}	D	Total fish caught in trawl samples in the south Delta during a survey
$N_{w\delta}$	C	Five-day running mean of total fish caught centered on day δ (weighting factor)
P_d	C	Total number of samples on day d (fish facilities or Chipps Island)
P_S	C	Proportional salvage of fish leaving Delta
P_L	CD	Proportional loss of fish to export effects
Q_{SD}	D	Daily flow to the south Delta (= Old and Middle River flow) (m^3d^{-1})
S	D	Survival (fraction); subscripts indicate time-period or cohort j
S_{HT}	C	Fraction of fish surviving handling and trucking
S_{Pi}	CD	Fraction of fish entrained that reach louvers
S_{Si}	C	Fraction of fish entrained that enter salvage facility
t	D	Any day between T_0 and the final date of the simulation (d)
T_0	D	Initial hatch date (d)
T_j	D	Initial hatch date (d) for cohort j
T_1	D	Final hatch date (d)
T_f	D	Final day of survey
u	C	Migration speed, m d^{-1}
V	D	Volume of habitat over which trawl catches are averaged (m^3)
V_{dpc}	C	Volume sampled by sample p on day d in the Chipps Island Trawl (m^3)
V_{SD}	D	Total volume filtered in survey s at South Delta stations (m^3)
W	C	Width of channel at Chipps Island (~ 1,000 m)
Z	C	Depth over which salmon are assumed to migrate (4 m)
θ	D	Efficiency ratio, a free parameter in adult loss equation (18)
λ	C	Ratio of loss to salvage, calculated from pre-salvage survival
Λ_{di}, Λ_i	D	Daily or cumulative loss to export facilities
Φ_{di}, Φ_i	CD	Daily or cumulative entrainment to export facilities
Φ_{dc}, Φ_c	CD	Daily or cumulative flux of fish past Chipps Island

Chinook salmon. For either method, the total salvage for a sampling period D is:

$$\hat{N}_i = \sum_{d=1}^{D} \hat{N}_{di} . \tag{3}$$

Entrainment is calculated as:

$$\hat{\Phi}_{di} = \frac{\hat{N}_{di}}{S_{Pi} E_i} , \tag{4}$$

and daily total loss is:

$$\hat{\Lambda}_{di} = \hat{\Phi}_{di} - \hat{N}_{Ri} = \hat{N}_{di} \left(\frac{1}{S_{Pi} \; E_i} - S_{HT} \right) . \tag{5}$$

$\Lambda = \Phi$ for delta smelt since they are assumed not to survive salvage. Proportional loss is calculated differently for salmon and for adult and young delta smelt (below).

Flow data were obtained from the Dayflow accounting program (Jassby et al. 1995; see http://iep.water.ca.gov/dayflow). Net flows in Old and Middle Rivers (Figure 1) have been determined by the U.S. Geological Survey since 1987 (Ruhl and Simpson 2005; Ruhl et al. 2006; P. Smith, USGS, pers. comm.). X_2, or the distance up the axis of the Estuary to where the tidally-averaged near-bottom salinity is 2 psu, was determined from daily Delta outflow as described in Jassby et al. (1995). Data on salmon-tagging studies and trawl data were obtained from the Interagency Ecological Program's Bay Delta and Tributaries Project (BDAT) website (http://bdat.ca.gov/). Salvage data for all species, sample data and abundance indices for delta smelt, and zooplankton abundance data were obtained from the California Department of Fish and Game (K. Fleming, R. Gartz, K. Hieb, and K. Souza, pers. comm.). Zooplankton biomass was determined from abundance data (Kimmerer 2006).

Chinook Salmon

Migrating salmon suffer a one-time risk of entrainment, in that fish that survive through the Delta either arrive at the export facilities and are entrained, or migrate past Chipps Island and presumably become invulnerable to entrainment. Salmon that arrive at the export facilities and are successfully salvaged also pass Chipps Island on their way to sea, and are vulnerable to capture there.

The general approach was to use recapture rates of coded-wire-tagged (CWT) hatchery smolts released in or near the upper Sacramento River and recaptured in the Delta fish facilities or at Chipps Island. The number of fish recaptured at each location was used to calculate salvage and losses at the fish facilities and flux of fish past Chipps Island, which were accumulated over the season and then used to calculate proportional salvage and loss.

The Livingstone Stone National Fish Hatchery (LSNFH) on the upper Sacramento River has released winter Chinook smolts marked with CWT and clipped adipose fins each spring since 1998. The Coleman National Fish Hatchery (CNFH) has released tagged fall and late-fall Chinook smolts each spring since 1981. Tagged fish have been released in groups of 81 to approximately 300,000 with unique tag codes, and up to 14 separate tag codes with up to approximately one million fish have been released on a single date. Tagged fish are recaptured at various locations, and data are stored in the BDAT database. I estimated the flux of tagged fish past Chipps Island and the losses to the fish facilities for years starting with brood-year 1998.

The following assumptions were made throughout this analysis:

1. The proportional loss of CWT hatchery fish represents that of naturally-spawned Chinook salmon.
2. Mortality factors at the fish facilities are constant in time and with export flow.
3. Fish are randomly distributed in time and across the Chipps Island channel in the top 4 meters, and migrate equally by day or night at a constant speed unaffected by flow.
4. Sampling at Chipps Island and at the fish facilities is unbiased, and the net is 100% efficient.
5. All CWT fish caught have their tags read.

Assumption 1 is fundamental to this approach as well as to numerous other studies (e.g., Newman and Rice 2002), but at present is untestable. Possible biases introduced by the other assumptions are discussed below.

Each year, CWT smolts in several tag groups have been released on a single day (Table 2). LSNFH winter Chinook have been released between January 27 and February 5, except that fish were released on April 9 in 1998. CNFH Chinook have been released in November through April, with one release in July 2005 which was not used in this analysis. I treated all groups of fish released on a single day as a single release; recaptures were too few to estimate variability among groups within single days.

Parameter values in Equation 5 were previously established for regulatory purposes (NMFS 2004). A series of experiments with marked juvenile Chinook salmon was used to estimate the pre-screen proportional loss for the state facility ($1 - S_{p1}$), which had a mean of 85% and range of 63–99% (Gingras 1997). The regulatory value is 75% (NMFS 2004). The pre-screen loss term for the federal facility has been set at 15% without any justification other than that the federal facility lacks the large forebay (Clifton Court) leading to the state facility, which may enhance predation on fish arriving at the facility. Studies conducted when the louvers were installed (Skinner 1973) gave a louver efficiency E_1 of ~ 90%, although more recent data suggest lower louver efficiency: Karp et al. (1995) reported overall efficiency of 50% at the federal facility with substantial variation, and Bowen et al. (2004) reported 85% efficiency for the secondary louvers at the federal facility. Handling and trucking loss terms ($1 - S_{HT}$) together amount to 4%. Given the high uncertainty about the pre-screen loss and louver efficiency, and the low rate of loss due to handling and trucking, I simplified Equation 5 by setting $S_{HT} = 1$ for both facilities, and assuming the same pre-salvage survival term S_S for both facilities, combining both pre-screen mortality and loss through the screens:

$$\hat{\Lambda}_i = \left(\frac{1}{S_S} - 1\right)\hat{N}_i = \lambda\hat{N}_i \qquad (6)$$

Tagged fish are captured by the U.S. Fish and Wildlife Service (USFWS) Chipps Island trawl survey, which takes 10–20 trawl samples daily in spring and less often during other seasons (Brandes and McLain 2001). The number of tagged fish collected by the Chipps Island trawl during each survey was extrapolated to a "fish flux" from the mean catch per volume and the migration speed past Chipps Island. The midwater trawl net is 4.6 meters deep and 9.1 meters wide (Brandes and McLain 2001), and the volume sampled is based on readings of a flowmeter in the net mouth. Fish were caught at the fish facilities slightly more often by night than by day (data from 1996–2004, 39% of all salmon and 49% of the samples were by day), which could be due to higher predation rates during daylight, so we are justified in assuming roughly equal passage at Chipps Island by day and night.

The fish flux past Chipps Island for each day on which a survey was conducted was calculated as:

$$\hat{\Phi}_{dc} = \frac{\sum_{p=1}^{P_d} N_{dpc}}{\sum_{p=1}^{P_d} V_{dpc}} WZu\ , \qquad (7)$$

which is the fish per unit volume multiplied by cross-sectional area and migration speed. Previous analyses have used the time spent sampling to provide a time-scale for migration (Brandes and McLain 2001), but that approach does not account for the migration speed of the fish, and is appropriate only for a stationary sampler. Migration speed u in Equation 7 was estimated at about 6 km/d based on the median date of recapture of tagged late-fall Chinook released at Ryde on the Sacramento River and caught at Chipps Island (Brandes and McLain 2001; Newman 2003). The fish flux was calculated for each day when a survey was conducted, and values were interpolated for days with no survey, then summed over the period between the first and last days when fish were captured:

$$\hat{\Phi}_c = \sum_{d=1}^{D} \hat{\Phi}_{cd}\ . \qquad (8)$$

Table 2. Chinook salmon. Summary of data from mark-recapture studies. Source is Coleman National Fish Hatchery (C) or Livingstone Stone National Fish Hatchery (L). LSNFH fish were all winter Chinook; Coleman fish were fall, late-fall, or spring Chinook. Dates are for the brood year if later than October, or for the next year if in January–June.

Source	Brood Year	Release Date	Recapture Dates		Length at Release (mm)	Number Released	Catch		
			Initial	Final			Chipps Is.	SWP	CVP
C	1997	11/10	11/26	03/09	118	66316	22	2	0
C	1997	12/09	12/19	03/16	134	66244	34	11	5
C	1997	01/12	01/18	03/18	137	61048	26	0	1
C	1997	01/13	01/19	03/16	141	63100	63	0	0
C	1997	01/14	01/20	03/16	137	67408	54	0	3
C	1997	01/22	01/27	03/18	138	57046	31	0	3
C	1997	03/04	03/25	05/15	56	27628	34	0	0
C	1997	03/06	03/27	05/11	59	35122	23	0	0
C	1997	03/31	04/16	05/22	64	37067	162	0	0
C	1997	04/07	04/19	05/29	65	33392	87	0	0
C	1997	04/22	04/28	06/03	72	28585	336	0	0
C	1997	04/23	05/01	06/03	66	32007	53	0	0
C	1998	11/12	11/24	02/05	116	66119	32	1	0
C	1998	12/15	12/22	03/30	120	64546	48	2	1
C	1998	01/04	01/11	05/26	126	59032	110	5	1
C	1998	03/31	04/29	05/09	59	29869	3	1	0
C	1998	04/20	04/26	05/20	78	24239	158	7	0
C	1998	04/21	05/01	05/23	69	32464	37	0	0
C	1998	04/27	05/05	05/28	75	34513	133	3	2
C	1998	04/28	05/05	05/13	78	34037	28	0	0
C	1999	11/12	11/27	01/28	110	70500	6	2	1
C	1999	12/09	12/20	02/19	110	75948	16	8	3
C	1999	12/21	01/03	02/21	110	83383	9	6	0
C	1999	01/04	01/19	04/20	120	79868	53	63	28
C	1999	01/12	01/21	03/21	120	81680	14	8	6
C	1999	04/07	04/15	04/28	75	33820	50	1	0
C	1999	04/14	04/20	05/21	77	32504	258	2	0
C	1999	04/21	04/26	05/29	78	35228	256	0	0
C	2000	11/03	12/11	01/21	113	58050	6	1	2
C	2000	12/08	12/25	02/26	119	54568	0	5	1
C	2000	01/02	01/17	04/23	128	62127	53	51	18
C	2000	01/09	01/20	03/15	129	65284	11	9	4
C	2000	04/13	04/23	05/13	73	62634	186	0	1
C	2000	04/27	05/07	05/30	76	62325	217	2	0

Source	Brood Year	Release Date	Recapture Dates		Length at Release (mm)	Number Released	Catch		
			Initial	Final			Chipps Is.	SWP	CVP
C	2001	11/14	11/28	04/27	120	88039	11	4	4
C	2001	12/12	12/21	03/01	120	73856	9	23	5
C	2001	01/04	01/10	03/08	135	65237	55	15	6
C	2001	01/08	01/14	04/23	120	77418	283	155	51
C	2001	04/18	04/25	05/27	77	79730	419	2	0
C	2001	04/25	05/03	05/29	77	71246	289	0	0
C	2002	11/08	12/06	01/06	102	67650	13	5	3
C	2002	12/02	12/18	05/01	117	59887	50	81	29
C	2002	01/02	01/08	03/31	125	66571	166	656	221
C	2002	01/15	01/22	03/21	131	74760	21	46	15
C	2003	11/28	12/11	02/27	126	65339	37	16	6
C	2003	12/31	01/08	04/06	130	72716	166	333	81
C	2003	01/02	01/08	03/24	127	69247	137	222	67
C	2003	01/30	02/11	03/17	146	64983	3	35	6
C	2003	04/16	04/24	05/14	79	75162	58	0	0
C	2004	11/05	12/10	01/03	121	87000	3	1	1
C	2004	11/29	12/14	01/31	117	69993	24	1	1
C	2004	01/04	01/11	03/03	134	32348	231	124	20
C	2004	01/13	01/27	02/27	134	69795	6	25	1
C	2005	12/02	12/12	02/10	116	80014	47	18	5
C	2005	01/03	01/08	03/22	141	82691	126	14	5
C	2005	01/19	01/27	03/06	141	65496	20	2	1
L	1998	01/28	03/15	04/19	70	10243	21	8	0
L	1999	01/27	02/22	05/01	80	1145	4	1	0
L	2000	02/01	03/05	04/04	80	4826	8	2	0
L	2001	01/30	03/07	05/07	80	62138	24	2	2
L	2002	01/30	02/14	04/14	82	8131	34	26	12
L	2003	02/05	02/20	04/09	88	11568	21	26	6
L	2004	02/03	02/22	03/31	87	8584	21	1	1
L	2005	02/02	02/17	03/27	86	15603	20	3	6

All recaptured fish from each release group were included in estimates of fraction salvaged and lost at the export facilities. Smolts were recaptured over various time intervals, with occasional stragglers recaptured weeks to months later than others in the same group (Figure 2). A relationship was calculated between proportional salvage and export flow averaged over the migration period (see below), but averaging export flow evenly over the migration season would give excessive weight to the later period when few fish were migrating. I therefore calculated a weighted mean export flow during the migration season, using the total daily catch at the fish facilities and Chipps Island as the weighting factor. The total daily catch was first interpolated to fill in days with no survey, then smoothed using a 5-day running mean:

$$N_{w\delta} = \frac{\sum_{d=\delta-2}^{\delta+2} \sum_{p=1}^{P_d} (N_{dp1} + N_{dp2}) + N_{dc}}{5}. \tag{9}$$

For each release group, I calculated total salvage and total losses (Equation 6) over the season as a proportion of the fish leaving the Delta. Proportional salvage P_S is unaffected by pre-salvage survival, whereas proportional loss P_L is very sensitive to the magnitude of S_S (see below). The proportional salvage for the migration period is the ratio of total salvage to the sum of salvage and migration past Chipps Island:

$$\hat{P}_S = \frac{\hat{N}_1 + \hat{N}_2}{\hat{N}_1 + \hat{N}_2 + \Phi_c}. \tag{10}$$

This proportion has a slight bias (<10%) because some fish are salvaged but not counted and subsequently pass Chipps Island. This calculation does not require knowledge of mortality patterns within the Delta or the details of alternative migration pathways. Proportional salvage was related to weighted export flow by a generalized linear model with a log link function and error distribution proportional to the mean (McCullagh and Nelder 1989). This model was fit for the combined data from the two hatcheries, including all data points with > 6 fish recaptured, and with source (hatchery) as a covariate. Additional covariates tried in this model were Sacramento River flow and position of Delta cross-channel gates (0 = both gates closed, 1 = both gates open), both weighted means over the migration season as described above for export flow.

Proportional loss is the total loss divided by the total number of fish departing the Delta either via loss at the export facilities or migration past Chipps Island:

$$\hat{P}_L = \frac{\hat{\Lambda}_1 + \hat{\Lambda}_2}{\hat{\Lambda}_1 + \hat{\Lambda}_2 + \Phi_c} = \frac{\lambda}{\lambda + \frac{1}{\hat{P}_S} - 1}, \tag{11}$$

in which the bias due to double-counting is negligible. The difference in denominators of the left-hand term of Equation 11 and Equation 10 arises because pre-salvage mortality is not included in Equation 10. The principal sources of uncertainty in the calculations of proportional loss arise from great uncertainty about the pre-salvage survival of fish at the fish facilities, and the migration speed of the fish. Although the estimate of migration speed could be refined, the lack of resolution of the pre-salvage survival is the principal impediment to even estimating —much less reducing—the errors in the estimates of

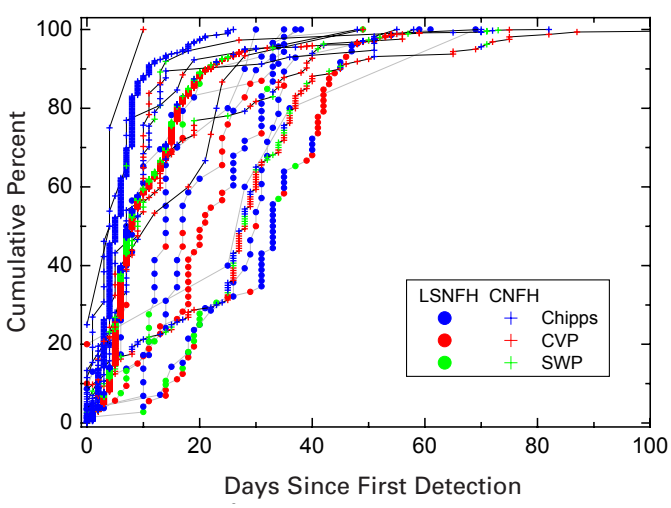

Figure 2. Chinook salmon. Examples of cumulative percent of coded-wire-tagged smolts captured at the fish facilities and at Chipps Island. All releases from LSNFH are shown, and a sample of 10 releases from CNFH. Each symbol represents an individual fish.

proportional losses. I estimated $\hat{P}_L$ as a function of export flow based on the fitted value of $\hat{P}_s$ from the above relationship with export flow, and alternative assumed values of pre-salvage survival.

Delta Smelt

In contrast to the situation for salmon, the loss of delta smelt to entrainment can be considered a continuous mortality, for which a greatly simplified expression in the absence of natural mortality is:

$$P_L = 1 - \prod_{d=1}^{D}\left(1 - \frac{\Lambda_x}{A}\right) . \qquad (12)$$

The product is calculated over the entire season of vulnerability.

Two groups of delta smelt are prominent in the salvage estimates from the fish facilities: adults from mid-December to mid-April, and larvae and juveniles from mid-April to mid-July (Figure 3). From approximately mid-July to mid-December, the fish are in brackish water, and few are salvaged in the fish facilities. I therefore focused on losses of adults and larvae/juveniles. Adults are also captured in the spring Kodiak trawl survey (Bennett 2005, see http://www.delta.dfg.ca.gov/data/skt/), and young fish are captured in the spring–summer 20-mm survey of late larvae and juveniles (Dege and Brown 2004, see http://www.delta.dfg.ca.gov/data/20mm/).

The general approach was to estimate entrainment as a mortality (since successful salvage is assumed to be negligible), and multiply the corresponding survival values for each day of exposure to entrainment (Equation 12). The sum of net flows in Old and Middle Rivers (Figure 1) was used to estimate the movement of fish toward the fish facilities. Net flow is southward toward the export facilities when export pumping is large compared to flow in the San Joaquin River. Salvage of adult and young delta smelt is usually low when this flow is positive, although substantial salvage of adult smelt occurred at the federal facility in some years of positive Old and Middle River flow (Figure 4).

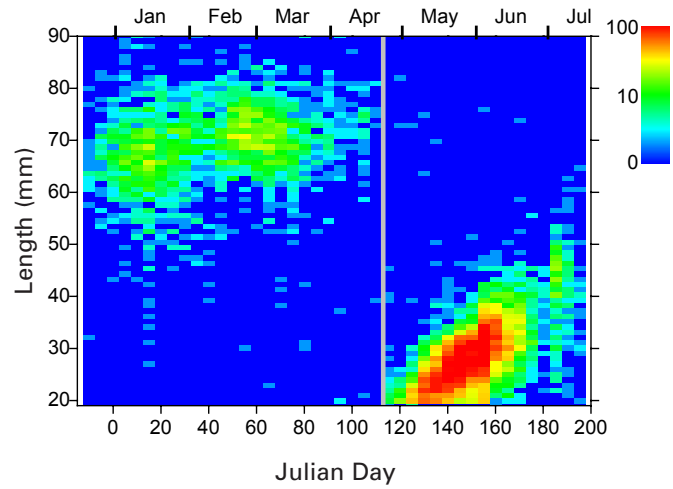

Figure 3. Delta smelt. Combined salvage at south Delta fish facilities for 1997–2005. Image plot showing numbers of fish by length and day, according to log scale at right. Larger fish are adults, and small ones are larvae and juveniles, roughly separated by the vertical line. Larvae smaller than 20 mm are generally not counted. Very few fish were caught between July and mid-December.

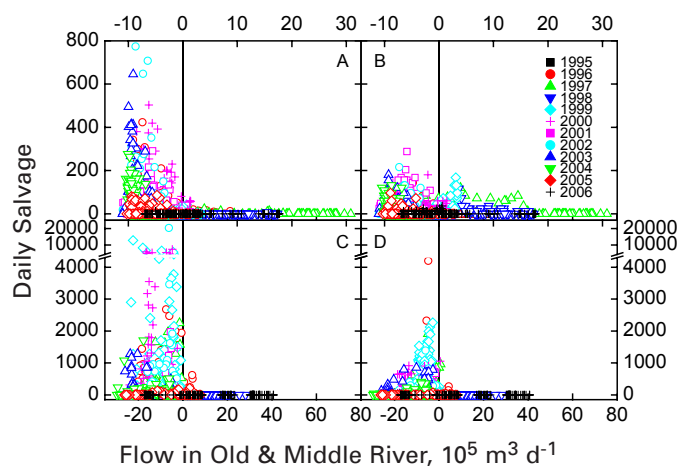

Figure 4. Daily salvage of delta smelt at the fish facilities vs. flow in Old and Middle Rivers, positive northward, 1995-2006. (A) and (B) are adults; (C) and (D) are juveniles. (A) and (C) are for the state facility; (B) and (D) are for the federal facility.

Adults

The general approach for adult delta smelt was to divide estimated daily entrainment by the monthly estimated population size from the Kodiak trawl survey to get a daily proportional loss rate, which was accumulated over each day in the month and each month in the season (December–April):

$$\hat{P}_L = 1 - \prod_{mo=12}^{4} \prod_{d=1}^{d(mo)} \left(1 - \frac{\Phi_{dx}}{A_{mo}}\right). \quad (13)$$

Natural mortality was not considered explicitly in this formulation because most of the losses occur early in the season before the population begins to decline. The principal difficulty with this method is that the fish flux is determined from the salvage sampling program, whereas the population size is determined from the Kodiak trawl data; thus, differences in efficiency between the two programs introduce an unknown parameter. I estimated this parameter as explained below by using Kodiak trawl data from stations in the southern Delta, where the fish are most vulnerable to entrainment.

Principal assumptions were:

1. The Kodiak trawl survey takes a representative sample of the adult delta smelt population.
2. Entrainment is proportional to the combined southward flow in Old and Middle Rivers.
3. All delta smelt entrained toward the export facilities are lost from the population.
4. The efficiency of sampling by the fish salvage facilities is constant.

The first assumption is unlikely to be true given the fixed stations of the Kodiak survey and the concentration of stations in some areas. An alternative approach is to calculate mean catch by sub-region, extrapolate to abundance by sub-region, and sum these values across sub-regions. Doing so results in only a small change in the calculated population size (e.g., see Kimmerer and Nobriga 2005). Assumption 2 is not strictly true since some adult delta smelt are reported from the salvage facilities even when flow is northward, probably because of dispersion (Figure 4A and B). However, this relationship was applied only during times when flow was southward, when advection would have dominated the entrainment flux. Although adult smelt do not drift passively, the patterns in Figure 4A and B support the idea that entrainment is related to the southward flow toward the export facilities. Adult and juvenile delta smelt do not tolerate much handling, and most are probably killed in the salvage process (Bennett 2005). Assumption 4 is unlikely to be true, and violation of this assumption introduces error variance into the calculations.

The Kodiak trawl program has taken surveys from January–May since 2002 but only the three to four surveys using standard stations were included (surveys designated by single digits). Based on reported lengths, all fish appeared to be adults, except for those smaller than 60 mm in May. Catch per volume was calculated assuming a volume filtered of 6,223 m^3, which is the median based on flowmeter readings and a mouth area of 12.5 m^2 (R. Baxter, California Department of Fish and Game, pers. comm.). The Kodiak trawl samples the upper ~ 2 meters of the water column, and adult delta smelt are most abundant in the upper half of the water column, ~ 4 meters. Population size throughout the habitat was calculated as the mean catch per m^3 multiplied by the volume of habitat shallower than 4 meters, about 0.9×10^9 m^3.

Data from the fish facilities included length for about 90% of the fish identified. Fewer than 1% of the fish caught and measured in May were adults—i.e., larger than 60 mm—so data from May were eliminated. About 40% of the fish measured in April were larger than 50 mm, and considered adults. This fraction was used to draw a random sample of the fish salvaged but not measured, which was added to salvage data for fish measured as > 50 mm in April. These fish, and all fish collected in December–March, were included in the analysis.

The daily proportional loss rate for both facilities is (from Equations 4 and 5, assuming no salvage is successful):

$$\hat{P}_{Ld} = \frac{E_k(\hat{\Phi}_{d1} + \hat{\Phi}_{d2})}{\hat{D}_s V} = \frac{E_k\left(\frac{\hat{N}_{d1}}{S_{P1}E_1} + \frac{\hat{N}_{d2}}{S_{P2}E_2}\right)}{\hat{D}_s V} \quad (14)$$

The efficiency E_2 for the federal facility is about 13% (M. Bowen, U.S. Bureau of Reclamation, pers. comm.). However, neither E_1 nor the pre-screen survivals S_{Pi} are known for delta smelt, nor is E_k. To simplify the analysis, I combined the two parameters into one for each facility, and assumed that the two resulting values scale as the mean catch at the two facilities. For adult delta smelt from 1995–2006, on days when both facilities had non-zero catches (a total of 235 days), the median ratio of the catch per volume at the state facility to that at the federal facility was 0.95, with 10th and 90th percentiles of 0.2 and 3.8. If fish were arriving at the two facilities in equal abundance per unit volume, the combined efficiency parameters are not consistently different between the two facilities. Therefore, Equation 14 was rearranged to give:

$$\hat{P}_{Ld} = \frac{\theta\,(\hat{N}_{d1} + \hat{N}_{d2})}{D_s V}, \text{ where}$$

$$\theta = \frac{E_k}{E_1 S_{P1}} = \frac{E_k}{E_2 S_{P2}}. \quad (15)$$

Entrainment can also be estimated as the product of abundance per volume in the south Delta times flow in the south Delta, so:

$$\frac{N_{SD}\,Q_{SD}}{V_{SD}} = \theta\left(\hat{N}_{d1} + \hat{N}_{d2}\right). \quad (16)$$

The value of θ was estimated using the Kodiak trawl catches from four south Delta stations (902, 906, 914, and 915). Data from 2006 were excluded because flow in Old and Middle Rivers was northward most of the time. The model used for this calculation was rearranged from Equation 16, and N_{SD} was assumed to have a Poisson error distribution:

$$\hat{N}_{SD} \sim \text{Poisson}\left[\frac{V_{SD}\theta}{Q_{SD}}\left(\hat{N}_1 + \hat{N}_2\right)\right], \quad (17)$$

which was fit using a generalized linear model with a Poisson error distribution to determine θ. Inserting θ into Equations 15 and then 13 gives:

$$\hat{P}_L = 1 - \prod_{mo=12}^{4} \prod_{d=1}^{d(mo)} \left(1 - \frac{\theta\,(\hat{N}_{d1} + \hat{N}_{d2})}{A_{mo}}\right). \quad (18)$$

Salvage data for each day in a month were inserted into Equation 18 and divided by the monthly estimate of population size. Monthly estimates were extrapolated for two missing cases (April 2002 and January 2003), and to the previous December for all years, using the nearest non-missing month's data.

Usable salvage data are available for as early as 1995, but the Kodiak trawl data started in 2002. The mean catch per trawl in the fall midwater trawl survey for November–December was moderately well correlated with the subsequent population size from the Kodiak trawl (r = 0.86 for log-transformed data). This relationship was therefore used to estimate mean population size in spring of 1995–2006 from the midwater trawl data. This mean population size was then inserted into Equation 18 as a constant for December–April of each year to calculate annual proportional losses for 1995–2006.

Larvae/Juveniles

The general approach for young fish was similar to that for adults except that this calculation does not rely on reported salvage data, which can underestimate the abundance of small fish, and the extrapolation from daily to seasonal loss involves several additional complications. A flow-chart (Figure 5) shows the calculations required to estimate the seasonal loss, and to test some of the assumptions listed below. Several sources of error were propagated through the calculations.

The 20-mm survey has sampled twice a month during March or April to July from 1995–2005, at up to 52 stations throughout the upper Estuary (Dege and Brown 2004). I dropped surveys having fewer than 20 stations, and dropped stations in San Pablo Bay where delta smelt are uncommon. Catch per tow was converted to catch per volume (CPUE, catch per

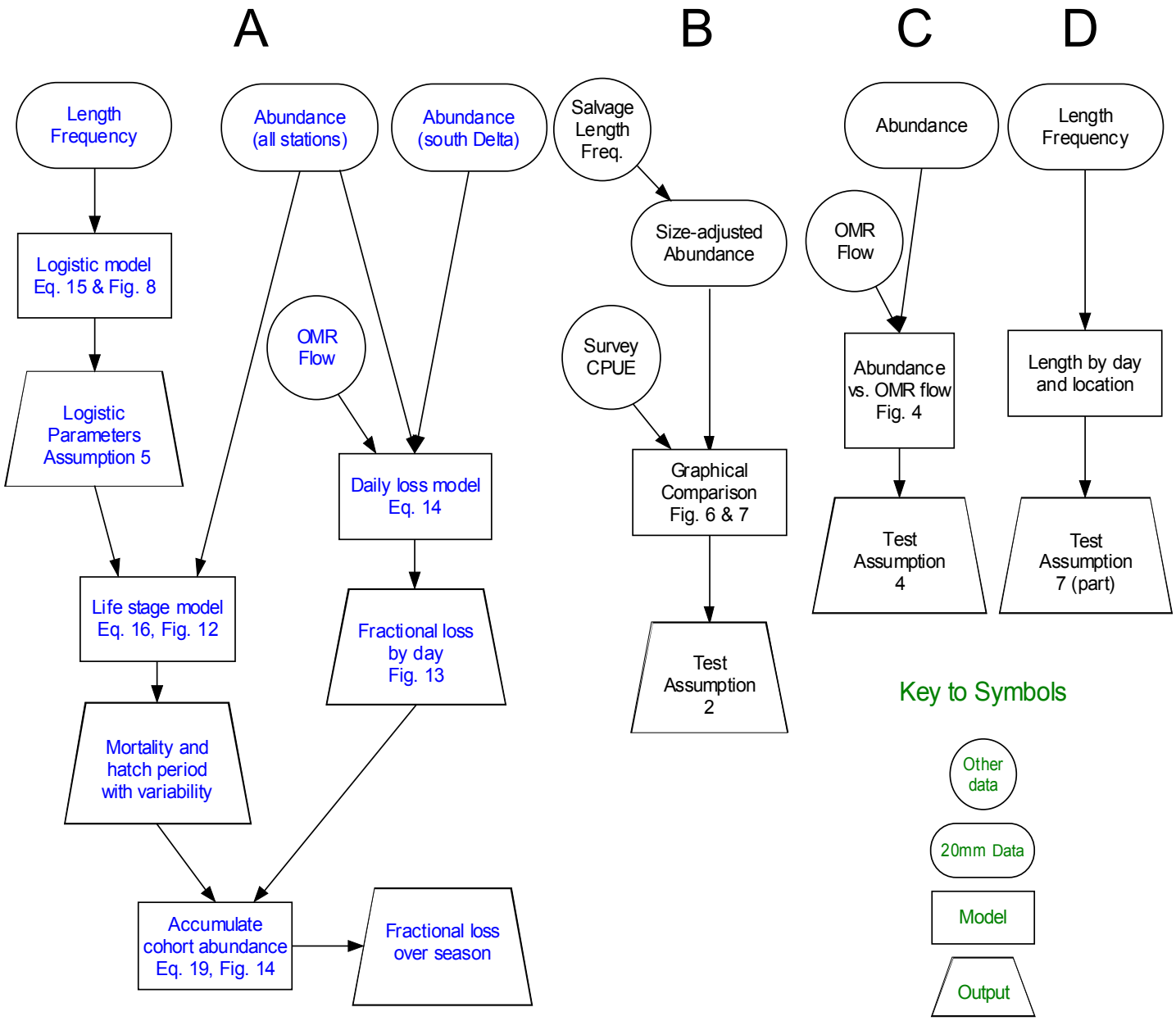

Figure 5. Flow diagram for calculations to estimate losses of juvenile delta smelt. (A) Main calculation of seasonal loss as a percentage of the population. B, C, and D are ancillary calculations to test assumptions: (B) Assumption 2; (C) Assumption 4; (D) Assumption 7. A key to symbols is shown at the bottom. OMR = Old and Middle River flows. CPUE = catch per volume.

unit effort) assuming 855 m^3 volume per tow and net efficiency that increased to 100% with increasing size of the fish (see below). The proportional daily loss of fish to the export facilities based on a single survey was estimated as:

$$\hat{P}_{Ld} = \left(\frac{N_{SDs}}{A_s}\right)\frac{Q_{SD}}{V_{SD}}. \tag{19}$$

Six stations (902, 906, 910, 914, 915, and 918) in the southern Delta nearest the fish facilities were used to calculate N_{SD} for each survey.

To calculate the total loss for the entire time-period of the 20-mm survey involves several complicating factors. Delta smelt hatch over a period of several weeks to months. The proportional loss to entrainment early in the season applies only to the fish that have hatched, so the product of daily survival values (Equation 12) underestimates overall survival. Furthermore, natural mortality (i.e., that not attributable to export pumping) suffered by the fish that hatch early requires a further discount of the proportional loss suffered by these fish. This occurs because all of the fish leave the Delta about the same date, after which vulnerability to export effects is considered negligible (the last date of the survey; see Assumption 8 below). Fish that hatch early suffer a longer period of mortality before this date, and thus contribute less to the population; therefore, losses of fish from these cohorts have less effect on subsequent population size.

Assumptions: Principal assumptions for calculating daily loss for each survey were:

1. Delta smelt that arrive in the vicinity of the export facilities are lost from the population.
2. The six stations listed above provide estimates of CPUE that represent the part of the population in the water going to the export facilities.
3. Mean CPUE in all stations represents the entire population.
4. The relevant flow toward the export facilities is the southward flow in Old and Middle Rivers.

Additional assumptions needed to extrapolate daily to seasonal losses (explained below) were:

5. Capture efficiency of the 20-mm net can be described by a logistic function, increasing from 0 to 100% as fish length increases.
6. Fish hatch at a constant daily rate over some time-period.
7. Daily mortality is constant from the beginning of the hatch period until the last survey.
8. Fish remain in the Delta until some date (or temperature) rather than moving to higher salinity at a certain age.
9. Fish hatch at a 5-mm length and grow at ~ 0.3 mm d^{-1}.

Assumption 1 seems reasonable since most of the smaller delta smelt go through the louvers at the fish facilities and are lost from the system (see below), and the few that are salvaged probably do not survive (Bennett 2005). Assumption 3 is probably true for surveys of pelagic fish (Kimmerer and Nobriga 2005). A constant hatch rate (Assumption 6) greatly simplifies the calculations, and is unlikely to have a big effect on the outcome. Daily mortality

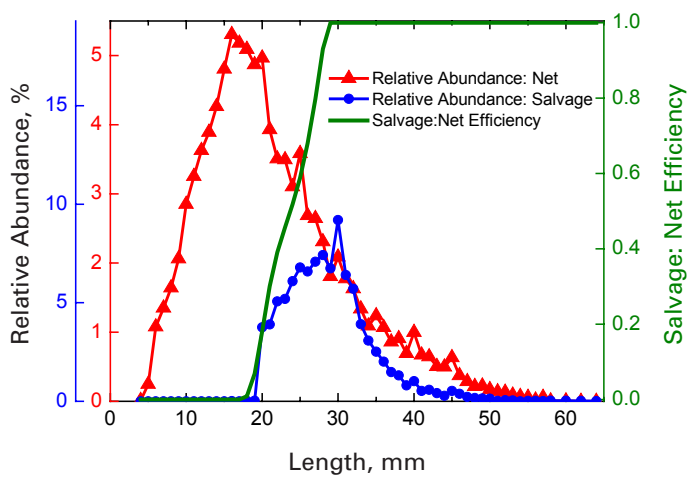

Figure 6. Larval/juvenile delta smelt. Length distributions for all fish caught in the 20-mm survey or in salvage, shown on different scales (left) so relative abundances overlap at ~ 30 mm. Also shown is the ratio of capture efficiency of the salvage sampling to the net sampling (right axis, solid line).

(Assumption 7) is almost certainly not constant, but there are no data on which to base reliable estimates. The growth rate value is supported by Figure 6 in Bennett (2005), and is also the approximate mean value obtained by fitting straight lines to data on length at date.

Assumption 2 is supported by the similar temporal pattern of catches in the south Delta sampling stations and the salvage facilities (Figure 5B). To match these catches, it was necessary to account for poor sampling of small fish in the salvage facilities (Figure 6). A relative capture efficiency of the salvage facilities was calculated as the ratio of catch at each size in salvage to that in the net samples, normalized to a total of 1. Since the decline in relative abundance in the salvage data at lengths greater than the modal length was likely due to movement of the fish rather than capture efficiency, the efficiency above the mode was set to 1 (Figure 6). Then the abundance in net samples in the southern Delta was reduced by the calculated relative capture efficiency. The resulting catches per volume (examples in Figure 7) matched reasonably well in timing and magnitude, and were weakly but significantly correlated across all days when data co-occurred ($r = 0.4$, $p < 0.01$).

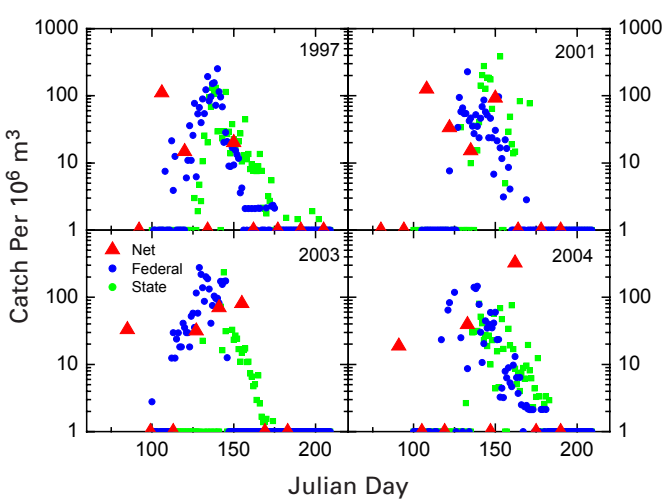

Figure 7. Examples comparing abundance of young delta smelt in the 20-mm survey and in the two fish facilities. Data from the 20-mm survey have been corrected by the relative capture efficiency of the fish facilities (green line in Figure 6) to allow direct comparison.

Assumption 4 (Figure 5C) is supported by the pattern of catch of juveniles in the salvage facilities vs. Old and Middle River flow (Figure 4C, D). Larval/juvenile delta smelt were rarely caught when flow was northward (positive).

Assumption 8 (Figure 5D) is supported by the salvage data in Figure 3: if smelt were moving to brackish water (and then becoming invulnerable to export entrainment) at a certain age, life stage, or length, the mean size in the export facilities would initially rise and then level off. Instead, the mean size increases throughout the spring, and the fish rather abruptly disappear (Figure 3, lower right). This pattern is also supported by the similarity in apparent growth rate from the 20-mm catches from the south Delta compared to that from catches from the entire system (not shown).

Net efficiency: The function describing capture probability as a function of fish length is:

$$E_L = \left(1 - \frac{1}{1 + ae^{bL}}\right) e^{kL}, \qquad (20)$$

where a, b, and k are parameters to be determined. The logistic term in parentheses is small at small size and increases sigmoidally to 1 at large size. The other term contains mortality (and declining capture efficiency) per increment of length to express the decreasing catch as fish grow. This term was used only to fit this equation, and only the logistic parameters a and b were used in subsequent analyses. Parameters were determined by using a least-squares optimization procedure (function *optim* in S-Plus, Venables and Ripley 2003) to fit Equation 20 to the overall length-frequency distribution. Data from each year were used to determine these parameters, which provided means and confidence intervals for each parameter.

The logistic fits to the length-frequency data show that the 20-mm net is 50% efficient at about 16 mm, with a 12-mm window around that value in which efficiency increases from 10% to 90% (mean parameters; Figure 8). The fit of the model to the overall length frequencies is good ($r^2 = 0.99$). The proportion of the population at 5-mm length (hatch

length) varied approximately three-fold with parameters at their upper and lower 95% confidence limits (Figure 8B). These values for the logistic parameters were used to propagate error in subsequent analyses.

Mortality rates and hatch dates: These were estimated by fitting data from all stations for each year to the following equations:

$$\left\{\begin{array}{ll} A_{L,t} = H\ e^{-m\,(t\,-\,T_j)}, & T_0 \le T_j \le T_1 \\ A_{L,t} = 0, & T_j < T_0 \text{ or } T_j > T_1 \end{array}\right\},$$
$$L = (t - T_j)\ g \qquad (21)$$

which describes the number of fish of cohort j on each day t given that H fish hatched on day T_j during an interval (T_0, T_1), with constant growth rate g and mortality rate m. The daily hatch rate H cancels out of calculations of proportional losses, so this is an arbitrary parameter that was set to 1. The calculated abundance values $A_{L,t}$ were adjusted for inefficient sampling of small fish using the logistic function from Equation 20, then the length data were aggregated into four length classes of equal size to reduce the number of zeros in the data. The data from each year were then fitted to these equations by an iterative search procedure that minimized the sum of squared deviations between the data and the model to estimate the hatch period (T_0, T_1) and the mortality m.

Daily and seasonal losses. The proportional loss for each survey was determined from Equation 19. To determine daily losses P_{Ld} from the proportional loss by survey, I interpolated the fraction in parentheses in Equation 19 for days between surveys, and extrapolated the fraction for the first survey back to the calculated first hatch date T_0. These fractions were then multiplied by the daily value of Q_{SD}, the southward flow in Old and Middle Rivers. The resulting daily proportional loss is a mortality rate and comprises part of the mortality m determined using Equation 21. Natural mortality (i.e., mortality not due to export losses) was calculated as the difference between mortality determined using Equation 21 and the effective mortality due to export effects:

$$\hat{m}_n = \hat{m} - \overline{\ln\,(1 - \hat{P}_{Ld})} \qquad (22)$$

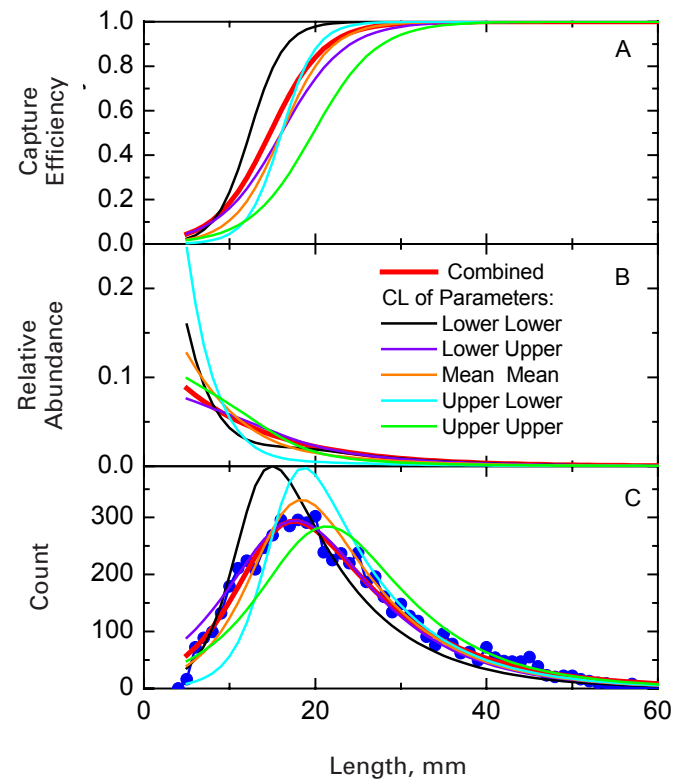

Figure 8. Fit of the net-efficiency model (Equation 20) to the count data from the 20-mm survey. Data for each year have been reduced to the same total number of fish (593) to even out all years. Each panel contains lines based on combinations of the two model parameters: both at their mean values, or either at their upper and lower 95% confidence limits. (A) Capture efficiency as logistic functions of length; (B) Relative abundance by length from the overall model; (C) Count data from the reduced data set (symbols) and model fits, which are proportional to the products of the curves in panels A and B.

where the average was taken over the season from T_1 to the last survey. I used these estimated mortality values for each year in the subsequent calculations, but made parallel calculations with no mortality for comparison.

Survival of each day's cohort j from its hatch date to the last survey day was calculated as:

$$\hat{S}_j = \prod_{T_j}^{T_f} e^{-\hat{m}_n}\,(1 - \hat{P}_{Ld}) \qquad (23)$$

The proportional loss of fish up to final day T_f was

then determined from the abundance of all cohorts on that day divided by the abundance in the absence of export losses:

$$\hat{P}_L = 1 - \frac{\sum_j \prod_{T_j}^{T_f} e^{-\hat{m}_n} (1 - \hat{P}_{Ld})}{\sum_j \prod_{T_j}^{T_f} e^{-\hat{m}_n}} \quad (24)$$

The calculation was run for each year of the 20-mm survey separately to determine a proportional loss. Each year's calculation was run 100 times using three sources of variability. Variability in abundance ratio (in parentheses in Equation 19) was determined by bootstrap sampling of the abundance ratios determined from field data for each year; this variability was propagated by sampling from a normal distribution with mean and standard error from the bootstrap analysis, truncated to 1.6 standard deviations (middle ~ 90% of the values) to prevent extreme values. The logistic parameters for each run (Equation 20) were determined by sampling from a normal distribution with the mean and standard deviation of the parameter, determined as described above. The growth rate used in the model was determined by sampling from a uniform distribution over the interval (0.2, 0.4), since there is insufficient information to determine variability in growth rate.

Equations 19 and 24 were also used to calculate proportional losses for hypothetical export flows. I calculated Old and Middle River flow by assuming a 1:1 reduction of Old and Middle River flow for each increase in export flow. I also assumed that the spatial distribution of delta smelt does not change with the changes in Old and Middle River flow, provided that flow remains negative.

Output from a particle tracking model (DSM-2 PTM, Kimmerer and Nobriga 2008) was used in a comparison with the results from this analysis. The PTM was run for 30 days with particles released at 31 locations in the Delta. The proportion of particles lost to the pumping facilities was determined for each release location. These results were aggregated using a weighting factor equal to the proportion of delta smelt < 10 mm at sampling stations close to each release site during dry years. The use of small fish in dry years was meant to ensure weighting toward likely spawning locations, i.e., initial locations for larvae. The PTM results were analyzed in a regression including export flow, inflow, and an interaction term, and the predictions of this statistical model were used to compare PTM output to results of the above analysis of proportional losses.

The fall index of delta smelt abundance is used as the principal measure of status of the population. Previous reports (Miller et al. 2005) documented a relationship between spatial co-occurrence of delta smelt in summer with calanoid copepods—their principal food—and the fall midwater trawl index of delta smelt abundance. Using a slightly different approach, I determined a relationship between zooplankton biomass and summer–fall survival. The independent variable was the biomass of calanoid copepods during July–October in a salinity range of 0.15–2.1 psu, the range over which 50% of the smelt occur in the summer townet survey. The dependent variable in a least-squares regression was the log ratio of the fall midwater trawl index to the summer townet index, which is an index of survival.

RESULTS AND DISCUSSION

Chinook Salmon

The capture of individual marked fish at Chipps Island and the fish facilities typically lasted for approximately 1 month, with the capture rate usually high for about half of the time and then gradually declining (Figure 2). On some occasions, timing was bimodal, with a few fish arriving early and the remainder in a later pulse. There was no consistent difference between timing at Chipps Island and that at either of the fish facilities.

The estimated proportion of migrating fish salvaged at the export facilities increased with increasing export flow (Figure 9). Four data points based on a small number of fish caught (four to six) were excluded from the analysis. Including these points gave a similar model fit, but diagnostic plots revealed an upward bias in the distribution of residuals. Entering the source or run of fish in the statistical model did not improve the fit according to the

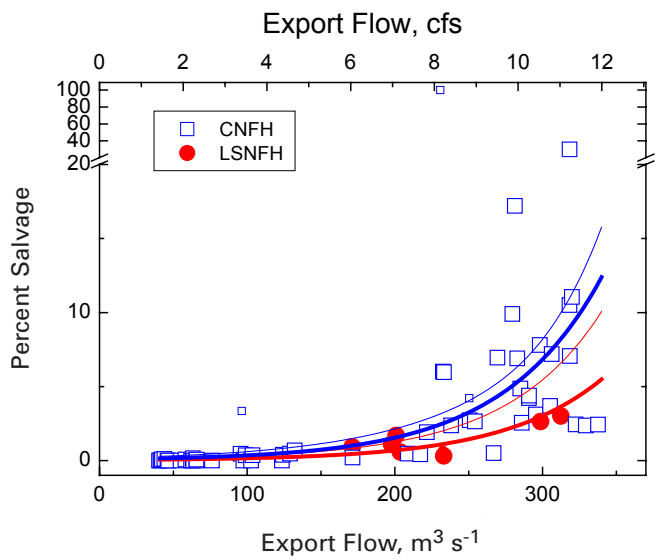

Figure 9. Chinook salmon. Relationship of estimated proportional salvage of tagged smolts at the fish facilities, P_S, to export flow. Small symbols represent data based on six or fewer fish caught, which were not used in determining the line. Lines are from a generalized linear model with log link function and variance proportional to the mean ($p < 0.0001$, 57 df), with source of fish as a categorical variable. Thick lines are predictions for fish from each hatchery; thin lines are upper 90% confidence limits of the predicted mean values.

Akaike Information Criterion (320.9 without, 321.3 with source of fish in the model), but the term for source of fish was marginally significant ($p < 0.1$), and the source term reflects the fact that the LSNFH values tended to be lower than those from CNFH at the higher export flows (Figure 9). Clearly, more data at high export flows would be useful in distinguishing between the results from the two hatcheries.

There was no apparent relationship between proportional salvage or total salvage and either Sacramento River flow or mean position of the gates controlling the Delta Cross-Channel. The relationship of proportional salvage to export flow (Figure 9) had a coefficient of variation for the prediction of about 20% at high export flows.

Proportional loss increased at an accelerating rate with decreasing pre-salvage survival (Figure 10). For pre-salvage survival of 50%, proportional loss is equal to proportional salvage. Proportional loss increases sharply as pre-salvage survival approaches 0, as is clear from Equation 6. Confidence limits on proportional loss are large (Figure 10), but the uncertainty about pre-salvage survival means that constraints on the true value of proportional loss are weak. Pre-salvage survival depends partly on pre-screen predation (Gingras 1997), but also on louver efficiency. NMFS (2004) raised questions about the efficiency of the louver systems under routine operations, when louvers must be lifted out of the water for cleaning and repairs.

Post-salvage mortality was assumed to be small, and is generally considered to be low because of high survival in tests of handling and trucking procedures (NMFS 1997). However, there is no information on survival of these fish after release, and anecdotal evidence suggests high predation rates on the released fish. If survival is low, salvage (Figure 9) would have to be reduced by the fraction of released fish that do not survive. This would have a substantial influence on losses only if pre-salvage survival were high (Figure 10).

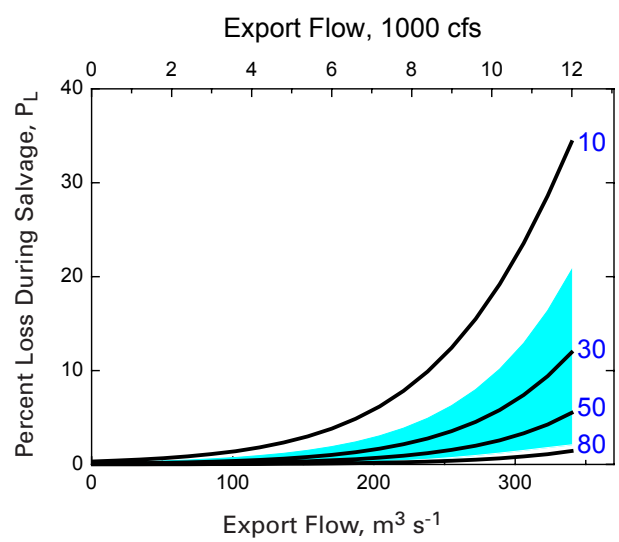

Figure 10. Calculated proportional loss of Chinook salmon, P_L, as a function of export flow and the pre-salvage survival term S_S, assumed to be the same for both fish facilities (Equations 6 and 11). Numbers on right give S_S as percent. Band gives 90% confidence limits around the 30% value based on the error term from Figure 9.

Other sources of uncertainty include the swimming speed of the fish, sampling efficiency, and differences between results from fish raised in the two hatcheries. None of these is likely to be comparable to the uncertainty in pre-salvage survival. Swimming speed may vary among releases, e.g., with net flow at Chipps Island or temperature. It may also be biased, which would influence the absolute values of the salvage and loss proportions.

Since the Chipps Island flux is determined using nets, and that at the export facilities using salvage, any difference in efficiency between the two sampling methods that is not taken into account will introduce error. I assumed that net efficiency is 100%; a lower efficiency would result in an underestimate of the fish flux past Chipps Island. A comparison between a midwater trawl and a larger Kodiak trawl in the Sacramento River revealed no difference in fish per volume, suggesting that the efficiency of the midwater trawl is high (Brandes et al. 2000).

All of these calculations refer to direct losses only. Indirect losses may be large (NMFS 1997) but have not been estimated, nor has a method been developed to estimate them. This was supposed to have been the focus of investigations using mark-recapture approaches, but to date these studies have not provided insights into this question (Brown and Kimmerer 2006). Mark-recapture studies have shown that survival of fish released into the interior Delta is lower than that of fish released in the lower Sacramento River, and the ratio of these survivals is a weak function of export flow (Newman 2003). However, these results say nothing about the potential role of indirect mortality, i.e., the likelihood that fish die during migration from the Delta as a result of altered hydrodynamic conditions. This is clearly an area for further investigation.

Even without estimates of indirect loss, the losses in Figure 10 are higher than expected based on management targets for the Delta. Take limits at the state and federal fish facilities for winter Chinook salmon are based on a calculated 2% of the estimated passage through the Delta. This assumes that roughly half of the fish identified by size as winter Chinook are actually winter Chinook. The sources of the hatchery-tagged fish are unambiguous, and considerably more than 1% of them are lost at high export flows for any value of pre-salvage survival < ~ 20% (Figure 10).

Delta Smelt Adults

Monthly population estimates declined beginning approximately in March, when the adults begin to spawn and die (Figure 11A). Estimated losses to entrainment began in mid-December, peaked in January, and then declined sharply (Figure 11B) as the population declined and the southward flow in Old and Middle Rivers decreased (Figure 11C).

The calculated value of θ was 29 $\pm$ 20 (95% confidence limit, 13 df). If the Kodiak trawl were 100% efficient, approximately 30 times more fish were entrained than salvaged. This ratio would be even higher if the Kodiak trawl were <100% efficient. A louver efficiency of 13% (see above) combined with 75% pre-screen losses for both facilities gives an overall pre-salvage loss of 97%, consistent with the above ratio but likely coincidental given the uncertainties in both estimates.

With the estimated value of θ, the cumulative loss over the season ranged from 3% to 50% (Table 3). If the upper confidence limit of θ is used, the values range from 6% to 69%. These confidence limits are somewhat underestimated because sampling error in the Kodiak trawl survey could lead to higher or lower estimates of population size.

Examining data back to 1995, southward flow in Old and Middle Rivers was highest in 2002–2004 and low during the wet years of the mid-1990s (Figure 12A).

Table 3. Estimated cumulative losses of adult delta smelt to entrainment in the south Delta water export facilities.

Year	Cumulative % Loss	95% Confidence Limits
2002	15	5 – 24
2003	50	19 – 69
2004	19	6 – 31
2005	7	2 – 12
2006	4	1 – 6

This pattern was followed by annual salvage estimates for December–March. Spring abundance was estimated accurately from the midwater trawl data, except for an over-estimate in 2003 (Figure 12B). During that year, no Kodiak trawl survey was taken in January, and the abundance in March was higher than that in February (Figure 11A), so that value is highly uncertain. The extrapolated Kodiak trawl estimates were higher for years before 2002 than during or after 2002 (Figure 12B). Calculated losses followed those determined above, with 2003 again the exception. The highest monthly salvage occurred during January 2003 (Figure 11B), again possibly reflecting an underestimate of population size in the Kodiak trawl data. Overall, mean proportional losses varied from near 0 to 23% (Figure 12C), with a trend reflecting that of Old and Middle River flow (P_L = -3.7 + (1.1 ± 0.4) Q_{SD}, r^2 = 0.75, 10 df). The relationship of percent loss to X_2 was weak and not significant, presumably because Old and Middle River flow is a more proximate cause of variability in percent loss than X_2.

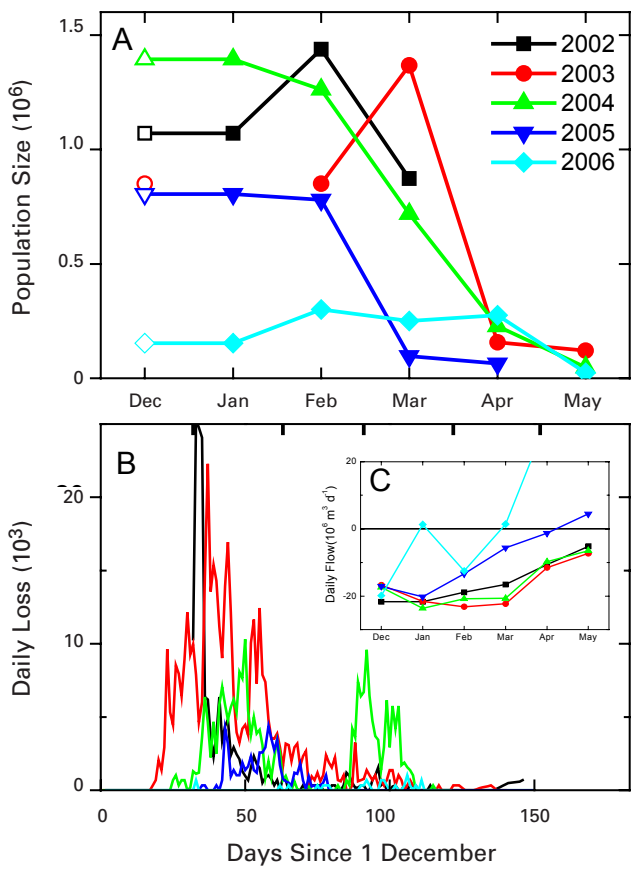

Figure 11. Adult delta smelt. (A) Estimated population size based on the Kodiak trawl survey; open symbols indicate that data for December were extrapolated back from the first survey of the following year; (B) Daily entrainment toward the fish facilities, which is salvage corrected for the ratio of capture efficiency of the Kodiak trawl to that of the fish facilities, so that these values are directly comparable to those in panel A; (C) Monthly mean of the daily combined flow in Old and Middle Rivers (positive northward, away from the export facilities).

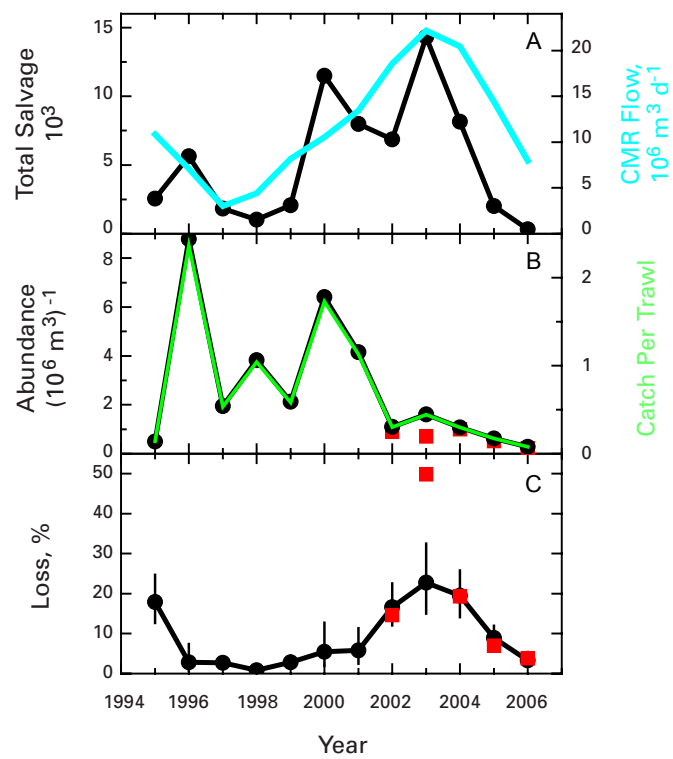

Figure 12. Reconstruction of export losses of adult delta smelt for 1995–2006. (A) Total salvage (line with circles) and Old and Middle River flow (line, right axis); (B) Predicted (line with circles) and measured (squares) population abundance, and mean catch per trawl for the fall trawl surveys in November and December (line, right axis); (C) Predicted (error bars, 5th and 95th percentiles) and measured (squares) proportional losses to export entrainment.

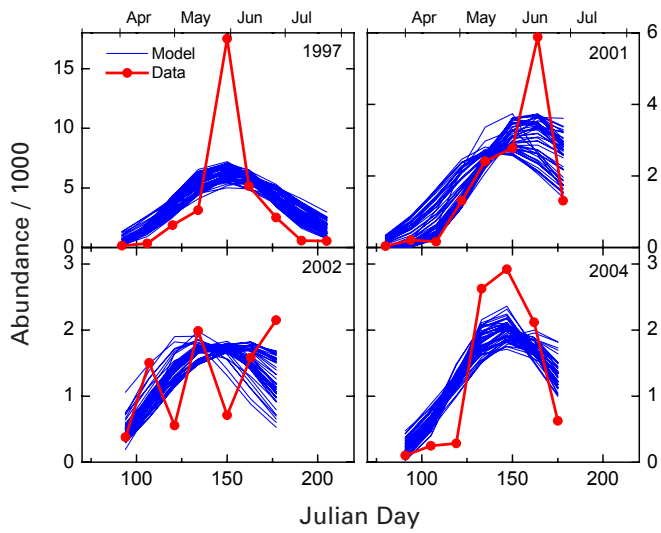

Figure 13. Larval/juvenile delta smelt. Examples of abundance by survey (line with circles) and example trajectories from repeated model runs with parameters sampled from their respective statistical distributions (thin lines).

Delta Smelt Larvae/Juveniles

The fits of the model of hatch dates and mortality (Equation 21) for each year were variable; of course the model failed to capture peaks in abundance (Figure 13), but the trends through the season were satisfactory for accumulating losses through the season. Modeled hatch dates and mortality rates varied among years (Table 4). These mortality rates seem low, but this is probably an artifact of the use of a single mortality rate for the entire period from hatch to migration.

The proportional loss data for each 20-mm survey showed a broad peak centered approximately in early April (Figure 14). Losses were low after mid-May and zero after mid-June. The seasonal or annual proportional loss was also highly variable among years, and roughly followed the maximum daily loss for each year (Figure 15). During the dry years 2001–2003, the losses were ~ 25%. Setting the natural mortality to zero raised the highest percentage loss to 37% (Figure 15). Increasing export flow to the maximum resulted in proportional losses up to 62%. The variation in annual loss was related to flow conditions ($P_L = -0.4 + (1.7 \pm 0.6)\ Q_{SD}$, $r^2 = 0.79$, 9 df), but this

Table 4. Juvenile delta smelt. Estimated hatch dates and mortality by year from the 20-mm survey.

Year	Natural Mortality mn, d-1	Hatch Dates Earliest	Hatch Dates Latest
1995	0.034	03/14	06/07
1996	0.039	03/16	05/13
1997	0.040	03/20	05/12
1998	0.027	03/11	05/02
1999	0.052	03/21	06/09
2000	0.029	03/25	05/15
2001	0.027	03/19	05/09
2002	0.038	03/07	05/12
2003	0.024	03/10	06/09
2004	0.030	03/13	04/28
2005	0.028	03/12	05/03

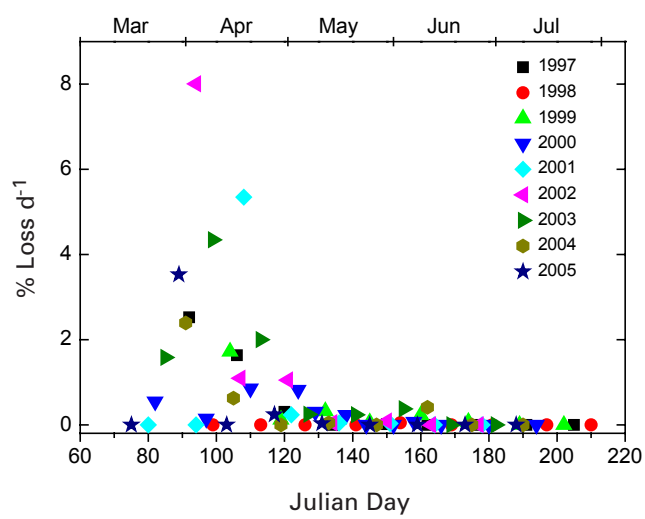

Figure 14. Seasonal pattern of daily proportional loss from the larval/juvenile delta smelt population with symbols and colors for each year.

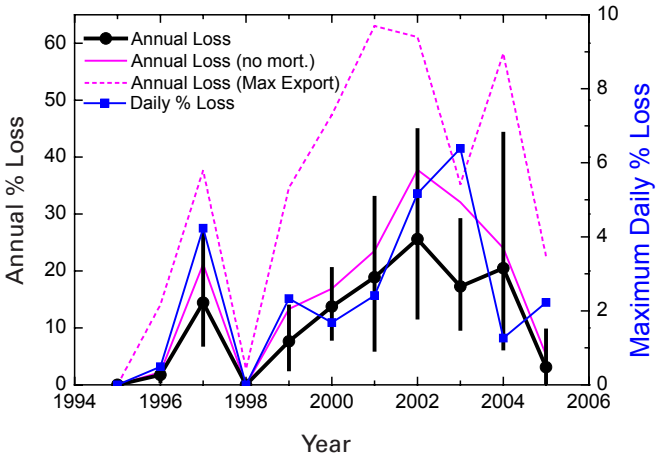

Figure 15. Estimated annual losses to export pumping of delta smelt from the 20-mm survey. The black line gives the estimated loss with 95% confidence limits allowing for mortality; red lines give annual losses without mortality (solid), and at the maximum export flow rate (dashed). The blue line with squares (right axis) gives the maximum daily percent loss determined in a single survey for each year.

relationship is tautological, since Old and Middle River flow was used explicitly in the calculations. This contrasts somewhat with the situation for adult delta smelt, for which the calculated losses were not based on flow, although flow was used in the calculation of θ (Equation 17).

The statistical analysis of output from the particle tracking model showed a reasonable ability to predict the loss of particles to export pumping from inflow and export flow (Figure 16). Placing the data from Figure 15 in the same framework gives predicted and calculated values that fall rather close to the same line, except for several values below the line at intermediate flow conditions and predicted loss rates (Figure 16). The calculated percent loss for 2005 was especially low, possibly because population abundance was so low.

The relationship of proportional loss to Old and Middle River flow (by assumption) and inflow and export flow (Figure 16) guarantees a relationship with X_2. Could this relationship underlie the weak negative relationship between X_2 and summer townet index for delta smelt after 1981 (Kimmerer 2002 Figure 8E)? A regression of summer townet index on X_2 for 1995–2005 had a slope of -0.11 ± 0.18 (95% CL, 22 df, p ~ 0.2). A regression of survival (1 – proportional loss) from the above analysis on X_2 had a slope of -0.009 ± 0.004 (9 df). The large confidence interval around the slope for the townet index includes the slope for the survival data. Applying the relationship in Figure 16 to all of the historical data for inflow and export flow replicates the X_2 effect that existed after 1981, but, in contrast to the historical data (Kimmerer 2002), there is no apparent change in the slope of the calculated X_2 effect. Thus, while the relationship of townet index to X_2 after 1981 is consistent with a mechanism based on high export losses during periods of landward X_2, this mechanism cannot explain the positive slope with X_2

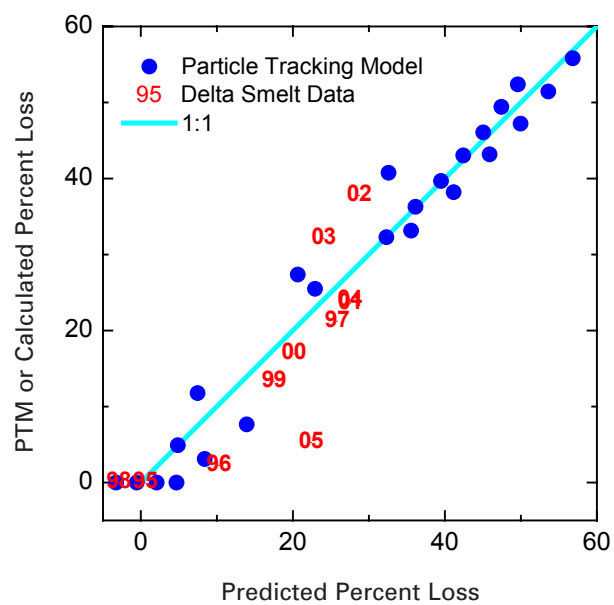

Figure 16. Larval/juvenile delta smelt. Predicted percent loss to the population by regression using log of Delta inflow and log of export flow as predictors (with interaction), and particle-tracking model results as the dependent variable (circles), with the line indicating a 1:1 relationship. The regression is: log (y) = 4.29 – (0.36 ± 0.17) log(inflow) – (0.90 ± 0.11) log(export flow) + (0.10 ± 0.03) log(inflow) × log(export flow), parameters with 95% confidence limits. Estimates of delta smelt losses from Figure 15 with no natural mortality (to match the particle tracking model results) are plotted against predictions from the above statistical model using mean flow conditions during the hatch period; numbers indicate years.

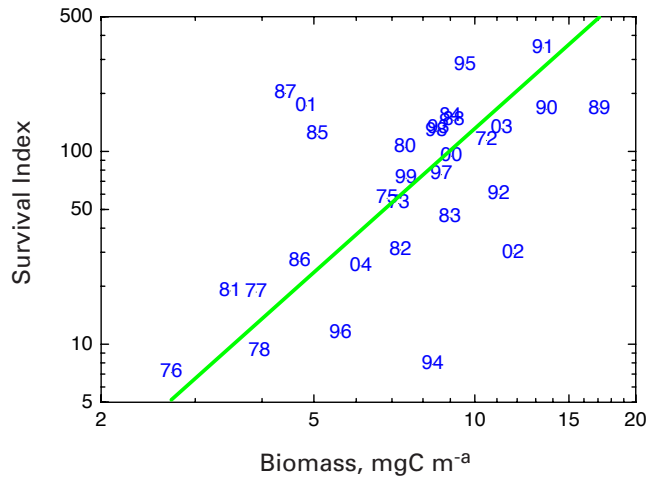

Figure 17. Relationship of survival index (fall trawl index / summer townet index) of delta smelt vs. mean zooplankton biomass during July–September for all stations in a salinity range of 0.15 to 2.09, the central 50% of the summer delta smelt distribution. The line is the geometric mean regression for log(10)-transformed data, y = 2.48x – 0.36. The correlation coefficient for the log-transformed data is 0.58 with a 95% confidence interval of (0.26, 0.78).

observed before 1981 (Kimmerer 2002). The causal mechanism for that relationship, and the reasons for the change, remain unknown (Bennett 2005).

The summer–fall index of survival varied over a range of 50-fold, and was significantly related to summer zooplankton biomass in the low-salinity zone (Figure 17). This may indicate food-limited survival. Observations of evidence for food shortage using histopathological methods (Bennett 2005) provides some support for this interpretation.

Population Consequences

Are these proportional loss rates excessive? This question cannot be answered using science alone. From a scientific perspective, all we can do is compare these losses with other sources of mortality or other data about the populations.

For Chinook salmon, a loss rate on the order of 10% or less, depending on pre-screen mortality (Figure 10), is less than fishing mortality: harvest index for all Chinook salmon off California in recent years has been around 40% (Williams 2006), which is close to fishing mortality rate for reasonable values of natural mortality. The harvest index for winter Chinook has probably been closer to 20% in recent years (Grover et al. 2004). From a population maintenance standpoint, the calculated loss rate at the export facilities would be a significant component of direct anthropogenic mortality. Furthermore, to the extent that the ocean fishery is supported by the large fall-run hatcheries, fishery losses could be offset by higher hatchery production. However, this level of additional mortality at the export facilities may place constraints on the rate of recovery of the listed winter- and spring-run stocks, and on ocean harvest of stocks (such as the fall run) that are not listed. Furthermore, these constraints may grow for winter Chinook if export flows continue to be kept high in winter to reduce impacts in spring.

Clearly, the big unknown is the pre-screen mortality. Although experiments have been conducted to attempt to determine this value, these have been hampered by incomplete design and by high variability. Furthermore, systemic problems with the operations and maintenance of the fish facilities (NMFS 2004) may prevent not only determining these factors but reducing them to an acceptable level. Thus, it is imperative that experimental designs be developed to better quantify pre-salvage survival if the current export configuration is to remain.

Delta smelt may suffer substantial losses to export pumping both as pre-spawning adults and as larvae and early juveniles. In contrast to the situation for salmon, pre-salvage mortality has been constrained in the calculations for adult delta smelt, and its effects eliminated from the calculations for larval/juvenile delta smelt. Combining the results for both life stages, losses may be on the order of 0–40% of the population throughout winter and spring. The estimates have large confidence limits, which could be reduced by additional sampling, particularly to estimate θ in Equation 18. If there is interest in improving these estimates further, some attempts should be made to examine the assumptions not fully tested above, particularly those used in extrapolating larval abundance to hatch dates.

Although the upper bound of this range represents a substantial loss, the effect of this loss is complicated by subsequent variability in survival (Figure 17). If this variability is uncorrelated with entrainment losses, then these losses will contribute little to the variability in fall abundance index. The simplest way to evaluate this is by regression of fall midwater trawl index on winter–spring export flow, but this relationship is contaminated by the downward step change in abundance in approximately 1981–1982, together with the long-term upward trend in export flow (mainly up to the mid-1970s, see Kimmerer 2004). Including this step in a regression model eliminates the effect of export flow on the fall midwater trawl index (coefficient = -1.5 ± 2.4, 95% CL, 36 df). It seems unlikely that the downward step change was due to the earlier increase in export flow; furthermore, despite substantial variability in export flow in years since 1982, no effect of export flow on subsequent midwater trawl abundance is evident.

This is not to dismiss the rather large proportional losses of delta smelt that occur in some years; rather, it suggests that these losses have effects that are episodic and that therefore their effects should be calculated rather than inferred from correlative analyses. In the absence of density dependence, using means in Figure 15 with natural mortality, fall abundance should have been reduced by ~ 10% during 1995–2005. This would have an equivalent effect of reducing the summer–fall survival index by 10%. This would have made little difference to fall abundance in the context of the approximately 50-fold variation in summer–fall survival (Figure 17), and would be difficult to detect through correlation.

Although summer–fall survival appears to dominate variability in abundance of delta smelt in fall (Figure 17), this does not imply that control of export effects would be fruitless, as these effects can be considerable during dry years. Management of delta smelt should incorporate any opportunities that arise to improve habitat or food supply and to reduce any negative impacts of predation or toxic contamination. However, current evidence does not provide a clear path toward improving the status of delta smelt using these factors. Manipulating export flow (and, to some extent, inflow) is the only means to influence the abundance of delta smelt that is both feasible and supported by the current body of evidence, even though export effects are relatively small. The results presented here can be used to suggest when, and under what conditions, control of export effects would be most helpful.

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Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR)

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Abstract. Four species of pelagic fish of particular management concern in the upper San Francisco Estuary, California, USA, have declined precipitously since ca. 2002: delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*). The estuary has been monitored since the late 1960s with extensive collection of data on the fishes, their pelagic prey, phytoplankton biomass, invasive species, and physical factors. We used multivariate autoregressive (MAR) modeling to discern the main factors responsible for the declines. An expert-elicited model was built to describe the system. Fifty-four relationships were built into the model, only one of which was of uncertain direction a priori. Twenty-eight of the proposed relationships were strongly supported by or consistent with the data, while 26 were close to zero (not supported by the data but not contrary to expectations). The position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow) and increased water clarity over the period of analyses were two factors affecting multiple declining taxa (including fishes and the fishes' main zooplankton prey). Our results were relatively robust with respect to the form of stock–recruitment model used and to inclusion of subsidiary covariates but may be enhanced by using detailed state–space models that describe more fully the life-history dynamics of the declining species.

Key words: Bayesian analysis; delta smelt; expert models; longfin smelt; Sacramento River, California, USA; San Joaquin River, California, USA; striped bass; threadfin shad; threatened species; water management.

Introduction

Estuaries, especially those associated with large rivers near major cities, are among the ecosystems most adversely affected by land use change (Nichols et al. 1986). Impacts of human actions in all upstream watersheds (catchments) are concentrated in the estuaries (Kennish 2002, Townend 2004). Diversion of water affects the location of boundaries between fresh, brackish, and saline water (Drinkwater and Frank 1994, Gillanders and Kingsford 2002, Gleick 2003). Large settlements often are located along shorelines, which convey contaminants and effects of boating and fishing to estuarine systems (Dauer et al. 2000). Shipping has led to introductions of many aquatic invasive species (Bollens et al. 2002, Williams and Grosholz 2008). Climate change will affect interactions between oceans and estuaries and will reduce catchment inflows in many regions (Scavia et al. 2002, Vicuna and Dracup 2007, Cai and Cowan 2008, Schindler et al. 2008).

The San Francisco Estuary is an archetype of a stressed estuarine system (Kimmerer et al. 2005*a*). The social, economic, and ecological effects of freshwater flows and diversions throughout the San Francisco Estuary have received much attention. Some 25 million Californians and 12 000 km^2 of agricultural land rely on water diversions from the delta created by the Sacramento and San Joaquin rivers. Annual agricultural

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revenue from California's Central Valley, which accounts for about half of the production of fruits and vegetables in the United States, frequently approaches US$15 billion.

Populations of many aquatic species in the estuary have declined since extensive human activities began in the mid-1800s (Bennett and Moyle 1996, Brown and Moyle 2005). However, conflicts over water management recently have intensified because of the apparently precipitous decline in four species of pelagic fish (delta smelt [*Hypomesus transpacificus*], longfin smelt [*Spirinchus thaleichthys*], striped bass [*Morone saxatilis*], and threadfin shad [*Dorosoma petenense*]) since ca. 2002 (Thomson et al. 2010). Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993. Recent litigation to protect the species resulted in court orders to halt water diversions temporarily (Wanger 2007*a*, *b*). Longfin smelt was listed as threatened under the California Endangered Species Act in 2009, although a petition for federal listing was declined. Striped bass was deliberately introduced to the Sacramento–San Joaquin Delta from the east coast of the United States in 1879 and supports a sport fishery (Moyle 2002). Threadfin shad was introduced into California reservoirs as a forage fish in 1954 and spread to the Delta (Moyle 2002, Feyrer et al. 2009).

To date, models and statistical analyses to identify mechanisms causing fish declines in the San Francisco Estuary generally have been on a species-by-species basis (Jassby et al. 1995, Kimmerer et al. 2001, Bennett 2005). These efforts suggest that several abiotic factors (e.g., water flows, salinity, turbidity), bottom-up biotic effects (e.g., zooplankton abundances, invasion of a filter-feeding, non-native clam [*Corbula amurensis*]), and top-down factors (e.g., incidental mortality associated with water diversions to pumping facilities) may play important roles. However, the relative importance of these factors remains unclear (Sommer et al. 2007). Identification of processes causing declines is critical because possible solutions include major investments in infrastructure, changes in water management, and rehabilitation of species' habitats, which would cost billions of dollars.

Although detailed analyses of the population dynamics of any one declining species are valid, it is plausible that more insight might be gained through multivariate analyses that consider community dynamics, including direct and indirect effects of interacting species and abiotic factors. These analyses might yield inferences on the biotic and abiotic factors that best explain patterns of abundance for multiple species in the community and on the relative influences of density dependence, among-species interactions, and abiotic factors on species abundances.

We used a multivariate statistical technique called multivariate autoregressive modeling (MAR) (Ives et al. 2003) with 40 years of data for pelagic fishes and their principal prey within the upper San Francisco Estuary. In a manner similar to path analysis (Shipley 1997), MAR uses time series data for multiple taxa to estimate the degree of association between the different taxa as well as between covariates and each taxon. Multivariate autoregressive modeling includes autoregressive terms for each species' abundance. Ives et al. (2003) provided a detailed introduction to the underlying theory and assumptions of MAR along with methods for estimating model parameters. Multivariate autoregressive modeling has been used in analyses of community dynamics in lakes in Wisconsin (Ives et al. 2003), Lake Washington (Hampton and Schindler 2006), and Lake Baikal (Hampton et al. 2008).

We developed a Bayesian implementation of MAR. Bayesian methods allow propagation of and account for multiple sources of uncertainty in complex models (Punt and Hilborn 1997) and allow great flexibility in model structure (Cressie et al. 2009). The Bayesian MAR modeling is a complementary approach to methods we used in a companion paper, which presented a Bayesian change point analysis (Thomson et al. 2010). The two methods were developed in tandem to evaluate whether the different strengths of the MAR and change point analyses provided similar inferences about factors potentially underlying causes of declines in the fish species. Multivariate autoregressive modeling is based on a food web structure, which allows both direct and indirect influences on the focal species (fish) to be represented. Moreover, MAR models the dynamics of all species (including prey) simultaneously. It is based on linear relationships (on a log-abundance scale), both within the food web and with covariates, over the entire time period.

Our implementation of MAR is underlain by an expert-elicited model, which draws on expert knowledge to specify whether particular trophic or covariate effects may be influential. The change point analysis is not embedded in a food web context, although availabilities of prey taxa can be used as covariates, but it does explicitly employ time dependence and nonlinearity in covariate relationships between log-abundances of the focal species and covariates. The change point method uses Bayesian variable selection (Green 1995) so that relationships do not need to be specified a priori. Both individual-species (species-specific model parameters) and multiple-species (common hyper-parameter distributions) versions of the change point analyses were implemented (Thomson et al. 2010), with the latter having some overlap, therefore, with the MAR analyses.

Here, we describe the upper San Francisco Estuary, the four species of fish on which we focused and their principal prey, and the set of covariates included in the MAR model. Multivariate autoregressive models are heavily parameterized because they describe many among-taxa interactions and relationships to covariates. Therefore, we developed an expert-elicited, circumscribed model that reduced the number of parameters to be estimated. We review the relative importance of

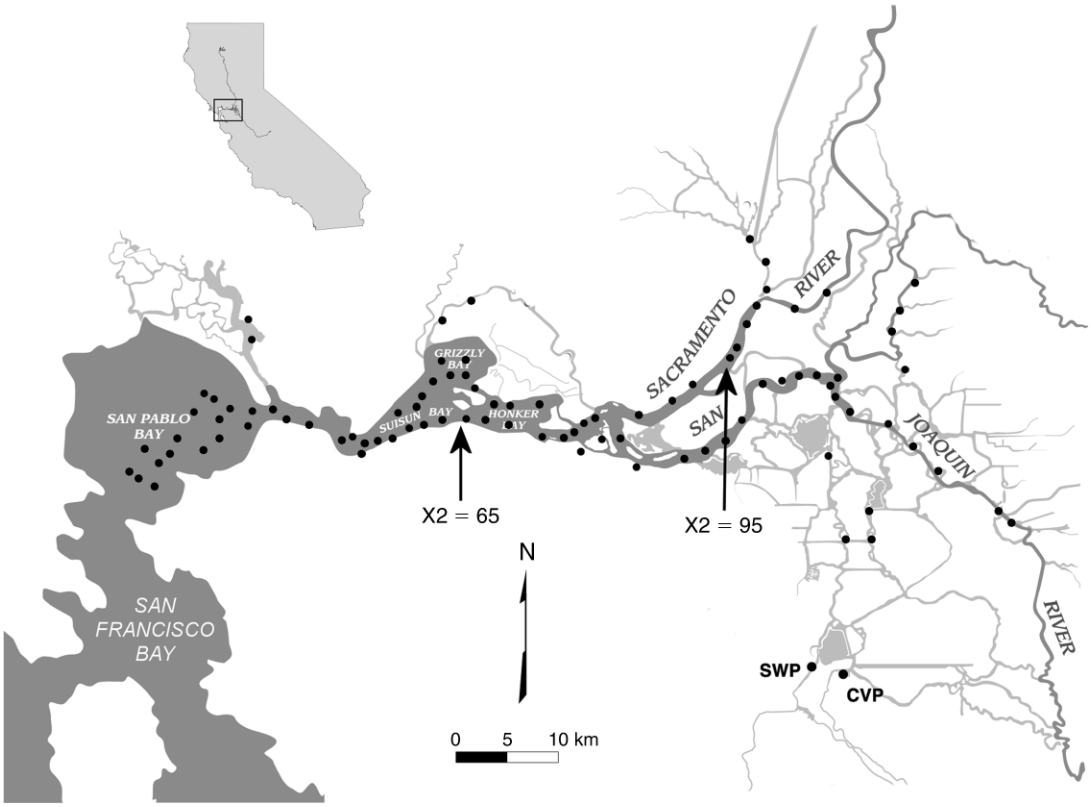

FIG. 1. Location and physiography of the upper San Francisco Estuary, California, USA. The solid circles denote sampling locations of the autumn midwater trawl surveys; arrows indicate two representative positions of the 2‰ isohaline (X2); SWP (State Water Project) and CVP (Central Valley Project) are locations of water exports from the estuary.

different factors in driving the temporal dynamics of our four declining fish species and comment on the usefulness and limitations of MAR models. Last, we comment on the agreement or otherwise between the MAR and change point approaches.

METHODS

The San Francisco Estuary

The San Francisco Estuary consists of three major regions: San Francisco Bay, the most seaward region; Suisun Bay, an intermediate brackish region; and the generally freshwater Sacramento–San Joaquin Delta (Fig. 1). The watershed has wet winters and dry summers. The Delta is the core of a massive system of dams and canals that store and divert water from the estuary for agricultural, industrial, and domestic use throughout California (Nichols et al. 1986). The water diversion facilities export ~30% of the annual freshwater flow into the Delta, although that percentage has exceeded 60% during many recent summers. Regulations, including standards for the position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow; Jassby et al. 1995), locally termed "X2," have become increasingly stringent.

Response variables: declining fish and their principal prey

Delta smelt is endemic to the San Francisco Estuary and reaches 60–70 mm standard length (SL) (Bennett 2005), feeding on zooplankton, mainly calanoid copepods, throughout life. The delta smelt is weakly anadromous, migrating between the brackish waters of Suisun Bay and the freshwaters of the Delta. Upstream migration begins in the late autumn or early winter and spawning occurs from March through May in freshwater. Most delta smelt spawn ~12 months after hatching, with a small percentage surviving for another year to spawn. Young delta smelt move downstream in early summer and remain in the low-salinity zone (0.5–10‰) until they migrate for spawning.

Longfin smelt is native to the San Francisco Estuary. The species usually reaches 90–110 mm SL (Moyle 2002, Rosenfield and Baxter 2007) and is anadromous. It spawns at age 2 yr in freshwater in the Delta from December to April. Young longfin smelt occur from the low-salinity zone seaward throughout the estuary and into the coastal ocean. Longfin smelt feed on copepods as larvae and mysids and amphipods as young and adults.

Striped bass is a potentially large (>1 m), potentially long-lived (>10 yr) anadromous species. Females begin

TABLE 1. Definitions of variables used in the multivariate autoregressive modeling, years for which data were available, and ranges of values for variables.

Variable	Years (missing)	Range	Definition
Response variables			
Delta smelt (*Hypomesus transpacificus*)	1967–2007 (3)	0.06–4.02	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Longfin smelt (*Spirinchus thaleichthys*)	1967–2007 (3)	0.03–113.16	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Striped bass (*Morone saxatilis*)	1967–2007 (3)	0.12–59.38	autumn (Sep–Dec) midwater trawl, mean age-0 catch per trawl
Threadfin shad (*Dorosoma petenense*)	1967–2007 (3)	1.36–31.21	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Calanoid copepods, spring	1972–2007 (1)	0.98–43.87	mean biomass of calanoid copepodites and adults during spring (Mar–May) in low-salinity zone
Calanoid copepods, summer	1972–2007 (1)	2.93–27.62	mean biomass of calanoid copepodites and adults during summer (Jun–Sep) in low-salinity zone
Mysids	1972–2007 (0)	0.42–35.05	mean biomass of mysid shrimp during Jun–Sep in low-salinity zone
Covariates			
Northern anchovy (*Engraulis mordax*)	1980–2006 (1)	0.22–490.42	mean catch per trawl of northern anchovy in the Bay Study midwater trawl (Jun–Sep) in the low-salinity zone
"Other zooplankton" in spring	1972–2006 (0)	3.79–56.86	mean biomass of other zooplankton (not including crab and barnacle larvae, cumaceans) during spring (Mar–May) in the freshwater zone
Spring chlorophyll *a* (freshwater zone)	1972–2006 (0)	2.35–43.54	mean chl *a* (mg/m^3) during spring (Mar–May) in freshwater zone
Spring chlorophyll *a* (low-salinity zone)	1975–2006 (0)	1.12–21.32	mean chl *a* (mg/m^3) during spring (Mar–May) in low-salinity zone
Summer chlorophyll *a*	1975–2006 (0)	1.23–20.15	mean chl *a* (mg/m^3) during summer (Jun–Sep) in low-salinity zone
Cyclopoid copepod *Limnoithona tetraspina*	1972–2006 (0)	0–7.78	mean biomass of *Limnoithona* copepodites and adults during summer (Jun–Sep) in low-salinity zone
Inland silverside (*Menidia beryllina*)	1994–2006 (0)	19.88–116.54	mean catch per seine haul of inland silverside in the USFWS survey during Jul–Sep (for stations within the delta)
Largemouth bass (*Micropterus salmoides*)	1994–2006 (0)	0.02–8.00	mean catch per seine haul of largemouth bass in the USFWS survey during Jul–Sep (for stations within the delta)
Spring X2 (isohaline)	1967–2006 (0)	48.53–91.74	mean Mar–May position of the 2‰ isohaline (X2)
Autumn X2 (isohaline)	1967–2006 (0)	60.24–93.18	mean Sep–Dec position of the 2‰ isohaline (X2)
Water clarity	1967–2006 (0)	0.44–11.00	mean Secchi depth (m) for the autumn midwater trawl survey
Winter exports	1967–2006 (0)	0.13–12.00	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Dec–Feb
Spring exports	1967–2006 (0)	0.37–13.00	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Mar–May
Invasive clam *Corbula amurensis*	1967–2006 (0)	0–1	binary variable for presence (1987–2006, 1) or absence (1967–1986, 0)
Duration of spawning window for delta smelt	1975–2007 (0)	24–85	no. days for which mean temperature was between 15° and 20°C,† mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta
Mean summer water temperature	1967–2006 (0)	20.45–23.65	mean water temperature (°C), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta during Jun–Sep

Notes: Mean catch per trawl was measured in terms of individuals. Biomass was measured as mg C/m^3. The freshwater zone was determined to be <0.5‰. The low-salinity zone was determined to be at 0.5–10‰. The X2 position was measured in km upstream from the Golden Gate Bridge.

† Range of water temperatures that best induce spawning by delta smelt (15°C) and limit larval survivorship (20°C).

to spawn at age 4 yr in the Sacramento River and, to a lesser extent, in the San Joaquin River, from April through June. Eggs drift with the current as they develop and hatch. Larvae drift into the low-salinity zone where they grow, later dispersing throughout the estuary. Adults occur primarily in saline waters of the estuary and the coastal ocean, except during spawning migrations. Age-0 striped bass feed mainly on copepods, later switching to macroinvertebrates and then to fish.

Threadfin shad typically is <100 mm total length and primarily inhabits freshwater. It switches between filter- and particle-feeding, consuming phytoplankton, zoo-

plankton, and detritus. Most threadfin shad spawn in their second summer, although some may spawn at the end of their first year. Spawning occurs mainly in June and July. Threadfin shad is the most abundant pelagic fish in the upper San Francisco Estuary.

While other fish and plankton groups might be included in our model as response variables, we chose to limit our analysis to species of zooplankton that are especially important for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad. Adult and juvenile (copepodites) calanoid copepods have different relationships with the fish in spring and summer, so we considered the two life stages as different "taxa" in our models. Mysid shrimps were regarded as most important to the fishes in the mid to late summer (Table 1).

Covariates

The covariates used in the MAR (Table 1) relate to factors thought to be important for one or more of the response variables (Table 2). Covariates included fish species that are potential competitors or predators of the four declining fish species (possibly at only certain life-history stages), food for the latter fishes or their crustacean prey (including phytoplankton), competitors (*Limnoithona*) or predators (*Corbula*) of the crustaceans, the primary surrogate of the fishes' habitat (X2) in spring and autumn, amounts of water extracted from the Delta in winter and spring, water clarity (measured using Secchi discs), and two water temperature variables (duration of the delta smelt spawning window, mean summer water temperature).

The expert model (Table 2) was based on extensive, long-term knowledge and experience of several of the authors (W. J. Kimmerer, F. Feyrer, W. A. Bennett, L. Brown, S. D. Culberson, G. Castillo), and justifications for expected relationships were drawn from the literature. Although Bayesian model selection (Green 1995) might have been incorporated into the MAR model, as was done for the complementary change point analyses (Thomson et al. 2010), we believe that there is didactic value in concentrating on the evidential support for the expert-elicited model.

Statistical Estimation

MAR: Gompertz dynamics

We used a variant of a MAR model (Ives et al. 2003) to represent dynamics of the response variables. We represented population dynamics with the Gompertz model (Dennis et al. 2006). We began with a deterministic version of the Gompertz model (Reddingius 1971):

$$n_{i,t} = n_{i,t-1} \exp(\gamma_i + \delta_i \ln n_{i,t-1}) \tag{1}$$

in which $n_{i,t}$ is abundance of species i at time t, $n_{i,t-1}$ is abundance of species i at time $t-1$, γ_i is the intrinsic rate of population growth for species i, and δ_i, which has been interpreted as the degree of density dependence.

We extended Eq. 1 first by allowing propagation for longer lags (up to L years prior to the current year), that is, an Lth-order Gompertz model (Zeng et al. 1998):

$$n_{i,t} = n_{i,t-1} \exp(\gamma_i + \sum_{l=1}^{L} \delta_{il} \ln n_{i,t-l}). \tag{2}$$

It is possible that the γ_i may vary, so we allowed linear time dependence: $\gamma_i(t) = \gamma_{i,0} + \gamma_{i,1}t$. We expected the $\gamma_{i,1}$ parameters to be <0 given the declines in the abundances of the fishes. Taking logarithms, setting $x_{i,t} = \ln n_{i,t}$, and allowing species-specific lags (L_i), we have

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l}. \tag{3}$$

Interspecific interactions among the seven taxa included as response variables were incorporated by appending terms relating to the previous year $\beta_{ij}x_{j,t-1}$, excluding self-terms:

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j\neq i}^{J} \beta_{ij} x_{j,t-1}. \tag{4}$$

We included effects of covariates u_k through α coefficients for the current year t:

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j\neq i}^{J} \beta_{ij} x_{j,t-1} + \sum_{k=1}^{K} \alpha_{ik} u_{k,t}. \tag{5}$$

MAR implementation

We used a Bayesian framework for implementing the model. There are many advantages to so doing. First, propagation of measurement uncertainties is straightforward using hierarchical models. Second, missing data are easily accommodated and estimated within the same process by which the parameters estimated are made, rather than a clumsier two-stage imputation–estimation approach. Third, we believe that the prior expectations, which also are easily implemented in a Bayesian framework, are critical encapsulations of the state of knowledge before the modeling was undertaken and need to be made explicit, as we have done.

We implemented Eq. 5 using the following model in WinBUGS, version 1.4 (Spiegelhalter et al. 2003):

$$z_{i,t} \sim \mathcal{N}(x_{i,t}, \omega_{i,t}^2) \qquad x_{i,t} \sim \mathcal{N}(\mu_{i,t}, \sigma_i^2) \qquad c'_{k,t} \sim \mathcal{N}(u_{k,t}, \zeta_k^2)$$

$$\mu_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j\neq i}^{J} \beta_{ij} x_{j,t-1} + \sum_{k=1}^{K} \alpha_{ik} u_{k,t} \tag{6}$$

($\mathcal{N}$ denotes the normal distribution). The model states

TABLE 2. Matrix of effects included in the model with explanations.

Response variable or covariate	Response variable							Explanation
	DS	LFS	SB	TFS	CA-SP	CA-SU	MYS	
Delta smelt (DS)					–	–		Calanoid copepods are consumed by delta smelt (Hobbs et al. 2006).
Longfin smelt (LFS)					–	–	–	Calanoid copepods and mysids are consumed by longfin smelt (Feyrer et al. 2003).
Striped bass (SB)					–	–	–	Calanoid copepods and mysids are eaten by young striped bass (Feyrer et al. 2003, Bryant and Arnold 2007).
Threadfin shad (TFS)								Threadfin shad consume phytoplankton and copepods but are most abundant in freshwater (Turner and Kelley 1966, Feyrer et al. 2007).
Calanoids, spring (CA-SP)	+	+	+					Key food for young fish in spring.
Calanoids, summer (CA-SU)	+	+	+				+	Key food for young fish in summer; mysids consume calanoids (Siegfried et al. 1979, Siegfried and Kopache 1980).
Mysids (MYS)		+	+			–		Key food for young longfin smelt and striped bass in summer.
Anchovy					–	–	–	Biomass dominant, consumes all plankton (Kimmerer 2006).
Other zooplankton				+				Threadfin shad consume zooplankton in freshwater (Turner and Kelley 1966).
Chlorophyll *a*, spring, freshwater					+			
Chlorophyll *a*, spring, low-salinity zone					+		+	Calanoids eat microplankton, including phytoplankton (Gifford et al. 2007) and respond positively to phytoplankton blooms (Kimmerer et al. 2005*b*).
Chlorophyll *a*, summer, low-salinity zone						+	+	Mysids eat phytoplankton and small zooplankton (Siegfried and Kopache 1908).
Limnoithona tetraspina						–		Indirect effect through depression of food resource (ciliates; not measured) (Bouley and Kimmerer 2006, Gifford et al. 2007).
Inland silverside	–				–	–		Silversides consume copepods and potentially delta smelt eggs and larvae (Bennett and Moyle 1996).
Largemouth bass	–		–	–				Potentially important predator on small fish in freshwater (Nobriga and Feyrer 2008).
X2, spring		–	–		+/–		–	Effects of spring X2 on subsequent abundance in the following autumn (Jassby et al. 1995, Kimmerer et al. 2009).
X2, autumn	–	–	–					X2 affects surface area available for fish through salinity distribution (Feyrer et al. 2007).
Water clarity	–	–	–	–				Turbidity favors all fish at various life-history stages by offering increased protection from predators (Feyrer et al. 2007, Nobriga and Feyrer 2008, Kimmerer et al. 2009).
Export flow, winter	–	–						Adult smelt are entrained by pumping facilities during winter (Baxter et al. 2008, Kimmerer 2008).
Export flow, spring	–	–	–	–				Juvenile and adult smelt and shad and juvenile striped bass are entrained by pumping facilities during spring (Baxter et al. 2008).
Corbula amurensis					–	–		Nauplius larvae of copepods are consumed by *Corbula* (Kimmerer et al. 1994).
Spawning window	+							Spawning window for delta smelt is constrained by temperature (Bennett 2005).
Mean summer water temperature	–							Delta smelt are negatively influenced by high water temperatures, reducing time spent in the freshwater Delta (Swanson et al. 2000).

Notes: A "+" denotes that the covariate was expected to exert a positive influence on the response variable (e.g., food source). A "–" indicates that the covariate was expected to have a negative influence on the response variable (e.g., by consumption). All null entries were deemed likely to be unimportant by expert knowledge. The abbreviations "X2" refers to the position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow).

that the (ln-transformed) observed values ($z_{i,t}$) represent the true values ($x_{i,t}$). The former have observation errors, which are included by use of (ln-transformed) unobserved values ($x_{i,t}$) and observation errors, $\omega^2_{i,t}$. The observation errors were estimated from SEs of mean values for the response variables for each time period. Given that the $z_{i,t}$ were ln-transformed, we used a Taylor functional expansion to approximate the ln-transformed SEs [$\mathrm{SE}(\ln(\bar{n})) \approx \mathrm{SE}(\bar{n})/\bar{n}$] (Seber 1973, Stuart and Ord 1987). Process variances (σ^2_i) were allowed to be species-specific and were implemented with priors on σ_i of U(0.01, 10) (Gelman 2005) (U = Uniform). The true,

unobserved values ($\mu_{i,t}$) are driven by the population dynamic parameters, trophic interactions, and covariates as described by the MAR model (Eq. 5).

Observed covariates $c_{k,t}$ were standardized for all available years of data (subtract mean $\bar{c}_k$, divide by standard deviations SD_k over all years, $c'_{k,t} = (c_{k,t} - \bar{c}_k)/SD_k$). Standardizing is helpful for model convergence and for equalizing numerical ranges among different scales of measurement. Uncertainties in covariate measurements (within-year SEs) correspondingly were scaled by the interannual standard deviations (i.e., $SE_{k,t}/SD_k$). The model specifies that the true (standardized) covariate values ($u_{k,t}$) are related to the observed standardized values ($c'_{k,t}$) but include the covariate-specific uncertainties [$\zeta_k^2 = (SE_{k,t}/SD_k)^2$]. Uncertainties for most covariates were included in the models (a few variables, such as presence of *Corbula*, were regarded as fixed). There were sporadic missing data for some covariates, which we allowed to be interpolated within the Markov chain Monte Carlo (MCMC) modeling. These missing covariate values need to be segregated from the main estimation of effects by using the "cut()" function in WinBUGS. If the uncertainties are not so isolated, the model will "sacrifice" fitting precision for the parameters describing dynamics of the response variables to better "fit" missing covariate values, which is not intended (Carrigan et al. 2007).

Priors

Relatively uninformative priors were assigned for these model parameters:

$$\gamma_{i,0} \sim \mathcal{N}(0,1) \qquad \eta_\gamma \sim \mathcal{N}(0,10^3) \qquad \sigma_\gamma \sim \mathrm{U}(0.01,10)$$
$$\sigma_i \sim \mathrm{U}(0.01,10) \qquad \delta_{il} \sim \mathcal{N}(0,1). \tag{7}$$

Use of standard Normal priors for the γ_0 and δ parameters is consistent with the expected values being within approximately ± 1 (i.e., constrained to reasonable values) given the ln-transforms for the response variables and the standardized covariates. From expert elicitation, species-specific lags were 2 (delta smelt), 3 (longfin smelt), 5 (striped bass), 2 (threadfin shad), and 1 (calanoids and mysids).

For the key α, β, and γ_1 parameters, we used a Weibull distribution to represent the prior beliefs of the expert-elicited model (Table 2). Use of the Weibull allows long tails in the expected direction if these are supported by the data. We used the construction ψ_0Weibull(2, 1) + ψ_1, where $\psi_0 = 1$ for expected influences in a positive direction and is -1 for negative expected influences, while ψ_1 is -0.55 for expected influences in a positive direction and 0.55 for negative ones. These configurations invest ~3:1 prior probability mass in favor of the expected influence. Only one α parameter had a neutral expected influence (Table 2), so this was assigned a $\mathcal{N}(0, 10^3)$ prior (i.e., low precision). Many of the potential relationships were specifically excluded from the model (i.e., deemed unlikely to be important). For such relationships, coefficients were assigned $\mathcal{N}(0, 10^{-6})$ priors (i.e., 0 with high certainty).

Parameter inference

We inferred importance of model parameters from the probability distributions of the parameters. We computed the proportion of the posterior probability distribution for each parameter exceeding 0 (designated as PPM), which is computed in WinBUGS with the "step()" function. The posterior odds are PPM/(1 − PPM) for a positive parameter and (1 − PPM)/PPM for a negative parameter. The ratio of these posterior odds to the prior odds is termed the odds ratio (OR). Common decision criteria for ORs are 3.2–10 (substantial evidence) and 10–100 (strong evidence) (Jeffreys 1961). For an uninformative prior, in which the ratio of prior probabilities for the parameter is unity, the OR is PPM/(1 − PPM) (or (1 − PPM)/PPM for negative parameters). We used a decision criterion of $\geq$10 for such parameters.

For informative priors, the prior odds were 3 (positive or negative). If the OR $\geq$ 3.2, we concluded that there was substantial support in the data for the expected relationship. If $1 \leq \mathrm{OR} < 3.2$, the data did not invalidate the expectation but there was less support (Jeffreys 1961). If $1 \geq \mathrm{OR} > 1/3.2$, then the data weakly contradicted the expectation. If OR $\leq$ 1/3.2, then the prior ratio of 3:1 had been shifted to 1:1 (or more extreme), suggesting that the expected relationship was inconsistent with the data but likely to be null. We interpreted OR $<$ 1/10 (viz. from 3:1 prior expectation to 1:3.2 posterior odds) as clear refutation of the expected relationship.

Modeling details and model fit

Parameters were estimated from three MCMC chains of 20 000 iterations after 10 000 iterations of burn-in ("model settling"). We checked MCMC mixing and convergence using the "boa" package (Smith 2006) in *R* (R Development Core Team 2006).

We determined relative importance of the autoregressive (A), among-response variables (R), and covariate (C) factors of the best model. To do so, we calculated the r^2 for eight models: null (fitting constant-only averages for the seven response variables), A, R, C, A + R, A + C, R + C, A + R + C (full model). These models were effected by deleting terms from Eq. 6 as appropriate. The γ_i terms were retained for all models. The r^2 are the squared Pearson correlation coefficients between the z and μ values from the seven response variables and all years. To decompose variance we used hierarchical partitioning (Chevan and Sutherland 1991, Mac Nally 2000), which identifies independent contributions from individual terms (viz. A, R, and C) and joint variance explanation. We used the R package "hier.part" (Walsh and Mac Nally 2003) to perform the decomposition.

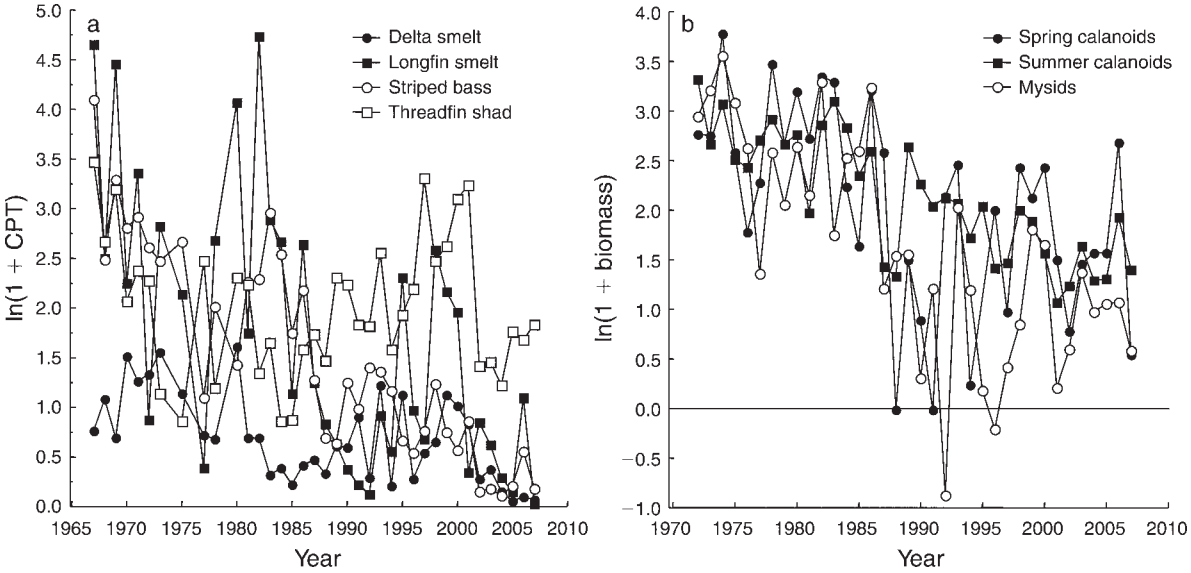

FIG. 2. Population trends (log-transformed) of (a) four fish species (mean catch per trawl [CPT]) and (b) zooplankton taxa (biomass, originally measured in mg C/m^3).

RESULTS

Abundance trajectories

Abundances of all four species of fish declined over the period of data collection, especially since about 2002 (Fig. 2a). Biomasses of the three crustacean groups have been declining consistently since the 1970s, with less evidence of a sudden decline in the 2000s (Fig. 2b).

Overall model characteristics

We used the r^2 (squared Pearson correlation coefficient) between the observed values and the posteriors of the fitted means as our measure of model fit. The full model (autoregressive components, among-response variables interactions, covariates) had an $r^2 = 0.69$. This explained variance was decomposed into independent explanatory amounts of (a) 0.13 for the autoregressive components (A), (b) 0.21 for among-response variable components (R), and (c) 0.35 for covariate relationships (C) (hence 1:1.62:2.69). Thus, the covariates were roughly 66% more important in explaining variation than the response variables, which in turn were ~62% more important than autoregressive elements.

Specific relationships

Parameter estimates and related details are provided in Appendix A. Some covariates appeared to affect more than one response variable (Fig. 3a, b). For expectations that seemed strongly supported by the data, the large values of spring X2 (upstream location) were negatively related to abundances of longfin smelt, biomass of calanoids in spring, and biomass of mysids (Fig. 3a). High water clarity was associated negatively with abundances of striped bass and threadfin shad, while high mean summer water temperatures had an inverse relationship with delta smelt abundance (Fig. 3a).

Several expectations were more weakly supported by the data, but were not refuted. Spring exports were negatively associated with abundances of delta smelt and threadfin shad (Fig. 3b). Many of the trophic interactions among response variables were supported to some extent, including negative relationships between the abundance of longfin smelt and delta smelt and biomass of calanoids in summer, negative correlations between abundance of striped bass and calanoid biomass in spring, and a positive relationship between concentration of chlorophyll *a* in spring and biomass of mysids and calanoids. Calanoid biomass in spring and summer was negatively associated with presence of the nonnative clam *Corbula amurensis*, while abundance of largemouth bass and volume of winter exports were negatively associated with abundance of delta smelt (Fig. 3b).

For all four declining fish species, the parameters indicating density dependence (δ) from the previous year were strongly negative, ranging from -0.79 ± 0.26 (mean $\pm$ SD) for threadfin shad to -1.03 ± 0.18 for longfin smelt (Appendix A). Current abundances were positively related to those for two years previous for longfin smelt (0.30 ± 0.16). Other lag effects were deemed unimportant, although a four-year lag (positive) for striped bass had OR = 9.2.

For the γ parameters, only one result seemed unexpected. The anticipated negative slope for threadfin shad was positive, with high certainty (OR $< 1/57.8$; Appendix A). This suggested, counterintuitively, that the intrinsic population growth parameter had increased over the duration of study.

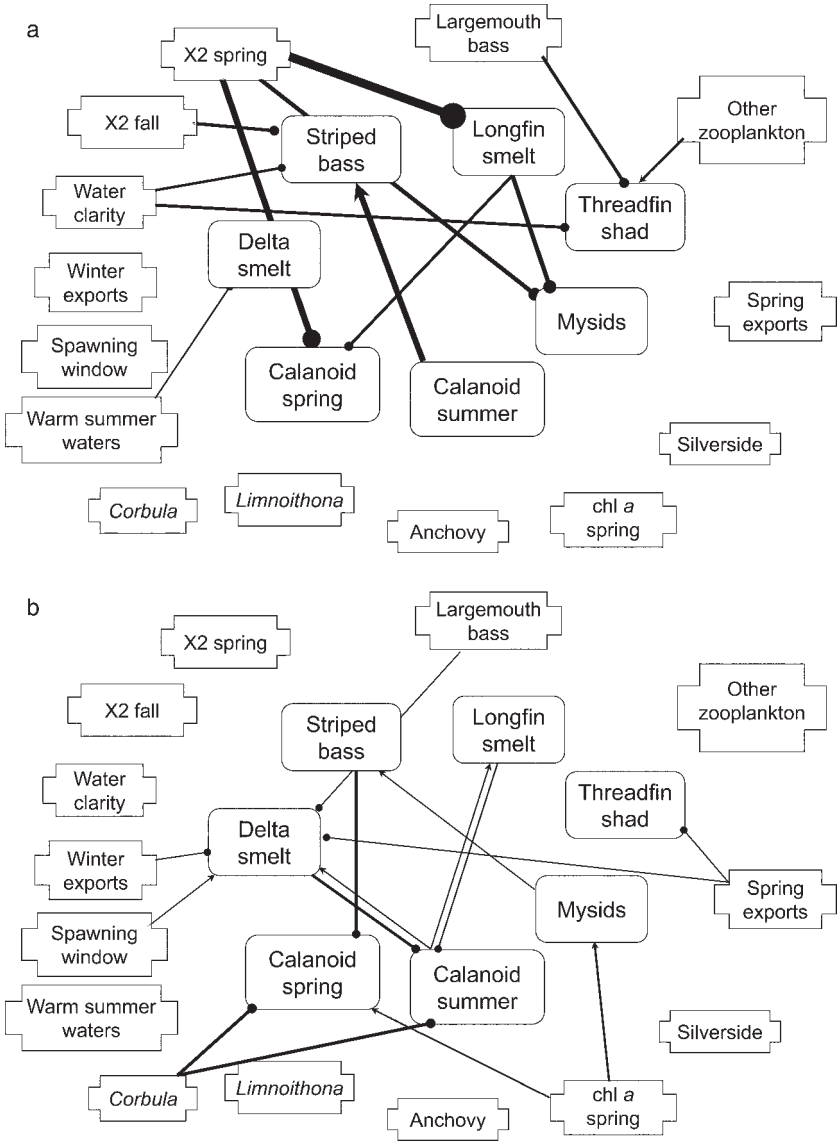

FIG. 3. Relationships supported by the Bayesian multivariate autoregressive analysis of the expert-elicited model, with width of lines proportional to the regression coefficient divided by its standard error. Response variables (focal taxa) are enclosed in rounded boxes while covariates are in boxes with side tabs. Arrows toward a focal taxon indicate a positive effect related to the focal taxon or covariate of line origin, while solid circles indicate negative relationships. (a) Relationships for which the odds ratio ≥ 3.2. (b) Relationships for which the odds ratio falls between 1 and 3.2. The abbreviation "X2" refers to the 2‰ isohaline.

DISCUSSION

Overview of the MAR results

The importance of covariates (51% of explained variation) suggests that some aspects of the environment that can be managed are associated with the declining fish species (e.g., X2 and exports). However, other potential remedial actions would be difficult or impossible to enact (e.g., total removal of *Corbula amurensis*). The relatively large proportion of variance explained by interactions among the declining fishes and their prey suggests that trophic interactions also are important, but it is less clear how management actions could modify such relationships.

The MAR analysis largely supported the expert model, suggesting that existing knowledge is sufficient to identify important interactions and processes, although not all relationships were supported. The expert model included 54 relationships, all but one of which was assigned an expected direction (Table 2). The latter was an "uninformed" expectation that calanoids in spring would be affected by spring X2. The direction was found to be strongly negative (Fig. 3a), suggesting that spring calanoid abundance is greater when X2 is

more seaward. Of the 53 relationships with expected directions, 13 were strongly supported on the basis of odds ratios (OR) of $\geq$3.2 (Fig. 3a) and 15 were not inconsistent with the expected direction ($3.2 > \text{OR} \geq 1$) (Fig. 3b). The other 25 coefficients had posterior means close to zero, indicating that the data did not support the expected directions.

One advantage of using the MAR approach is that results can be represented easily in a form with which most ecologists are familiar, a (partial) food web (Fig. 3). The predator–prey relationships involving the calanoids and mysids support existing reports of direct and indirect effects on the four declining fish species. For example, abundance of striped bass was positively related to availability of calanoid copepods in summer (Fig. 3a). This was negatively associated with the occurrence of the introduced clam *Corbula amurensis* (Fig. 3b), which has induced an ongoing decrease of ~60% in chlorophyll *a* concentration in the low-salinity zone (Alpine and Cloern 1992). Other indirect food limitation relationships may be the chlorophyll *a* (spring) → mysids → striped bass and chlorophyll *a* (spring) → calanoids (spring) → striped bass pathways (Fig. 3b). Longfin smelt abundances had strong negative correlations with calanoids in spring and summer and mysids in spring (Fig. 3a, b). Abundance of delta smelt was related to calanoid biomass in summer (Fig. 3b). These results and relationships of copepods and mysids to chlorophyll *a* concentrations (Fig. 3b) suggest that food web dynamics are important for both smelt species. The isohaline position (X2) in spring had strong negative relationships with spring calanoids and mysids, which also would propagate back through those food pathways (Fig. 3a).

Few covariate relationships were expressed clearly for more than one of the four declining fish species (Fig. 3a, b). Increased water clarity appeared to be related negatively to both striped bass and to threadfin shad (Fig. 3a). Increased water clarity has been attributed to reduction of sediment supply in the rivers (Wright and Schoellhamer 2004) and to sediment capture by submerged aquatic vegetation. Water clarity affects fish feeding (Hecht and Vanderlingen 1992) and vulnerability to predation (Gregory and Levings 1998). Abundance of largemouth bass, a potential predator of the declining fish species (Nobriga and Feyrer 2008), was negatively related to abundance of threadfin shad and, more weakly, to abundance of delta smelt (Fig. 3). Abundance of largemouth bass has increased in the Delta concurrently with expansion of submerged aquatic vegetation (Brown and Michniuk 2007), which provides high-quality habitat for the species. Greater cover of submerged aquatic vegetation also reduces turbidity. Reduced water clarity has been identified as a key component of habitat for delta smelt, at least in autumn (Feyrer et al. 2007). The absence of a discernible relationship between water clarity and abundance of delta smelt may be due to an indirect expression through trophic relationships. Young delta smelt require suspended particles in the water column to feed properly (Baskerville-Bridges et al. 2002, Mager et al. 2002), so reduced prey availability (e.g., summer calanoids) may mask the direct water clarity effect. The multiple effects of temperature, feeding, exports, and introduced species are more consistent with understanding of delta smelt biology (Bennett 2005, Baxter et al. 2008) than are effects of individual covariates per se.

There were clear relationships between warmer summer waters (negative) and duration of water temperatures suitable for spawning (positive) (Fig. 3) and delta smelt, which were consistent with known effects of high temperatures on delta smelt survival (Swanson et al. 2000) and spawning requirements (Bennett 2005).

Increases in water exports in both winter and spring were negatively associated with abundance of delta smelt and increases in spring exports with abundance of threadfin shad. Losses of delta smelt previously have been related to exports through entrainment and mortality at pumping facilities and may be important to population dynamics under some circumstances, particularly during dry years (Kimmerer 2008). Effects of spring exports on threadfin shad have not been measured but possibly are important given that this is the only species of the four to occupy freshwater throughout its life cycle and whose main distribution is near the export facilities (Feyrer et al. 2009).

Modeling formulation: data and limitations

Using MAR, we identified plausible results, notwithstanding a number of important caveats within the model framework, which relate to the nature of the underlying data and to the structure of the analytical model.

Data limitations.—Three major forms of data limitation inherent in MAR are relevant to our study: (1) characterization of all variables and covariates by using a single value per year; (2) lack of spatially and temporally explicit data; and (3) selection of covariates and their measurement. For the declining fish species, we used an estimate of abundance based on average catch per sampling trawl over ~100 sampling stations over each of the four autumn months (September to December). Fish have been collected by other sampling methods (e.g., beach seine nets), but either not consistently over the duration of the data collection or only recently. We included observation error as the standard error from the ~400 trawls per year, but whether this is the most appropriate measure is arguable (Newman 2008).

Apart from allowing γ_i to be time-dependent (albeit linearly), the MAR model assumed process stationarity over the entire duration, which means that the structure of the model and distributions of model parameters are regarded as being the same over the 40+ years. It is possible that population dynamics of the declining taxa

changed greatly as a function of population size. It is plausible that per capita reproductive rates, age structures, social (e.g., schooling) behaviors, Allee effects (Stephens and Sutherland 1999), and vulnerability to predation may differ when there are many individuals compared to when there are few. This is a common tenet in conservation biology (Caughley 1994).

Given the high certainty that all four species declined in concert in 2002 (Thomson et al. 2010), we modified Eq. 6 to allow all parameters to have a two-phase structure. The first phase was the 1967–2001 period and the second phase was 2002–2007. Each parameter was represented by a term of the form $\varpi + \delta\varpi$, where $\delta\varpi$ was the deviation in the second phase from values in the first phase. There were no parameters in which $\delta\varpi$ differed substantially from zero using our OR criteria. This suggests that the stationarity assumption of the MAR model is reasonable, although the small number of years in phase two may make changes difficult to detect.

Stakeholders have commissioned extensive correlative analyses (D. Fullerton, W. J. Miller, and B. F. J. Manly, *unpublished data*), which suggest a wide range of possibilities for potential covariates that might have sparked the precipitous declines. We included eight commonly mentioned covariates in additional runs of the MAR model (Appendix B). Our inferences were little changed, which suggests that our expert model was resilient to inclusion of additional variables and that the latter were largely uninformative.

Model form and structure.—The MAR model is underlain by the Gompertz population dynamic model (Eq. 1). Inference on stock recruitment is contingent on the form of the model (Maunder 2003). We explored whether our inferences were highly dependent on the use of the Gompertz by replacing it with another widely used formulation, the Ricker model (Appendix C; Zeng et al. 1998). The Ricker model emphasized more strongly several relationships: for example, the negative relationships between striped bass and X2 (autumn) and between spring calanoids and X2 (spring) (Appendix C). The Ricker and Gompertz versions of the MAR model generally provided similar inferences but the Gompertz appeared to resolve with greater precision a larger number of relationships given our criteria for their identification (i.e., using ORs).

The values for the δ_{i1} coefficients for the four declining fish species suggested strong negative density dependence (values between −0.79 and −1.03 for one-year lag; Appendix A). Such results seem difficult to reconcile biologically given that the fish sampled each year are young-of-the-year and it is difficult to conceive of a mechanism producing such density dependence. It is possible that this apparent contradiction may be a statistical artifact of the parameterization of the usual Gompertz model. Estimates of γ and δ can be highly correlated and identifiability depends upon length of time series (J. Ponciano, *personal communication*). Even if there were estimation problems for γ and δ, these probably do not affect our estimates of trophic interactions and covariate relationships. From simulations of a Gompertz model with one covariate, we found that the estimate for the covariate coefficient was unbiased even though the estimates of γ and δ were biased (results not shown).

The MAR formulation assumed linear relationships (on the log-abundance scale) and no interactions among covariates, although many interactions are plausible. Interactions would add substantially to the complexity and difficulty of interpretation of an already highly parameterized model. Inclusion of nonlinear functions and interactions among covariates may reduce capacity to resolve drivers of responses if used injudiciously.

A comparison of major outcomes of the MAR analysis with those of the change point analyses, which did allow nonlinear functions of covariates, showed some commonalities, but also several differences. Relationships with water clarity were important in the change point analyses for delta smelt, striped bass, and longfin smelt, although the relationship for the latter was rather stronger in a multispecies model (Thomson et al. 2010). A correlation of water clarity with abundances of threadfin shad, but not with delta smelt, was identified in MAR. A pervasive relationship of spring X2 with abundances of longfin smelt was clear in both analyses. A correlation of winter exports with delta smelt was evident in the change point, but was weaker in the MAR (Fig. 3b). The MAR analysis, but not the change point analysis, identified a correlation between autumn X2 and striped bass. Spring exports appeared to be related to abundances of threadfin shad in both analyses, although the magnitude of the correlation was less in the MAR. Unlike the change-point analysis, the MAR analysis did not identify a relationship between winter exports and threadfin shad. However, in the change-point analysis the magnitude of the average regression coefficient for winter exports and threadfin shad was substantially less than that for spring exports (Thomson et al. 2010). The trophic interactions evident in the MAR, of which many were pronounced (Fig. 3), were less evident in the model selection procedures used in the change point analysis.

A broader life-history model with a more general state–space approach to modeling the pelagic species decline should be more informative (M. N. Maunder and K. B. Newman, *personal communication*). Such a model would incorporate multiple sources of survey data, including data pertinent to egg, larval, juvenile, and adult phases and covariates appropriate for each stage (Maunder 2004).

Estuarine management

Our application of the MAR model provides evidence from a multivariate analysis of how abiotic habitat factors directly relate to declining fish abundance in the upper San Francisco Estuary and indirectly to these fish

populations through the food web. Synthesis of previous univariate analyses have come to similar conclusions, albeit indirectly (Bennett 2005, Baxter et al. 2008). Before the fish species declined precipitously, the abiotic component of their habitat in the estuary was represented mainly as X2 because position of the salinity field was correlated with the abundances of many organisms (Jassby et al. 1995). Recent results have highlighted the importance of other abiotic variables, including water clarity and water temperatures, in the estuary (Feyrer et al. 2007, Nobriga and Feyrer 2008). Our results, which identify trophic relationships, suggest the need to better understand the processes underlying the influence of abiotic conditions on the food web of the estuary. The upper San Francisco Estuary is an exemplar, perhaps an extreme one, of severe, adverse ecological response to many of the stressors to which such systems increasingly are exposed (Fig. 3). Some of the key issues relate to how the isohaline position (X2), which seems to have a profound effect on the declining fish and on their prey, might be managed. While evidence that water exports directly affect striped bass or longfin smelt in a consistent linear manner is weak, there is evidence of potential effects of water exports on delta smelt and threadfin shad. Successfully managing the estuary, at least for the declining fish species, requires a more complete understanding of how the direct effects of water exports interact with the indirect effect of controlling abiotic conditions and the food web.

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APPENDIX A

Details of parameter estimates for the multivariate autoregressive (MAR) model including credible intervals of odds ratios (all model parameters are listed) (*Ecological Archives* A020-050-A1).

APPENDIX B

Details of parameter estimates for multivariate autoregressive (MAR) model with and without distinct variables suggested by other analyses (only parameters with large odds ratios are listed) (*Ecological Archives* A020-050-A2).

APPENDIX C

Details of parameter estimates for multivariate autoregressive (MAR) models underlain by Ricker and Gompertz population-dynamic formulations (only parameters with large odds ratios are listed) (*Ecological Archives* A020-050-A3).

Ecological Archives A020-050-A3

Ralph Mac Nally, James R. Thomson, Wim J. Kimmerer, Frederick Feyrer, Ken B. Newman, Andy Sih, William A. Bennett, Larry Brown, Erica Fleishman, Steven D. Culberson, and Gonzalo Castillo. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modelling (MAR). *Ecological Applications* 20:1417–1430.

Appendix C. Details of parameter estimates for multivariate autoregressive (MAR) models underlain by Ricker and Gompertz population-dynamic formulations (only parameters with large odds ratios are listed).

The Gompertz model is a representation of population dynamics often used in fisheries science (Dennis et al. 2006). We sought to determine the sensitivity of our results to the assumption of a Gompertz model form. To do so, we used another common model, the Ricker, with all parameter estimation and priors the same as for the Gompertz evaluation.

$$z_{i,t} \sim \text{Normal}(x_{i,t}, \omega_{i,t}^2); x_{i,t} \sim \text{Normal}(\mu_{i,t}, \sigma_i^2);$$
$$\mu_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} n_{i,t-l} + \sum_{j=1, j\neq i}^{J} \beta_{ij} x_{j,t-1} + \sum_{k=1}^{K} \alpha_{ik} u_{k,t}, \quad \text{(C.1)}$$

The principal change is that the autoregressive lags are related to the non-ln-transformed densities, n_i (Zeng et al. 1998), which also means that untransformed measurement uncertainties are incorporated. Unlike the Gompertz, this has the effect of mixing transformed and untransformed versions of the basic data in population dynamics. Inclusion of untransformed values, especially of measurement uncertainties, is likely to introduce noise in the estimation process and to reduce resolution in many instances.

Here, we present a comparison of inferences for the Ricker and Gompertz versions of the model. The Ricker model emphasized more strongly several relationships, indicated by increased odds ratios: the negative relationships between abundance of striped bass and X2 (autumn) and between biomass of calanoids (spring) and X2 (spring). Five strong Gompertz relationships were less well defined in the Ricker version (i.e., odds ratios declined to < 3): the negative association between abundance of delta smelt and warm summer waters, decreases in abundance of striped bass and threadfin shad as water clarity increased, negative association between biomass of calanoids in spring and abundance of longfin smelt, and negative association between abundance of threadfin shad and biomass of other zooplankton. The expected negative relationship between abundance of longfin smelt and volume of winter exports, which was close to 0 in the Gompertz model, was strongly positive in the Ricker version. Of the relationships depicted in Fig. 3b, three had odds reduced to < 1: association between abundance of delta smelt and abundance of largemouth bass (–) and summer biomass of calanoids (+) and abundance of striped bass and biomass of mysids (+). Model fit gauged by R^2 and $\overline{\sigma}_i^2$ was similar. We conclude that the models provide generally similar inferences, given the large number of parameters estimated, but that the Gompertz appears to identify more relationships given our odd-ratio criterion for their identification.

TABLE C1. Parameter details for Bayesian estimation of the multivariate autoregressive model for Ricker and Gompertz dynamics, focusing on relationships with large (= 3) odds ratios (posterior odds : prior odds) in either model (c.f. Fig. 3a; see Table 1 for variable definitions).

Response	Covariate	Ricker		Gompertz	
		Mean ± SD	Odds ratio	Mean ± SD	Odds ratio
Delta smelt	Water temperature, summer	-0.093 ± 0.090	2.0	-0.132 ± 0.075	8.7
Longfin smelt	X2 (spring)	-0.571 ± 0.230	44.1	-0.694 ± 0.199	466.3
Longfin smelt	Exports winter	0.243 ± 0.165	1/32.3	0.031 ± 0.177	1/4.2
Striped bass	X2 (autumn)	-0.374 ± 0.167	21.9	-0.265 ± 0.128	12.4
Striped bass	Exports spring	0.057 ± 0.088	1/9.2	0.031 ± 0.075	1/6.2
Striped bass	Water clarity	-0.095 ± 0.153	0.9	-0.217 ± 0.129	7.3
Threadfin shad	"Other zooplankton"	0.149 ± 0.146	1.9	0.192 ± 0.149	3.1

Threadfin shad	Largemouth bass	-0.222 ± 0.163	3.6	-0.267 ± 0.161	6.8
Threadfin shad	Water clarity	-0.138 ± 0.190	1.1	-0.245 ± 0.187	3.4
Spring calanoids	X2 (spring)	-0.509 ± 0.152	544.6	-0.498 ± 0.156	258.3
Mysids	X2 (spring)	-0.344 ± 0.149	26.0	-0.346 ± 0.150	25.0
Striped bass	Summer calanoids	0.363 ± 0.194	15.3	0.472 ± 0.157	Inf.
Spring calanoids	Longfin smelt	-0.167 ± 0.174	1.7	-0.246 ± 0.177	3.6
Mysids	Longfin smelt	-0.314 ± 0.154	15.5	-0.349 ± 0.159	19.1

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Ralph Mac Nally, James R. Thomson, Wim J. Kimmerer, Frederick Feyrer, Ken B. Newman, Andy Sih, William A. Bennett, Larry Brown, Erica Fleishman, Steven D. Culberson, and Gonzalo Castillo. **2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modelling (MAR). *Ecological Applications* 20:1417–1430.**

Appendix B. Details of parameter estimates for multivariate autoregressive (MAR) model with and without distinct variables suggested by other analyses (only parameters with large odds ratios are listed).

Previous analyses by D. Fullerton, B. F. J. Manly, and W. J. Miller (unpublished reports) suggested that certain other variables should be considered as influences on the abundance of delta smelt. Many of these variables are variants on, surrogates for, or identical to covariates used in our analyses. The distinct variables are **ecsepdec** (September-December electrical conductivity, µS/cm), **eupsJul** (average *Eurytemora* and *Pseudodiaptomus* density, July, m^3), **eupsAug** (average *Eurytemora* + *Pseudodiaptomus* density, August, m^3), **zooBJul** (average zooplankton biomass density, July, µg C m^3), **zooBAug** (average zooplankton biomass density, August, µg C m^3), **avgNH4Hood** (average of September–December ammonia at Hood, California, mg/L), **maxNH4Hood** (maximum average monthly ammonia at Hood, California, September–December, m/L), **NH4Load** (discharge of ammonia from Sacramento Regional Wastewater treatment plant, August–October, *t*).

We included these variables in the MAR model after standardizing variables, and included missing values to be imputed, in the same manner as for the main covariates. We included these variables for delta smelt, longfin smelt, striped bass, and threadfin shad, but not for mysids and calanoids. We provided the regression coefficients for these covariates with negatively or positively shifted Weibull priors according to the inferences given in the unpublished reports.

Model fit gauged by R^2 and $\overline{\sigma}_i^2$ was similar. Inferences on most of the key relationships derived from our model were sustained with the inclusion of the eight additional variables (Table B1). The inferential strength of three relationships was different: from one conforming with our model to ones with reduced odds ratios (direction of inference was the same). Relationships involving any of the eight additional variables ran strongly counter to expectations (Table B1). These outcomes suggested that our expert model was resilient to inclusion of those additional variables, but the latter were either uninformative or seemingly counter-intuitive.

TABLE B1. Parameter details for Bayesian estimation of the multivariate autoregressive model for Gompertz dynamics with and without the distinct variables suggested by other analyses. Again, we focus on relationships with large (= 3) odds ratios (posterior odds : prior odds) in either variable set.

Response variable	Covariate	With additional variables		Without additional variables	
		Mean ± SD	Odds ratio	Mean ± SD	Odds ratio
Delta smelt	Warm summer waters	-0.094 ± 0.091	1.8	-0.132 ± 0.075	8.7
Longfin smelt	X2 (spring)	-0.497 ± 0.252	11.7	-0.694 ± 0.199	466.3
Striped bass	X2 (autumn)	-0.301 ± 0.152	4.2	-0.265 ± 0.128	12.4
Striped bass	Exports spring	0.029 ± 0.076	1/6.0	0.031 ± 0.075	1/6.2
Striped bass	Water clarity	-0.301 ± 0.152	10.3	-0.217 ± 0.129	7.3
Threadfin shad	“Other zooplankton”	0.129 ± 0.190	1.0	0.192 ± 0.149	3.1

Threadfin shad	Largemouth bass	-0.270 ± 0.186	4.2	-0.267 ± 0.161	6.8
Threadfin shad	Water clarity	-0.322 ± 0.226	3.8	-0.245 ± 0.187	3.4
Spring calanoids	X2 (spring)	-0.495 ± 0.157	311.5	-0.498 ± 0.156	258.3
Mysids	X2 (spring)	-0.341 ± 0.152	23.8	-0.346 ± 0.150	25.0
Striped bass	Summer calanoids	0.361 ± 0.166	15.5	0.472 ± 0.157	Inf.
Spring calanoids	Longfin smelt	-0.226 ± 0.182	2.8	-0.246 ± 0.177	3.6
Mysids	Longfin smelt	-0.348 ± 0.154	20.5	-0.349 ± 0.159	19.1
Delta smelt	zooBAug	-0.165 ± 0.136	1/23.2	–	–
Longfin smelt	eupsJul	-0.198 ± 0.171	1/20.4	–	–
Striped bass	zooBJul	-0.125 ± 0.111	1/20.4	–	–
Threadfin shad	zooBAug	-0.126 ± 0.209	1/10.0	–	–

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Ralph Mac Nally, James R. Thomson, Wim J. Kimmerer, Frederick Feyrer, Ken B. Newman, Andy Sih, William A. Bennett, Larry Brown, Erica Fleishman, Steven D. Culberson, and Gonzalo Castillo. **2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modelling (MAR). *Ecological Applications* 20:1417–1430.**

Appendix A. Details of parameter estimates for the multivariate autoregressive (MAR) model including credible intervals of odds ratios (all model parameters are listed).

In Table A1, we provide explicit details for model parameters and for quantities used for inference on parameter importance; see Table 1 in main manuscript for definitions of variables.

TABLE A1. Parameter details for Bayesian estimation of the multivariate autoregressive (MAR) model. "Expected" denotes direction of relationship derived from the expert model, while the odds ratio (posterior odds : prior odds) is expressed as 1/*G* for results that were contrary to expectation (where *G* = odds ratio for the unanticipated result).

Response variable	Covariate	Mean ± SD	2.50% – 97.50%	Post-odds	Expected	Odds ratio
Delta smelt	Inland silverside	0.008 ± 0.078	-0.145 – 0.165	1.2	–	1/3.5
Delta smelt	Largemouth bass	-0.075 ± 0.092	-0.256 – 0.109	4.1	–	1.4
Delta smelt	X2 (autumn)	0.055 ± 0.106	-0.156 – 0.263	2.4	–	1/7.1
Delta smelt	Water clarity	-0.026 ± 0.126	-0.292 – 0.209	1.3	–	0.4
Delta smelt	Exports winter	-0.089 ± 0.102	-0.292 – 0.108	4.5	–	1.5
Delta smelt	Exports spring	-0.083 ± 0.079	-0.240 – 0.076	6.2	–	2.1
Delta smelt	Spawning window	0.081 ± 0.081	-0.073 – 0.245	5.5	+	1.8
Delta smelt	Warm summer waters	-0.132 ± 0.075	-0.280 – 0.017	26.0	–	8.7
Longfin smelt	X2 (spring)	-0.694 ± 0.199	-1.066 – -0.286	1399.0	–	466.3
Longfin smelt	X2 (autumn)	-0.046 ± 0.225	-0.518 – 0.359	1.3	–	0.4
Longfin smelt	Water clarity	-0.094 ± 0.225	-0.551 – 0.335	1.9	–	0.6
Longfin smelt	Exports winter	0.031 ± 0.177	-0.343 – 0.359	1.4	–	1/4.2
Longfin smelt	Exports spring	0.055 ± 0.143	-0.232 – 0.334	1.9	–	1/5.7
Striped bass	Largemouth bass	-0.027 ± 0.089	-0.203 – 0.149	1.6	–	0.5
Striped bass	X2 (spring)	0.040 ± 0.103	-0.174 – 0.234	2.0	–	1/5.9
Striped bass	X2 (autumn)	-0.265 ± 0.128	-0.512 – 0.004	37.3	–	12.4
Striped bass	Water clarity	-0.217 ± 0.129	-0.471 – 0.041	21.8	–	7.3
Striped bass	Exports spring	0.031 ± 0.075	-0.122 – 0.178	2.1	–	1/6.2
Threadfin shad	"Other zooplankton" in spring	0.192 ± 0.149	-0.094 – 0.485	9.7	+	3.2
Threadfin shad	Largemouth bass	-0.267 ± 0.161	-0.582 – 0.043	20.5	–	6.8
Threadfin shad	Water clarity	-0.245 ± 0.187	-0.628 – 0.122	10.3	–	3.4
Threadfin shad	Exports spring	-0.078 ± 0.119	-0.318 – 0.153	3.0	–	1.0
Spring calanoids	Anchovy	-0.068 ± 0.192	-0.488 – 0.302	1.8	–	0.6
Spring calanoids	Spring chlorophyll *a* (freshwater)	0.134 ± 0.200	-0.252 – 0.542	3.0	+	1.0
Spring calanoids	Spring chlorophyll *a* (low salinity)	0.026 ± 0.189	-0.329 – 0.416	1.2	+	0.4
Spring calanoids	Inland silverside	-0.042 ± 0.177	-0.406 – 0.294	1.4	–	0.5
Spring calanoids	X2 (spring)	-0.498 ± 0.156	-0.756 – -0.159	258.3	+/–	258.3
Spring calanoids	*Corbula*	-0.263 ± 0.291	-0.845 – 0.270	4.2	–	1.4
Summer calanoids	Anchovy	0.013 ± 0.115	-0.217 – 0.256	1.2	–	1/3.6

Summer calanoids	Summer chlorophyll *a* (low salinity)	-0.049 ± 0.134	-0.307 – 0.216	1.8	+	1/5.5
Summer calanoids	*Limnoithona*	0.080 ± 0.165	-0.267 – 0.387	2.3	–	1/7.0
Summer calanoids	Inland silverside	-0.004 ± 0.110	-0.220 – 0.212	1.0	–	0.3
Summer calanoids	*Corbula*	-0.262 ± 0.222	-0.694 – 0.125	7.0	–	2.3
Mysid	Anchovy	-0.010 ± 0.187	-0.451 – 0.305	1.2	–	0.4
Mysid	Spring chlorophyll *a* (low salinity)	0.180 ± 0.174	-0.154 – 0.532	5.8	+	1.9
Mysid	Summer chlorophyll *a* (low salinity)	0.109 ± 0.190	-0.252 – 0.496	2.5	+	0.8
Mysid	X2 (spring)	-0.346 ± 0.150	-0.640 – -0.049	75.1	–	25.0
Delta smelt	Spring calanoids	-0.025 ± 0.092	-0.198 – 0.161	1.6	+	1/4.9
Delta smelt	Summer calanoids	0.110 ± 0.161	-0.207 – 0.439	3.1	+	1.0
Longfin smelt	Spring calanoids	0.085 ± 0.198	-0.286 – 0.511	1.9	+	0.6
Longfin smelt	Summer calanoids	0.271 ± 0.254	-0.235 – 0.771	6.0	+	2.0
Longfin smelt	Mysids	0.085 ± 0.203	-0.283 – 0.508	1.9	+	0.6
Striped bass	Spring calanoids	0.000 ± 0.092	-0.182 – 0.187	1.0	+	1/3.1
Striped bass	Summer calanoids	0.472 ± 0.157	0.158 – 0.780	Inf.	+	Inf.
Striped bass	Mysids	0.073 ± 0.095	-0.108 – 0.274	3.8	+	1.3
Spring calanoids	Delta smelt	-0.062 ± 0.306	-0.722 – 0.435	1.2	–	0.4
Spring calanoids	Longfin smelt	-0.246 ± 0.177	-0.585 – 0.111	10.8	–	3.6
Spring calanoids	Striped bass	-0.227 ± 0.289	-0.811 – 0.294	3.4	–	1.1
Summer calanoids	Delta smelt	-0.235 ± 0.274	-0.815 – 0.261	4.1	–	1.4
Summer calanoids	Longfin smelt	-0.119 ± 0.102	-0.322 – 0.080	7.3	–	2.4
Summer calanoids	Striped bass	-0.122 ± 0.204	-0.518 – 0.270	2.6	–	0.9
Mysids	Longfin smelt	-0.349 ± 0.159	-0.656 – -0.026	57.3	–	19.1
Mysids	Striped bass	0.077 ± 0.227	-0.419 – 0.450	1.9	–	1/5.7
Mysids	Summer calanoids	0.054 ± 0.237	-0.388 – 0.530	1.4	+	0.5
Declining taxon	*Parameter*					
Delta smelt	Lag 1	-0.807 ± 0.271	-1.305 – -0.228	290.6		290.6
Delta smelt	Lag 2	0.296 ± 0.274	-0.262 – 0.824	6.0		6.0
Longfin smelt	Lag 1	-1.034 ± 0.183	-1.408 – -0.682	–Inf.		–Inf.
Longfin smelt	Lag 2	0.300 ± 0.159	-0.024 – 0.607	29.0		29.0
Longfin smelt	Lag 3	-0.103 ± 0.148	-0.392 – 0.197	3.2		3.2
Striped bass	Lag 1	-0.792 ± 0.215	-1.204 – -0.342	2332.2		2332.2
Striped bass	Lag 2	-0.052 ± 0.204	-0.460 – 0.355	1.6		1.6
Striped bass	Lag 3	0.048 ± 0.172	-0.302 – 0.385	1.6		1.6
Striped bass	Lag 4	-0.213 ± 0.166	-0.541 – 0.111	9.2		9.2
Striped bass	Lag 5	-0.007 ± 0.132	-0.259 – 0.261	1.1		1.1
Threadfin shad	Lag 1	-0.786 ± 0.262	-1.273 – -0.250	367.5		367.5
Threadfin shad	Lag 2	-0.025 ± 0.249	-0.510 – 0.468	1.2		1.2
Spring calanoids	Lag 1	-0.001 ± 0.010	-0.021 – 0.019	1.3		1.3
Summer calanoids	Lag 1	-0.001 ± 0.010	-0.021 – 0.018	1.2		1.2
Mysids	Lag 1	-0.001 ± 0.010	-0.021 – 0.018	1.3		1.3
Delta smelt	? intercept	0.270 ± 0.532	-0.783 – 1.268	2.3		2.3
Delta smelt	? slope	-0.004 ± 0.012	-0.026 – 0.020	1.9	–	0.6
Longfin smelt	? intercept	0.932 ± 0.774	-0.525 – 2.494	7.7		7.7

Longfin smelt	? slope	-0.023 ± 0.022	-0.064 – 0.021	5.6	–	1.9
Striped bass	? intercept	0.557 ± 0.701	-0.789 – 1.815	3.2		3.2
Striped bass	? slope	-0.011 ± 0.017	-0.043 – 0.023	2.9	–	1.0
Threadfin shad	? intercept	0.309 ± 0.487	-0.621 – 1.293	2.9		2.9
Threadfin shad	? slope	0.052 ± 0.022	0.005 – 0.098	1/57.8	–	1/73.4
Spring calanoids	? intercept	1.126 ± 0.777	-0.335 – 2.664	12.8		12.8
Spring calanoids	? slope	-0.018 ± 0.025	-0.068 – 0.030	3.2	–	1.1
Summer calanoids	? intercept	0.884 ± 0.643	-0.326 – 2.208	12.7		12.7
Summer calanoids	? slope	-0.016 ± 0.020	-0.057 – 0.023	3.6	–	1.2
Mysids	? intercept	0.251 ± 0.731	-1.240 – 1.672	1.7		1.7
Mysids	? slope	0.001 ± 0.019	-0.037 – 0.040	1.1	–	0.4

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A state–space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hyposmesus transpacificus*)

Mark N. Maunder and Richard B. Deriso

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Abstract: Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of populations. To provide appropriate management advice, the data should be used to determine which factors are important and what life stages they impact. It is also important to consider density dependence because it can modify the impact of some factors. We develop a state–space multistage life cycle model that allows for density dependence and environmental factors to impact different life stages. Models are ranked using a two-covariates-at-a-time stepwise procedure based on AIC_c model averaging to reduce the possibility of excluding factors that are detectable in combination, but not alone. Impact analysis is used to evaluate the impact of factors on the population. The framework is illustrated by application to delta smelt (*Hyposmesus transpacificus*), a threatened species that is potentially impacted by multiple anthropogenic factors. Our results indicate that density dependence and a few key factors impact the delta smelt population. Temperature, prey, and predators dominated the factors supported by the data and operated on different life stages. The included factors explain the recent declines in delta smelt abundance and may provide insight into the cause of the pelagic species decline in the San Francisco Estuary.

Résumé : Les multiples facteurs qui agissent sur les différents stades du cycle biologique influencent la dynamique des populations et compliquent l'évaluation et la gestion des populations. Afin de fournir des avis de gestion appropriés, il faut utiliser les données pour déterminer quels facteurs sont importants et quels stades du cycle ils affectent. Il est aussi important de considérer la densité dépendance, car elle peut modifier l'impact de certains facteurs. Nous mettons au point un type de modèle état–espace à stades de vie multiples qui tient compte de l'impact de la densité dépendance et des facteurs du milieu sur les différents stades de vie. Les modèles sont placés par ordre à l'aide d'une procédure pas-à-pas de deux covariables à la fois basée sur l'établissement de la moyenne des modèles de type AIC_c afin de réduire la possibilité d'exclure des facteurs décelables en combinaison, mais non isolément. Une analyse d'impacts sert à évaluer les effets des facteurs sur la population. Nous illustrons ce cadre d'analyse en l'appliquant à l'éperlan du delta (*Hyposmesus transpacificus*), une espèce menacée qui est potentiellement affectée par de multiples facteurs anthropiques. Nos résultats montrent que la densité dépendance et quelques facteurs clés affectent la population d'éperlans du delta. La température, les proies et les prédateurs dominent parmi les facteurs révélés par les données et ils agissent sur différents stades de vie. Les facteurs retenus expliquent les déclins récents de l'abondance de l'éperlan du delta et peuvent fournir une perspective sur la cause de la diminution des espèces pélagiques dans l'estuaire de San Francisco.

[Traduit par la Rédaction]

Introduction

Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of natural populations. To provide appropriate management advice, the available data should be used to determine which factors are important and what life stages they impact. It is also important to consider density-dependent processes because they can modify the impact of some factors, and the strength of density dependence can vary among life stages (Rose et al. 2001). Management can then better target limited resources to actions that are most effective. Unfortunately, the relationships among potential factors, the life stages that they influence, and density dependence are often difficult to piece together through standard correlation or linear regression analyses.

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Life cycle models are an essential tool in evaluating factors influencing populations of management concern (Buckland et al. 2007). They can evaluate multiple factors that simultaneously influence different stages in the presence of density dependence. They also link the population dynamics from one time period to the next propagating the information and uncertainty. This link allows information relating to one life stage (i.e., abundance estimates) to inform processes influencing other life stages and is particularly important when data is not available for all life stages for all time periods. The life cycle model should be fit to the available data to estimate the model parameters, including parameters that represent density dependence, and determine the data-based evidence of the different factors that are thought to influence the population dynamics. Finally, the model should be used to direct research or provide management advice.

Deriso et al. (2008) present a framework for evaluating alternative factors influencing the dynamics of a population. It extends earlier work by Maunder and Watters (2003), Maunder and Deriso (2003), and Maunder (2004) and is similar to approaches taken by others (e.g., Besbeas et al. 2002; Clark and Bjornstad 2004; Newman et al. 2006). The Deriso et al. framework involves several components. First, the factors to be considered are identified. Second, the population dynamics model is developed to include these factors and then fitted to the data. Third, hypothesis tests are performed to determine which factors are important. Finally, to provide management advice, the impact of the factors on quantities of management interest, are assessed. They illustrate their framework using an age-structured fisheries stock assessment model fit to multiple data sets. Their application did not allow for density dependence in the population dynamics, except through the effect of density on the temporal variation in which ages are available to the fishery.

Inclusion of density dependence is important in evaluating the impacts on populations. Without density dependence, modeled populations can increase exponentially. This is unrealistic and can also cause computational or convergence problems in fitting population dynamics models to data. Density dependence can also moderate the effects of covariates. This is important because factors affecting density-independent survival may be much less influential in the presence of density dependence compared with factors that affect carrying capacity (e.g., habitat). It is also important to correctly identify the timing of when the factors influence the population with respect to the timing of density dependence processes and available data. The approach also provides a framework for amalgamating the two paradigms of investigating population regulation outlined by Krebs (2002): the density paradigm and the mechanistic paradigm.

Here we develop a life cycle model that allows for density dependence at multiple life stages and allows for factors to impact different life stages. We apply the framework of Deriso et al. (2008) where the first component also includes identifying the life stages that are impacted by each factor and where density dependence occurs. We illustrate the framework by applying it to delta smelt (*Hyposmesus transpacificus*). Delta smelt is an ideal candidate to illustrate the modeling approach because there are several long-term abundance time series for different life stages and a range of hypothesized factors influencing its survival for which covariate data is available. Life cycle models have been recommended to evaluate the factors effecting delta smelt (Bennett 2005; Mac Nally et al. 2010; Thomson et al. 2010).

Delta smelt is of particular management concern because of declines in abundance and the myriad of anthropogenic factors that could be causing the decline. Delta smelt is endemic to the San Francisco Estuary, which has multiple stressors, including habitat modification, sewage outflow, farm runoff, and water diversions, to name just a few. Delta smelt was listed as threatened under the US and California Endangered Species Acts in 1993. Several other pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Recent studies have investigated the factors hypothesized to have caused the declines at both the species and ecosystem level, but the results were not conclusive (Mac Nally et al. 2010; Thomson et al. 2010).

Materials and methods

Model

The model is stage-based with consecutive stages being related through a function that incorporates density dependence. For simplicity and to be consistent with the predominant dynamics of delta smelt, we assume an annual life cycle. However, it is straightforward to extend the model to a multiple year life cycle or to stages that cover multiple years (i.e., adding age structure; e.g., Rivot et al. 2004; Newman and Lindley 2006). Within a year the number of individuals in each stage is a function of the numbers in the previous stage. The number of individuals in the first stage is a function of the numbers in the last stage in the previous year (i.e., the stock–recruitment relationship), except for the numbers in the first stage in the first year, which is estimated as a model parameter. The functions describing the transition from one stage to the next are modeled using covariates. A state–space model (Newman 1998; Buckland et al. 2004, 2007) is used to allow for annual variability in the equation describing the transition from one life stage to the next. Traditionally, state–space models describe demographic variability (e.g., using a binomial probability distribution to represent the number of individuals surviving based on a given survival rate; e.g., Dupont 1983; Besbeas et al. 2002); however, environmental variability generally overwhelms demographic variability (Buckland et al. 2007) so we model the process variability (e.g., Rivot et al. 2004; Newman and Lindley 2006) using a lognormal probability distribution (Maunder and Deriso 2003). Our approach differs from modeling the log abundance and assuming additive normal process variability (e.g., Quinn and Deriso 1999, page 103), and the population dynamics function models the expected value rather than the median. The difference in the expectation will simply be a scaling factor ($\exp(-0.5\sigma^2)$) unless the variance of the process variability changes with time.

$$(1) \qquad N_{t,s} \sim \text{Lognormal}\left[f(N_{t,s-1}), \sigma^2_{s-1}\right]; \qquad s > 1$$

$$(2) \qquad N_{t,1} \sim \text{Lognormal}\left[f(N_{t-1,\text{nstages}}), \sigma^2_{\text{nstages}}\right]$$

where t is time, s is stage, nstages is the number of stages in the model, and σ_s is the standard deviation of the variation

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not explained by the model (process variability) in the transition from stage s to the next stage.

The three-parameter Deriso–Schnute stock–recruitment model (Deriso 1980; Schnute 1985) is used to model the transition from one stage to the next. The Deriso–Schnute model is a flexible stock-recruitment curve in which the third parameter (γ) can be set to represent the Beverton–Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) stock–recruitment models (Quinn and Deriso 1999, page 95).

$$(3) \qquad f(N) = aN(1 - b\gamma N)^{\frac{1}{\gamma}}$$

where the parameter a can be interpreted as the number of recruits per spawner at low spawner abundance or the survival fraction at low abundance levels. In cases for which only the relative abundance at each stage can be modeled (as in the delta smelt example), a also contains a scaling factor from one survey to the next. The parameter b determines how the number of recruits per spawner or the survival rate decreases with abundance. Constraints can be applied to the parameters to keep the relationship realistic: $a \geq 0$, $b \geq 0$. The additional constraint $a \leq 1$ can be applied when the relationship is used to describe survival and the consecutive stages are modeled in the same units.

Covariates are implemented to influence the abundance either before density dependence ($g(N,x)$) or after density dependence ($h(x)$). Although, when no density dependence is present, the two methods are identical.

$$(4) \qquad f(N) = ag(N,x)[1 - b\gamma g(N,x)]^{\frac{1}{\gamma}}h(x)$$

$$(5) \qquad g(N,x) = N\exp\left(\sum \lambda x\right)$$

$$(6) \qquad h(x) = \exp\left(\sum \beta x\right)$$

where λ and β are the coefficients of the covariate (x) for before and after density dependence, respectively, and are estimated as model parameters.

For survival it might be important to keep the impact of the environmental factors within the range 0 to 1 and the logistic transformation can be used, e.g.,

$$(7) \qquad ag(N,x) = N\frac{\exp\left(a' + \sum \lambda x\right)}{1 + \exp\left(a' + \sum \lambda x\right)}$$

Where the parameter a' defines the base level of survival (i.e., $a = \frac{\exp(a')}{1+\exp(a')}$) and replaces a of the density dependence function.

If the covariate values are all positive, the negative exponential can be used, e.g.,

$$(8) \qquad g(N,x) = N\exp\left(-\sum \lambda x\right); \qquad \lambda \geq 0, \quad x \geq 0$$

A combination of the above three options may be appropriate depending on the application.

The importance of the placement of the covariates (i.e., before or after density dependence) relates to both the timing of density dependence and the timing of the surveys, which provide information on abundance. Covariates could be applied to the other model parameters. For example, covariates that are thought to be related to the carrying capacity (e.g., habitat) could be used to model b.

The model is fit to indices of abundance ($I_{t,s}$). The abundance indices are assumed to be normally distributed, but other sampling distributions could be assumed if appropriate. Typically, if the index of abundance is a relative index and not an estimate of the absolute abundance, the model is fit to the index by scaling the model's estimate of abundance using a proportionality constant (q, often called the catchability coefficient; Maunder and Starr 2003).

$$(9) \qquad I_{t,s} \sim \text{Normal}(qN_{t,s}, \nu_{t,s}^2)$$

However, the scaling factor is completely confounded with the a parameter of the Deriso–Schnute model, and therefore the population is modeled in terms of relative abundance that is related to the scale of the abundance indices for each life stage and only makes sense in terms of total abundance if the abundance indices are also in terms of total abundance. Therefore, the proportionality constant (q) should be set to one. Other data could also be used in the analysis if appropriate (e.g., information on survival from mark–recapture studies; Besbeas et al. 2002; Maunder 2004).

Model parameters to estimate

The model parameters estimated include the initial abundance of the first stage $N_{1,1}$; the parameters of the stock–recruitment model for each stage $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{\gamma}$; the coefficients of the covariates $\boldsymbol{\lambda}$, $\boldsymbol{\beta}$; the standard deviation of the process variability for each stage $\boldsymbol{\sigma}$; and the standard deviation of the observation error (used in defining the likelihood function) for each index of abundance $\boldsymbol{\nu}$. The observation error standard deviation, $\boldsymbol{\nu}$, is often fixed based on the survey design or restricted so that there is not a parameter to estimate for each survey and time period (e.g., Maunder and Starr 2003). The state–space model can be implemented by treating the process variability as random effect parameters (de Valpine 2002). The likelihood function that is optimized is calculated by integrating over these parameters (Skaug 2002; Maunder and Deriso 2003). Therefore, they are not treated as parameters to estimate. However, realizations of the random effects can be estimated by using empirical Bayes methods (Skaug and Fournier 2006), so that the unexplained process variation can be visualized. The estimated parameters of the model are $N_{1,1}$, $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{\gamma}$, $\boldsymbol{\lambda}$, $\boldsymbol{\beta}$, $\boldsymbol{\sigma}$, and $\boldsymbol{\nu}$.

Implementation in AD Model Builder

Dynamic models like the multistage life cycle model described here can be computationally burdensome if they are carried out in a state–space modeling framework (i.e., integrating over the state–space or equivalently the process variability), and efficient parameter estimation is needed if multiple hypotheses are being tested. Implementation is facilitated by the use of Markov chain Monte Carlo and related methods (Newman et al. 2009), and their use has increased in recent years (Lunn et al. 2009). In particular, authors have found a Bayesian framework convenient for implementation (Punt and Hilborn 1997). An alternative approach is to use the Laplace approximation to implement the integration (Skaug 2002). AD Model Builder (ADMB; http://admb-project.org/) has an

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efficient implementation of the Laplace approximation using automatic differentiation (Skaug and Fournier 2006). The realizations of the random effects are estimated by using empirical Bayes methods adjusted for the uncertainty in the fixed effects (Skaug and Fournier 2006). ADMB was originally designed as a function minimizer, and therefore likelihoods are implemented in terms of negative log-likelihoods, and probability distributions are implemented in terms of negative log-probabilities. A more complete description of ADMB and its implementation of random effects can be found at http://admb-project.org/.

The population is modeled using random effects to implement the state–space model (de Valpine 2002):

$$N_{t,s} = f(N_{t,s-1})\exp\left(\sigma_{s-1}\varepsilon_{t,s-1} - 0.5\sigma_{s-1}^2\right) \tag{10}$$

$$N_{t,1} = f(N_{t-1,\text{nstages}}) \times \exp\left(\sigma_{\text{nstages}}\varepsilon_{t-1,\text{nstages}} - 0.5\sigma_{\text{nstages}}^2\right) \tag{11}$$

$$\varepsilon_{t,s} \sim N(0, 1) \tag{12}$$

A penalty is added to the objective function to implement the random effects

$$0.5\sum_{t,s}\varepsilon_{t,s}^2 \tag{13}$$

The negative log-likelihood function for the abundance indices ignoring constants is

$$-\ln(L) = \sum_{t,s}\ln(\nu_{t,s}) + \frac{(I_{t,s} - qN_{t,s})^2}{2\nu_{t,s}^2} \tag{14}$$

Model selection

Model selection (Hilborn and Mangel 1997) can be used to determine if the data supports density dependence for a particular stage or the factors that impact the population dynamics. In our analysis different models are represented by different values of the model parameters. The relationship between one stage and the next is density independent if $b = 0$. Therefore, a test for density dependence tests whether $b = 0$. When $b = 0$, γ has no influence on the results, and unless a hypothesis about γ is made (i.e., Beverton–Holt, $\gamma = -1$; or Ricker, $\gamma \to 0$), testing between density independence and density dependence requires the estimation of two additional parameters (b, γ). A factor has no influence on the model when its coefficient (λ, β) is fixed at zero. Therefore, testing a factor requires estimating one parameter for each factor tested. There are a variety of methods available for model selection and hypothesis testing, each with their own set of issues (e.g., Burnham and Anderson 1998; Hobbs and Hilborn 2006). Given these issues, we rely on Akaike information criterion adjusted for sample size (AIC_c) and AIC_c weights to rank models and provide an idea of the strength of evidence in the data about an a priori set of alternative hypotheses (factors), but they are not used as strict hypothesis tests (Anderson et al. 2000; Hobbs and Hilborn 2006).

The AIC_c is useful for ranking alternative hypotheses when multiple covariates and density dependence assumptions are being considered. The AIC_c (Burnham and Anderson 2002) is given by

$$AIC_c = -2\ln L + 2K + \frac{2K(K+1)}{n-K-1} \tag{15}$$

where L is the likelihood function evaluated at its maximum, K is the number of parameters, and n is the number of observations. A better model fit is one with a smaller AIC_c score.

AIC_c weights are often used to provide a measure of the relative support for a model and to conduct model averaging (Hobbs and Hilborn 2006). AIC_c weights are essentially the rescaled likelihood penalized by the number of parameters, which is considered the likelihood for the model (Anderson et al. 2000).

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_j \exp(-0.5\Delta_j)} \tag{16}$$

where Δ is the difference in the AIC_c score from the minimum AIC_c score.

The correct modeling of observation and process variability (error) is important for hypothesis testing. If process variability is not modeled, likelihood ratio and AIC-based tests are biased towards incorrectly accepting covariates (Maunder and Watters 2003). Other tests, such as randomization tests, should be used if it is not possible to model the additional process variability (e.g., Deriso et al. 2008). Incorrect sampling distribution assumptions (e.g., assumed values for the variance) can influence the covariate selection process, and the weighting given to each data set can change which covariates are chosen (Deriso et al. 2007). If data-based estimates of the variance are not available, estimating the variances as model parameters or using concentrated likelihoods is appropriate (Deriso et al. 2007). Missing covariate data need to be dealt with appropriately, such as by using the methods described in Gimenez et al. (2009) and Maunder and Deriso (2010).

Parameter estimation of population dynamics models generally requires iterative methods, which take longer than calculations based on algebraic solutions, and therefore limit the number of models that can be tested (Maunder et al. 2009). This is problematic when testing hypotheses because, arguably, all possible combinations of the covariates and density-dependent possibilities should be evaluated. All possible combinations should be used because a covariate by itself may not significantly explain process variation, but in combination they do (Deriso et al. 2008), and some covariates may only be significant if density dependence is taken into consideration. However, modeling of process variability, as we suggest, may minimize this possibility. In many cases, time and computational resource limitations may prevent testing all possible combinations, and therefore we suggest the strategy described in Table 1.

We stop evaluating covariates when the lowest AIC_c model in the current iteration is at least four AIC_c units higher than the model with the lowest overall AIC_c (step 2e). The approach is based on a compromise between eliminating models for which there is definite, strong, or very strong evidence that the model is not the Kullback–Leibler (K–L) best model ($4 \leq \Delta$) and the fact that there is a maximum Δ when adding

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Table 1. Algorithm for evaluating covariates for the delta smelt (*Hyposmesus transpacificus*) application.

1	Evaluate density dependence.
(a)	Calculate all combinations of density-dependent processes without the inclusion of factors. Combinations include (*i*) density independent; (*ii*) Beverton–Holt; (*iii*) Ricker; and (*iv*) estimate both b and γ. These can be at any of the three stages.
(b)	Choose the density dependence combination that has the lowest AIC_c, or if there are several that have similar support, choose multiple combinations.
2	Evaluate covariates.
(a)	For each density dependence scenario chosen in 1b, run all possible one- and two-covariate combinations.
(b)	For each combination, set the AIC_c weight to zero if the sign is wrong for either of the coefficients in the combination or if the b parameter of a density dependence function is unrealistically high.
(c)	Sum AIC_c weights for a given covariate across all models that include that covariate.
(d)	Select the two covariates with the highest summed AIC_c weights to retain for the next iteration.
(e)	Iterate *a–d* until the AIC_c value of the best model in the current iteration is more than four units higher than the lowest AIC_c model.
3	Double check all included covariates.
(a)	Check confidence intervals of the estimated coefficients for all included covariates to see if they contain zero.
(b)	For all coefficients that contain zero, remove the associated covariate and see if the AIC_c is degraded. If the AIC_c is not degraded, exclude that covariate from the model.

covariates to the lowest AIC_c model. We have chosen to carry out the selection process by using the sum of the AIC_c weights over all models that include the corresponding factor (step 2d). This selection process chooses factors that have high support in general, work in combination with other factors, and are therefore less likely to preclude additional factors in subsequent steps. This approach embraces the multiple hypothesis weight of evidence framework and is somewhat consistent with model averaging. We also remove models for which any of the estimated covariate coefficients are the incorrect sign as assumed a priori (step 2b). Modification of this procedure may be needed depending on the available computational resources, the number of covariates and model stages, and the relative difference in the weight of evidence among models.

Burnham and Anderson (2002) note that in general, there are situations where choosing to make inferences using a model other than the lowest AIC_c model can be justified (their page 330) based on professional judgment, but only after the results of formal selection methods have been presented (their page 334). For example, model parameterizations that do not make sense biologically might be eliminated from consideration. Burnham and Anderson (2002) give an example (their page 197) where a quadratic model is rejected because it could not produce the monotonic increasing dose response that was desired. Sometimes AIC_c will select a model that fits to quirks or noise in the data but does not provide a useful model. The selected best model is a type of estimate, and so like a parameter estimate it can sometimes be a poor estimate (Ken Burnham, Colorado State University, Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, personal communication, 2010).

Parameter estimates from stock–recruitment models in integrated assessments are often biased towards extremely strong density-dependent survival (recruitment is independent of stock size) (Conn et al. 2010), and this is unrealistic for stocks that have obtained very low population sizes. We therefore identify values of the Deriso–Shnute stock–recruitment relationship (for the Beverton–Holt and Ricker special cases) b parameter that are realistic (see Appendix A). We assume that recruitment (or the individuals surviving) cannot be greater than 80% of that expected from the average population size when the population is at 5% of the average population size seen in the surveys during the period studied. Models with unrealistic density dependence are given zero weight in that step of the model selection prodecure (step 2b).

Impact analysis

To determine the impact of the different factors on the stock, we conducted analyses using values of the covariates modified to represent a desired (e.g., null) effect. Following Deriso et al. (2008), these analyses were conducted simultaneously within the code of the original analyses so that the impact assessments shared all parameter values with the original analyses. This allowed estimation of uncertainty in the difference between the models with the covariate included and with the desired values of the covariate. The results are then compared for the quantities of interest, which may be a derived quantity other than the covariate's coefficients. For example, if a covariate is related to some form of mortality, the coefficient is set to zero to determine what the abundance would have been in the absence of that mortality (e.g., Wang et al. 2009).

Application to delta smelt

The multistage life cycle model is applied to delta smelt to illustrate the application of the model, covariate selection procedure, and impact analysis. Delta smelt effectively live for 1 year and one spawning season. Some adults do survive to spawn a second year, but the proportion is low (Bennett 2005) and we ignore them in this illustration of the modeling approach. The delta smelt life cycle is broken into three stages (Fig. 1). The model stages are associated with the timing of the three main surveys, (*i*) 20 mm trawl (20 mm), (*ii*) summer tow net (STN), and (*iii*) fall midwater tow (FMWT), and roughly correspond to the life stages larvae, juveniles, and adults, respectively. The reason for associating the model stages with the surveys is because the surveys are the only data used in the model, and therefore information is only available on processes operating between the surveys. The population is modeled from 1972 to 2006 because these are the years for which data for most of the factors are available. The STN abundance index is available for the whole

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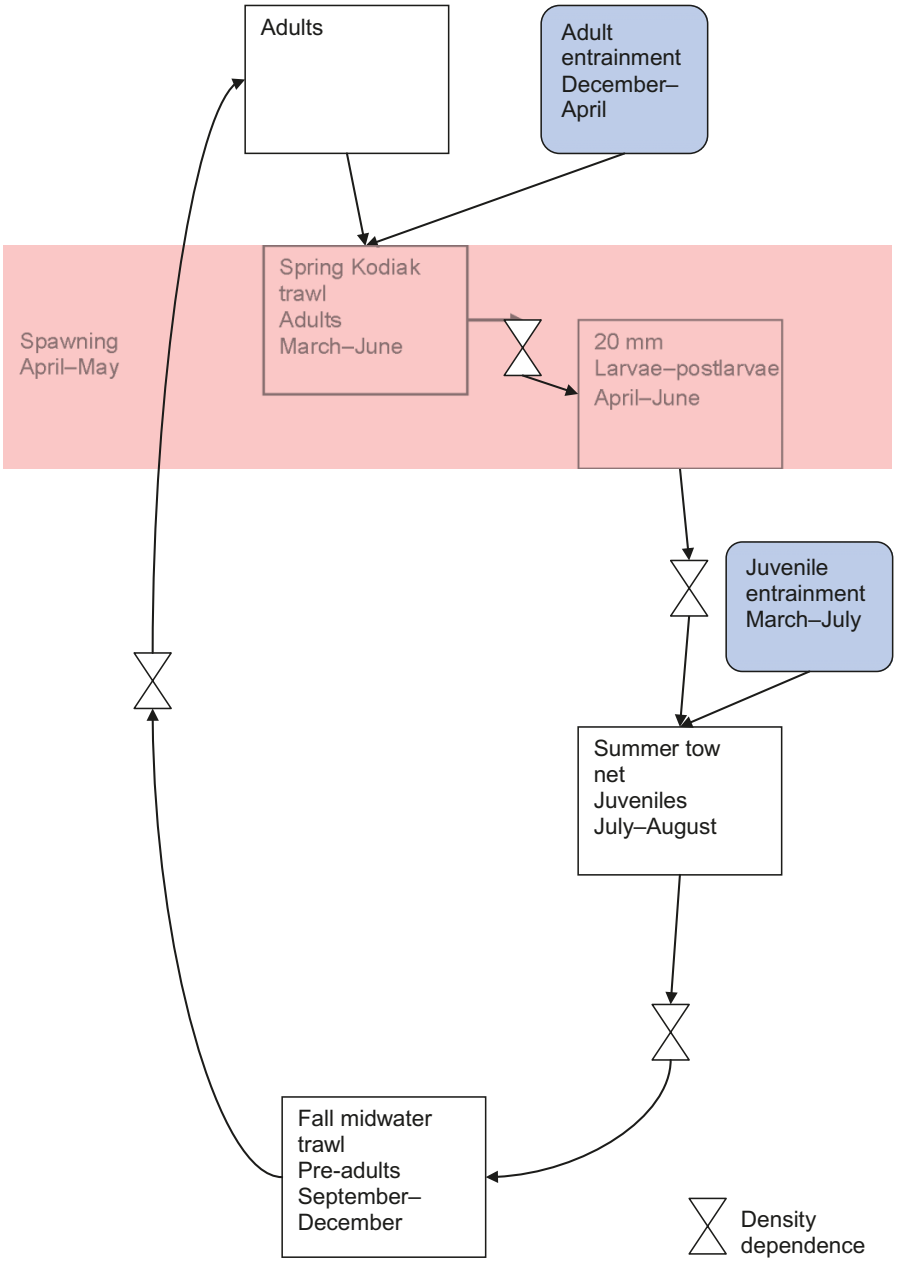
Fig. 1. Life cycle diagram of delta smelt (*Hyposmesus transpacificus*) with survey, entrainment, and density dependence timing.



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time period. The FMWT abundance index is available for the whole time period except for 1974 and 1979. The 20 mm abundance index is only available starting in 1995. Other survey data are available (e.g., the spring Kodiak trawl survey), but they are not used in this analysis.

The FMWT and STN survey indices of abundance are the estimates taken from Manly (2010*b*, tables 2.1 and 2.2). The standard errors were calculated by bootstrap procedures (Manly 2010*a*). The 20 mm survey index was taken from Nations (2007). The index values and standard errors are given in the supplementary material[1]. The results of the bootstrap analysis suggest that the abundance indices are normally distributed (Manly 2010*a*).

Two types of factors are used in the model (Table 2). The first are standard factors relating to environmental conditions. The second are mortality rates based on estimates of entrainment at the water pumps. The mortality rates are converted to the appropriate scale to use in the model. Let u represent the mortality fraction such that the survival fraction is $1 - \mu = \exp(\beta x)$, and x will be used as a covariate in the model. Setting $\beta = 1$ gives $x = \ln(1 - \mu)$.

Several factors were chosen for inclusion in the model (Table 3). These factors are used for illustrative purposes only, and they may differ in a more rigorous investigation of the factors influencing delta smelt. The environmental factors are taken as those proposed by Manly (2010*b*). The entrainment mortality rates are calculated based on Kimmerer (2008); the rates were obtained by fitting a piecewise linear

[1]Supplementary data are available with the article through the journal Web site (http://www.nrcresearchpress.com/cjfas).

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Table 2. The variables used as candidates to account for the changes in delta smelt abundance.

Factor	Name	Covariate	Stage	Before–After	Sign	Description	Data scaling	Justification
1	SpDys	1	A	Before	+	Days where temperature is in the range 11–20 °C	Norm	This measures the number of days of spawning — the longer the spawning season, presumably the better chance of survival
2	TpAJ	2	L	Before	– or +	Average water temperature in delta smelt habitat for April–June	Norm	Temperature affects growth rate and survival of early life stages
3	TpAJ	2	A	After	– or +			
4	TpJul	3	L	After	–	Average water temperature in delta smelt habitat for July	Norm	Higher water temperatures can be lethal; could also include August temperature
5	EPAJ	4	L	Before	+	Minimum eurytemora and pseudodiaptomus density for April–June	Norm	Measures height of food "gap" in spring, as eurytemora falls from spring maximum and pseudodiaptomus rises from ~0
6	EPAJ	4	A	After	+			
7	EPJul	5	L	After	+	Average eurytemora and pseudodiaptomus density for July	Norm	Measures food availability in summer until summer tow net survey, identified as problem by Bennett (2005) based on smelt condition
8	Pred1	6	J	After	–	September–December abundance of other predators	Mean	Predation is a source of direct mortality, measured as the product of relative density from beach seine data with the square of average Secchi depth
9	Pred1	6	A	Before	–			
10	Pred1	6	A	After	–			
11	StBass	7	J	After	–	September–December abundance of striped bass	Mean	A major predator, whose abundance is measured as actual number of adults
12	StBass	7	A	Before	–			
13	StBass	7	A	After	–			
14	DSLth	8	L	After	+	Delta smelt average length	Norm	See Bennett (2005) for length vs. fecundity relationship, linear for 1-year-olds
15	DSLth	8	J	After	+			
16	DSLth	8	A	After	+			
17	TpJS	9	J	After	–	Maximum 2-week average temperature for July–September	Norm	Measure of whether lethal temperature is reached in hot months
18	EPJA	10	J	After	+	Average eurytemora and pseudodiaptomus density for July–August	Norm	Measures food availability in summer between STN and FMWT surveys, identified as problem by Bennett (2005) based on smelt condition
19	Secchi	11	A	Before	–	January–February weighted Secchi depth	Norm	Protection from predators
20	Secchi	11	A	After	–			
21	Jent	12	L	After	+*	Juvenile entrainment	Raw	Entrained in by water pumps
22	Aent	13	A	Before	+*	Adult entrainment	Raw	Entrained in by water pumps
23	Pred2	14	L	Before	–	April–June abundance of other predators	Mean	Predation is a source of direct mortality, measured as the product of relative density from beach seine data with the square of average Secchi depth
24	Pred2	14	A	After	–			

Note: A = occurs between adult and larval stages; L = occurs between larval and juvenile stages; J = occurs between juvenile and adult stages; Norm = subtract mean and divide by standard deviation; Mean = divide by mean; Raw = not scaled. The covariate is attributed to after density dependence unless it is known to occur before density dependence. This is because density dependence generally reduces the influence of the covariate.

*The effect of entrainment on survival is negative, but the covariate is formulated so setting the coefficient to 1 implies the assumption that entrainment is known without error, so the coefficient should be positive.

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Table 3. AIC_c weights for all possible density dependence models without covariates.

		J–No	J–BH	J–R	J–DD	Sum
L–No	A–No	0.000	0.079	0.062	0.027	0.168
	A–BH	0.000	0.075	0.067	0.026	0.168
	A–R	0.000	0.059	0.052	0.020	0.131
	A–DD	0.000	0.069	0.064	0.023	0.156
	Sum	0.000	0.281	0.245	0.096	0.622
L–BH	A–No	0.000	0.022	0.017	0.007	0.047
	A–BH	0.000	0.020	0.018	0.007	0.045
	A–R	0.000	0.016	0.014	0.005	0.035
	A–DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L–R	A–No	0.000	0.022	0.017	0.007	0.047
	A–BH	0.000	0.020	0.018	0.007	0.045
	A–R	0.000	0.016	0.014	0.005	0.035
	A–DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L–DD	A–No	0.000	0.006	0.005	0.002	0.013
	A–BH	0.000	0.005	0.005	0.002	0.012
	A–R	0.000	0.004	0.004	0.001	0.009
	A–DD	0.000	0.004	0.004	0.001	0.010
	Sum	0.000	0.020	0.017	0.006	0.043

Note: L = survival from larvae to juveniles; J = survival from juveniles to larvae; A = the stock–recruitment relationship from adults to larvae; No = no density dependence; BH = Beverton–Holt density dependence; R = Ricker density dependence; DD = Deriso–Schnute density dependence (i.e., estimate γ).

regression model of winter Old Middle River flow to his adult entrainment estimates and his larval–juvenile entrainment estimates were fitted to a multiple linear regression model with spring Old Middle River flow and spring low salinity zone (as measured by X). The values from Kimmerer (2008) were used for years in which they are available, and the linear regression predictions were used for the remaining years. Manly (2010*b*) provided several variables as candidates to account for the changes in delta smelt abundance from fall to summer and summer to fall. The fall to summer covariates could influence the adult and larvae stages, while the summer to fall covariates could influence the juvenile stage. The factors proposed by Manly (2010*b*) are those that are considered to act directly on delta smelt. There are many other proposed factors that act indirectly through these factors. We also include Secchi disc depth as a covariate for water turbidity–clarity, since it was identified as a factor by Thomson et al. (2010). Exports were also identified as an important factor and were assumed to be related to entrainment. However, we chose to use direct measures of entrainment. Interactions among the factors were not considered in the application. However, some of the covariates implicitly include interactions in their definition and construction.

Some manipulation of the data was carried out before use in the model (the untransformed covariate values used in the model are given in the supplementary material[1]). Delta smelt average length was missing for 1972–1974, 1976, and 1979 and was set to the mean based on Maunder and Deriso (2010). The factors were normalized (mean subtracted and divided by standard deviation) to improve model performance, except for the covariates relating to predator abundance, which were just divided by the mean, and the entrainment mortality rates, which were not transformed. These exceptions are factors that are hypothesized to have a unidirectional impact, and setting their coefficients to zero is needed for impact analysis. Setting the coefficient for the entrainment mortality rate covariates to one can be used to determine the impact if the entrainment estimates are assumed to be correct.

The standard approach outlined above and in Table 1 is applied to the delta smelt application. The Ricker model was approximated by setting $\gamma = -\exp(-10)$. We also constrained $\gamma < 0$ to avoid computational errors. It is difficult to scale the survey data to absolute abundance, so they are all treated as relative abundance and are not on the same scale. The scaling parameter a is not limited to $a \leq 1$, and the exponential model is used for all covariates. To illustrate the impact analysis, we implement three scenarios. In the first scenario, the covariates are all set to zero. This means that environmental conditions are average, predation is zero, and entrainment is zero. We implement the second scenario if one or both of the entrainment covariates are selected for inclusion in the model. In this case, only the entrainment coefficients are set to zero. In the third scenario, we take the final set of covariates and add the entrainment covariates (or substitute them if they were already included in the model) with their coefficients set to one and rerun the model. In this case, only the entrainment coefficients are set to zero in the impact analysis.

Results

AIC_c values and weights were calculated for all possible combinations of density dependence that included no density dependence (No), a Beverton–Holt model (BH), a Ricker model (R), and estimation of both b and γ (DD) (Table 3). Density dependence was clearly preferred for survival from juveniles to adults (J), but it is not clear if the density dependence is Beverton–Holt, Ricker, or somewhere in between. The Beverton–Holt and Ricker models for juvenile survival appear to be influenced by three consecutive data points (years 1976–1978) of high juvenile abundance with corresponding average adult abundance (Figs. 2 and 3). The evidence for and against density dependence is about the same for the stock–recruitment relationship from adults to larvae (A), with slightly more evidence for no density dependence if survival from juveniles to adults is Beverton–Holt and slightly more evidence for Beverton–Holt density dependence if the survival from juveniles to adults is Ricker. The evidence for no density dependence in survival from larvae to juveniles (L) is moderately (three to four times) higher than that for density dependence. Therefore, we proceed with four density dependence scenarios: (*i*) Beverton–Holt density dependence in survival from juveniles to adults (JBH); (*ii*) Beverton–Holt density dependence in survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship from adults to larvae (JBHABH); (*iii*) Ricker density dependence in survival from juveniles to adults (JR); and (*iv*) Ricker density dependence in survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship from adults to larvae (JRABH).

The number and the type of factors supported by the data

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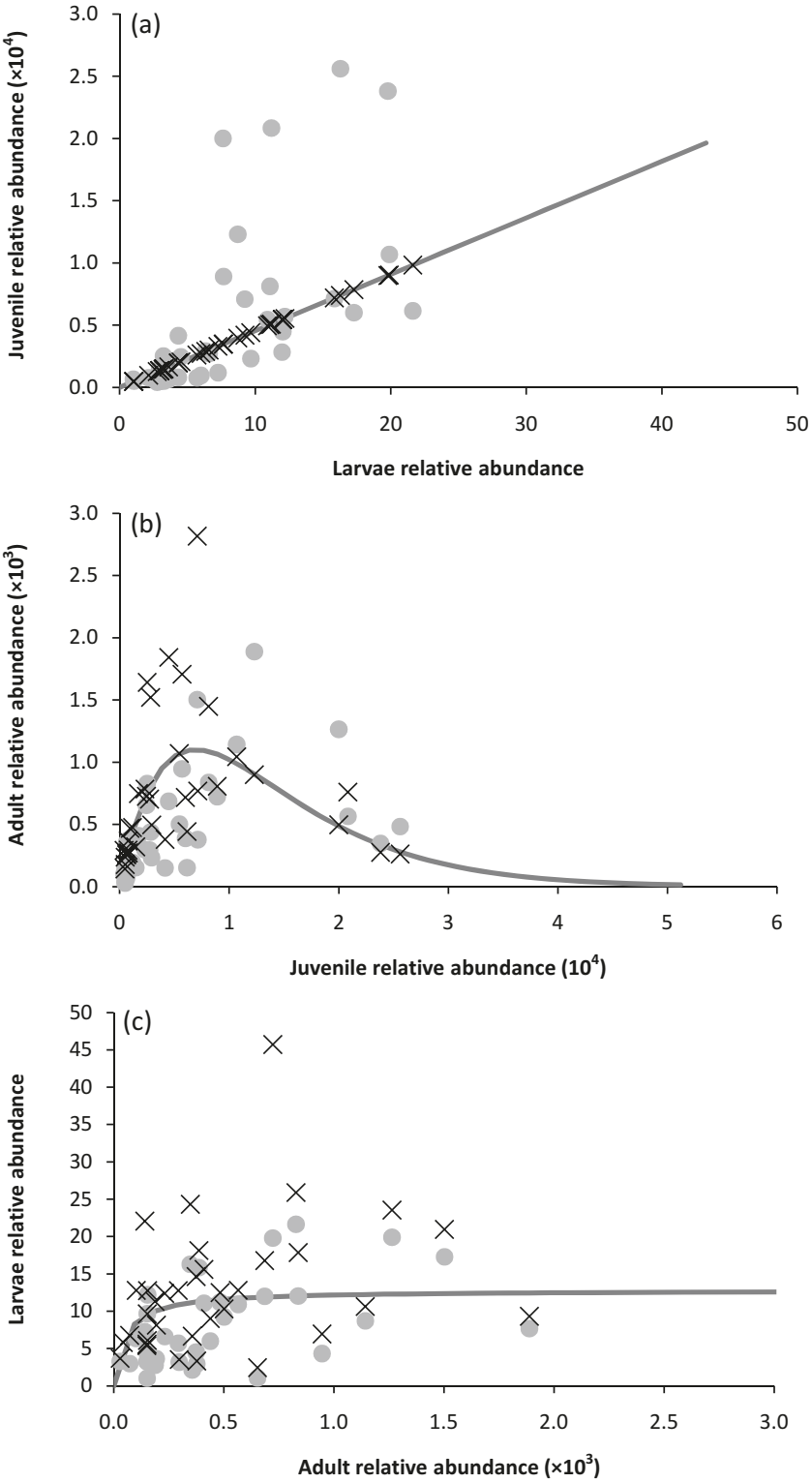
Fig. 2. Relationship among stages in the model for the lowest AIC_c model that has Ricker survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship. Points are the model estimates of abundance, lines are the estimates from the stock–recruitment models without covariates or process variation, crosses are the estimates without covariates.



depended on the assumptions made about density dependence (Tables 4 and 5). The models with density dependence for both survival from juveniles to adults and a stock–recruitment relationship for adults to larvae included more covariates in the lowest AIC_c models (eight and nine covariates for Beverton–Holt and Ricker density dependence in survival from juveniles to adults, respectively) than the models that included only density dependence for survival from juveniles to adults (five covariates each). Several temperature, prey, and predator covariates (TpAJ, EPAJ, EPJA, TpJul,

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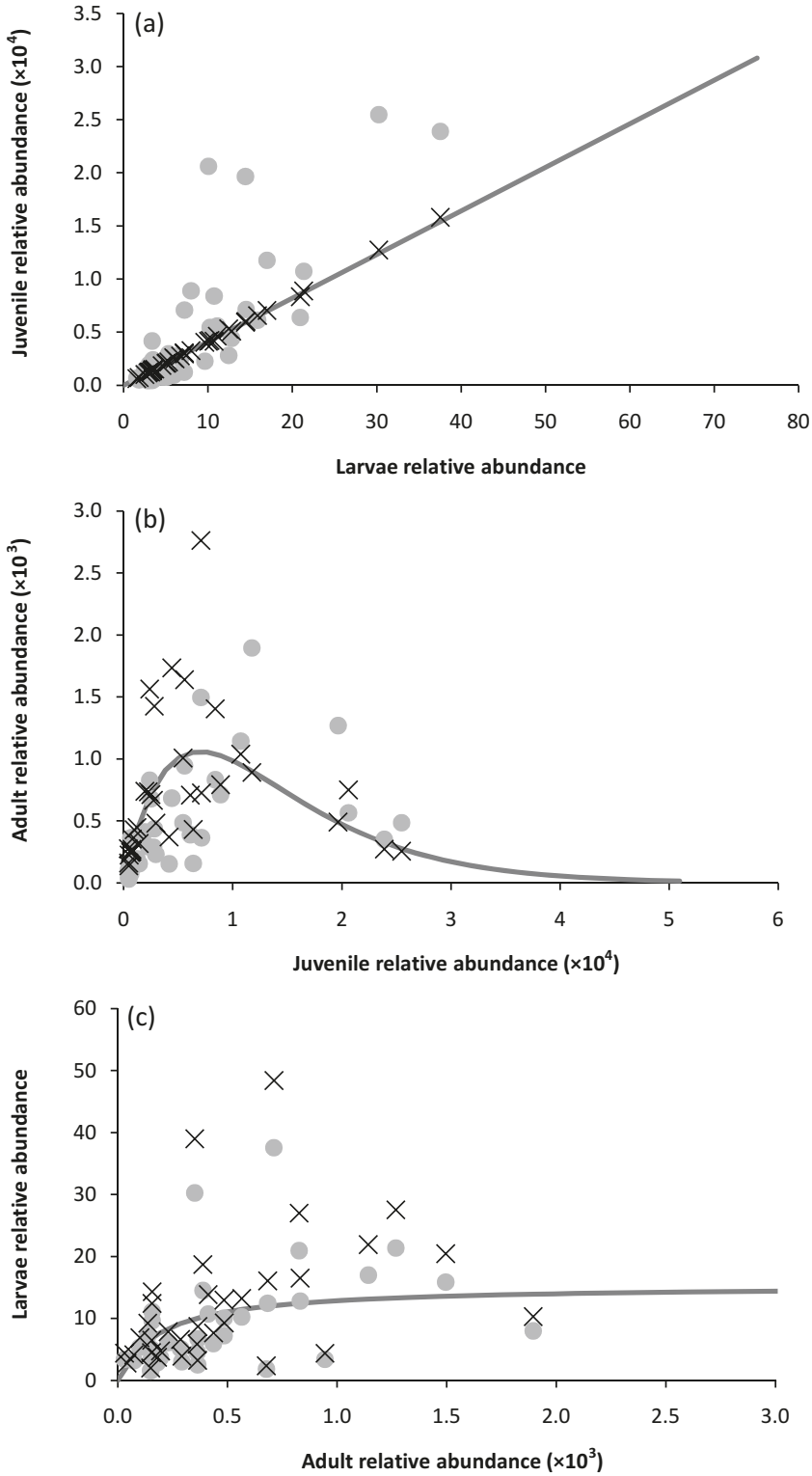
Fig. 3. Relationship among stages in the alternative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model). Points are the model estimates of abundance, lines are the estimates from the stock–recruitment models without covariates or process variation, crosses are the estimates without covariates.



Pred1) were selected in the first few steps and were included in all models. The April–June abundance of predators (Pred2) was selected in the first few steps in one model, but not selected at all in the others.

Overall, the model with Ricker density dependence in survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship from adults to larvae had better AIC_c scores than the other models (Table 5). This differs from the similarity in scores obtained when no covariates were included in the models (Table 3). For all density-

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Table 4. Order of inclusion of factors into the analysis.

Factor	Name	Stage	Before–After	JBH	JBHABH	JR	JRABH
2	TpAJ	L	Before	1	1	2	2
4	TpJul	L	After	2	2	2	3
5	EPAJ	L	Before	1	1	1	1
7	EPJul	L	After	—	4	—	5
8	Pred1	J	After	2	2	3	3
18	EPJA	J	After	3	3	1	2
19	Secchi	A	Before	—	3	—	4
22	Aent	A	Before	—	4	—	4
23	Pred2	L	Before	—	—	—	1*

Note: JBH = Beverton–Holt density dependence from the juvenile (J) to adult (A) stage; JBHABH = Beverton–Holt density dependence from the juvenile to adult stage and Beverton–Holt density dependence from the adult to larvae (L) stage (the stock–recruitment relationship); JR = Ricker density dependence from the juvenile to adult stage; JRBH = Ricker density dependence from the juvenile to adult stage and Beverton–Holt density dependence from the adult to larvae stage (the stock–recruitment relationship). See Tables 2 and 3 for definitions.

*This covariate was excluded from the final model because the confidence interval of its coefficient included zero and including the covariate degraded the AIC_c.

dependent assumptions, there were alternatives with more (or less) covariates than the lowest AIC_c model (within the models for that density dependence assumption), for which there was not definite, strong, or very strong evidence that the model is not the K–L best model ($4 \leq \Delta$), suggesting that these factors should also be considered as possible factors that influence the population dynamics of delta smelt (Table 5). However, the asymmetrical nature of the AIC_c scores for nested models should be kept in mind.

The magnitude and the sign of the covariate coefficients are generally consistent across models (Table 6). The covariates were standardized so that the size of the coefficients are generally comparable across covariates. The coefficients are similar magnitudes for most covariates except those for water clarity (Secchi) and, particularly, adult entrainment (Aent), which had much larger effects. These both occurred before the stock–recruitment relationship from adults to larvae, which had a very strong density dependence effect. Pred2 had a small effect. The confidence intervals on the coefficients support inclusion of the covariates in the lowest AIC_c models except for Pred2 (Table 6). The effects for Secchi and Aent appear to be unrealistically large, and their coefficients have a moderately high negative correlation. This appears to be a consequence of the unrealistically strong density dependence estimated in the stock–recruitment relationship from adults to larvae for those models (see Supplemental Table S6 online[1]).

The five lowest AIC_c models in iteration 6 of the two factors at a time procedure had a *b* parameter of the Beverton–Holt stock–recruitment relationship from adult to larvae that was substantially greater than the critical value used to define realistic values of the parameter. The sixth model had an AIC of 812.53, which is worse than the lowest AIC_c model of iteration 5. The lowest AIC_c model with Beverton–Holt survival from juveniles to adults and Beverton–Holt stock–recruitment relationship from adult to larvae also had an unrealistic *b* parameter, and the next lowest AIC_c model had an AIC of 812.33. Therefore, the lowest AIC_c model after accounting for realistic parameter values is the lowest AIC_c model from iteration 5 with Ricker survival from juveniles to adults and Beverton–Holt stock–recruitment relationship from adult to larvae with one additional covariate (Table 5, $AIC_c = 808.47$). The confidence intervals for the Pred2 covariate for this model contained zero and removing the Pred2 covariate essentially had no effect on the likelihood. Therefore, we chose this model without the Pred2 covariate as the lowest AIC_c model ($AIC_c = 806.63$). Several models had an AIC_c score within two units of this model; according to the Burnham and Anderson (1998, p. 128) guidelines, "there is no credible evidence that the model should be ruled out". Therefore, to illustrate the sensitivity of results to the model choice, we also provide results for the model with the fewest parameters that was within two AIC_c units of the lowest AIC_c model. This alternative model is that selected with two additional parameters in iteration 3 of the selection procedure (Table 5, $AIC_c = 810.20$). Removing the Pred2 covariate improved the AIC_c score (808.63), so we also eliminated the Pred2 covariate from this model.

The models fit the survey data well (Figs. 4 and 5), in fact better than expected from the survey standard errors, indicating that most of the variation in abundance was modeled by the covariates or unexplained process variability. The unexplained process variability differed among the stages (Fig. 6; Table 7). Essentially all the variability in survival between larvae and juveniles was explained by the covariates. The amount of variability explained in the survival from juveniles to adults was higher than that in the stock–recruitment relationship, but they show similar patterns (Fig. 6; Table 7).

There was substantial correlation among estimated parameters (see supplementary material[1]). The lowest AIC model has moderate and high correlation between the covariate coefficients and several model parameters and also among the covariate coefficients themselves (Supplemental Table S6[1]). The alternative model has fewer parameter correlations (Supplemental Table S7[1]). The parameters of the density dependence function were highly positively correlated. The relative number of larvae in the first year is negatively correlated with parameters influencing larval survival, including the survival fraction at low abundance (*a*), the standard deviation of the process variability, and the prey covariate coefficients. The coefficients for the prey and temperature covariates influencing larval survival are correlated. This is partly related

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Table 5. AIC_c values for each step in the model selection process.

	Step 1		Step 2		Step 3		Step 4		Step 5		Step 6		Step 7	
	Covar1	Covar2	Covar1	Covar2	Covar1	Covar2	Covar1	Covar2	Covar1	Covar2	Covar1	Covar2	Covar1	Covar2
JBH	841.06	833.44	827.58	824.00	823.01	823.30	824.61	825.95	828.28	831.08	—	—	—	—
JBHABH	832.46	824.68	818.25	815.18	813.92	814.32	814.17	811.85	812.33	814.75	—	—	—	—
JR	841.80	833.67	826.25	821.40	820.00	821.10	822.58	823.71	826.26	828.86	—	—	—	—
JRBH	833.16	824.93	817.96	814.72	811.60	810.20	810.72	810.38	808.47	809.23	810.86	813.39	817.03	820.83

Note: Shaded values are the lowest AIC_c for that density dependence configuration. See Table 4 for definitions.

to the fact that some of these covariates are also correlated (Supplemental Table S5[1]). The coefficients for water clarity (Secchi) and adult entrainment (Aent) in the lowest AIC model were highly negatively correlated and were correlated with the parameters of the density dependence survival function that relates adults and larvae. The coefficient for Aent is also unrealistically large. The coefficient for Pred1 is correlated with the parameters of the density dependence relationship for juvenile survival and is also highly positively correlated with year. The coefficient for EPJA is positively correlated with the parameter that controls density dependence for juvenile survival. The coefficient for EPJul in the lowest AIC model is correlated with several parameters.

The impact analysis of the selected covariates shows that the adult abundance under average conditions, with no predators and entrainment mortality set to zero, differs moderately from that estimated in the original model (Fig. 7). In particular, the recent decline is not as substantial under average conditions, indicating that the covariates describe some of the decline, although there is still substantial unexplained variation and a large amount of uncertainty in the recent abundance estimates. Entrainment is estimated to have only a small impact on the adult abundance in either the lowest AIC_c model, which uses the estimated adult entrainment coefficient and the juvenile entrainment coefficient is zero, or the alternative model, in which both the juvenile and adult entrainment coefficients are set to one (Fig. 8). The lowest AIC_c model with the two entrainment coefficients set at one did not converge, and results are not shown for that analysis, although the results are expected to be similar.

Discussion

We developed a state–space multistage life cycle model to evaluate population impacts in the presence of density dependence. Application to delta smelt detected strong evidence for a few key factors and density dependence operating on the population. Both environmental factors (e.g., Deriso et al. 2008) and density dependence (e.g., Brook and Bradshaw 2006) have been detected in a multitude of studies either independently or in combination (e.g., Sæther 1997; Ciannelli et al. 2004). Brook and Bradshaw (2006) used long-term abundance data for 1198 species to show that density dependence was a pervasive feature of population dynamics that holds across a range of taxa. However, the data they used did not allow them to identify what life stages the density dependence operates on. Ciannelli et al. (2004) found density dependence in different stages of walleye pollock (*Theragra chalcogramma*). In our application, we found evidence against density-dependent survival from larvae to juveniles, strong evidence for density dependence in survival from juveniles to adults, and weak evidence for density dependence in the stock–recruitment relationship from adults to larvae, which includes egg and early larval survival. Other studies have suggested that density dependence is more predominant at earlier life stages (e.g., Fowler 1987; Gaillard et al. 1998), although the life history of these species differs substantially from delta smelt. The density dependence in survival from juveniles to adults found in our study was probably heavily influenced by three consecutive years of data. Unfortunately, this is a common occurrence in which

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Table 6. Estimates of coefficients (and 95% confidence intervals) from the lowest AIC_c models for each density dependence assumption.

Factor	Name	Stage	B–A	JBH	JBHABH	JR	JRABH	JRABH, no Pred2	Alternative
2	TpAJ	L	B	–0.32 (–0.46, –0.18)	–0.21 (–0.36, –0.07)	–0.32 (–0.45, –0.19)	–0.20 (–0.34, –0.06)	–0.22 (–0.36, –0.09)	–0.31 (–0.44, –0.18)
4	TpJul	L	A	–0.29 (–0.50, –0.08)	–0.30 (–0.49, –0.12)	–0.28 (–0.49, –0.07)	–0.28 (–0.47, –0.09)	–0.32 (–0.50, –0.13)	–0.30 (–0.50, –0.11)
5	EPAJ	L	B	0.39 (0.15, 0.63)	0.40 (0.18, 0.62)	0.37 (0.13, 0.61)	0.32 (0.09, 0.55)	0.36 (0.14, 0.58)	0.47 (0.23, 0.71)
7	EPJul	L	A		0.32 (0.07, 0.58)		0.31 (0.05, 0.56)	0.33 (0.07, 0.59)	
8	Pred1	J	A	–0.45 (–0.84, –0.06)	–0.49 (–0.90, –0.08)	–0.37 (–0.71, –0.03)	–0.42 (–0.77, –0.07)	–0.44 (–0.78, –0.09)	–0.40 (–0.75, –0.05)
18	EPJA	J	A	0.21 (0.00, 0.42)	0.22 (0.00, 0.45)	0.44 (0.21, 0.66)	0.46 (0.22, 0.69)	0.46 (0.22, 0.69)	0.46 (0.23, 0.69)
19	Secchi	A	B		–1.08 (–1.97, –0.19)		–1.24 (–2.27, –0.22)	–1.15 (–2.11, –0.20)	
22	Aent	A	B		9.50 (0.62, 18.38)		10.97 (0.93, 21.01)	10.32 (0.99, 19.65)	
23	Pred2	L	B				–0.19 (–0.52, 0.13)		
	a	L		396 (334, 458)	451 (373, 529)	396 (337, 456)	593 (307, 879)	454 (376, 532)	410 (340, 481)
	a	J		0.74 (0.01, 1.48)	0.77 (–0.02, 1.56)	0.39 (0.18, 0.6)	0.42 (0.19, 0.65)	0.43 (0.2, 0.66)	0.41 (0.19, 0.63)
	a	A		0.03 (0.02, 0.04)	0.2 (–0.13, 0.53)	0.03 (0.02, 0.04)	0.27 (–0.24, 0.78)	0.25 (–0.18, 0.67)	0.08 (0, 0.16)
	b	L		0	0	0	0	0	0
	b ($\times 10^{-4}$)	J		8.38 (–0.19, 16.95)	7.95 (–0.57, 16.48)	1.43 (1.01, 1.84)	1.42 (1.01, 1.84)	1.44 (1.02, 1.85)	1.43 (1.01, 1.84)
	b ($\times 10^{-2}$)	A		0	1.48 (–1.41, 4.38)	0	2.35 (–2.77, 7.47)	1.93 (–1.96, 5.81)	0.52 (–0.34, 1.39)
	γ	L							
	γ	J		–1	–1	0	0	0	0
	γ	A			–1		–1	–1	–1
	σ	L		0.07 (–0.32, 0.45)	0 (–0.35, 0.35)	0.04 (–0.5, 0.59)	0 (–0.35, 0.35)	0 (–0.26, 0.26)	0.1 (–0.2, 0.39)
	σ	J		0.52 (0.36, 0.67)	0.55 (0.39, 0.71)	0.46 (0.31, 0.6)	0.48 (0.32, 0.63)	0.48 (0.32, 0.63)	0.47 (0.32, 0.62)
	σ	A		0.79 (0.57, 1.01)	0.61 (0.45, 0.77)	0.82 (0.59, 1.04)	0.61 (0.45, 0.77)	0.62 (0.46, 0.78)	0.71 (0.52, 0.9)
	$h_{0.05}$	L		1	1	1	1	1	1
	$h_{0.05}$	J		0.24 (0.09, 0.4)	0.24 (0.08, 0.4)	0.11 (0.09, 0.14)	0.11 (0.09, 0.14)	0.12 (0.09, 0.14)	0.11 (0.09, 0.14)
	$h_{0.05}$	A		1	0.29 (–0.06, 0.64)	1	0.38 (–0.09, 0.85)	0.34 (–0.07, 0.75)	0.15 (0, 0.3)

Note: Definitions of abbreviations and a description of the covariates can be found in Table 2 and the density dependence configurations in Table 4; B–A, before–after. The alternative model is the model that has the fewest covariates and the AIC_c is less than two AIC_c units greater than the lowest AIC_c model.

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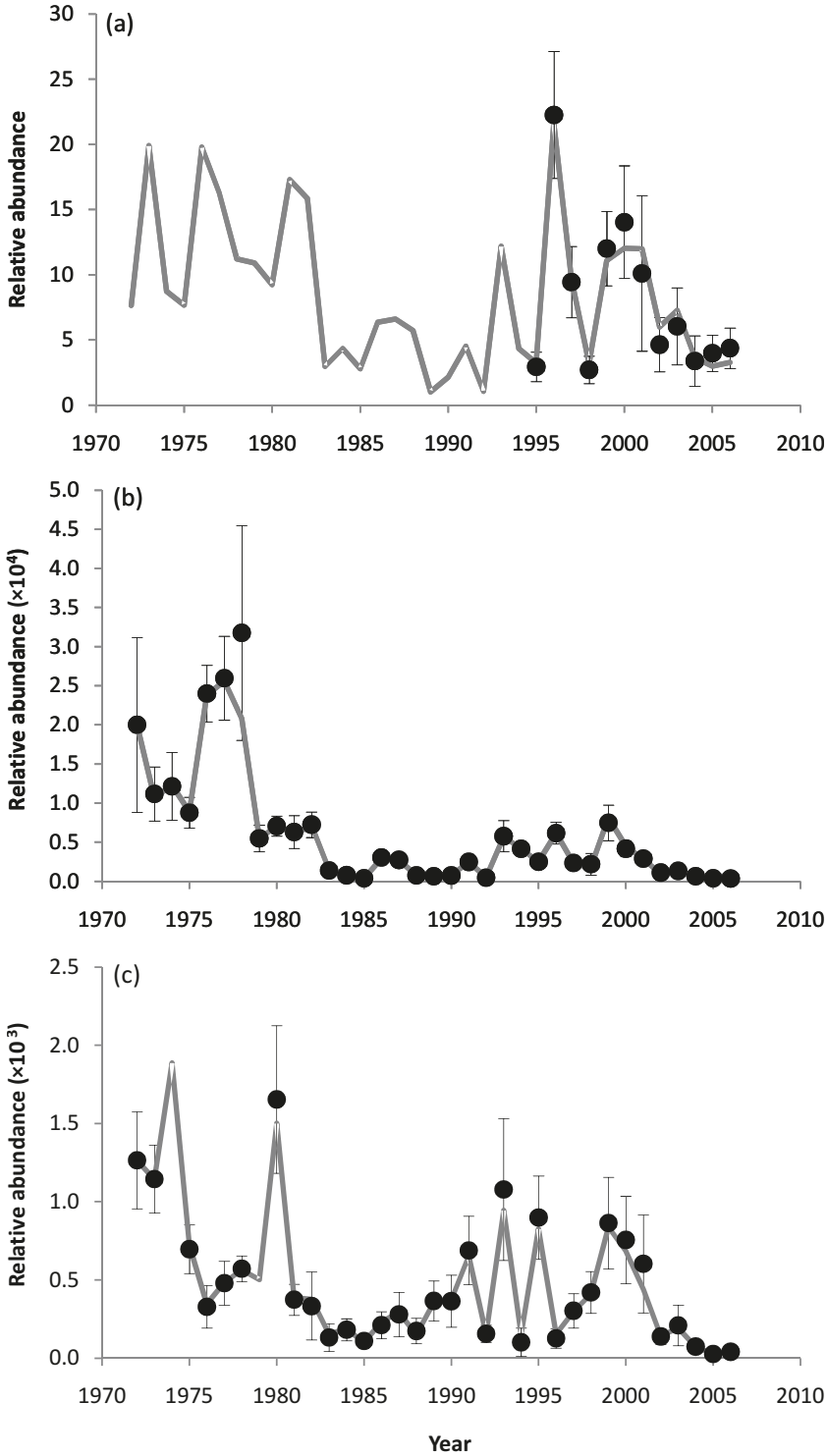
Fig. 4. Fit (line) to the survey abundance data (circles) for the lowest AIC_c model that includes Ricker survival between juveniles and adults and a Beverton–Holt stock–recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.



autocorrelated environmental factors cause autocorrelation in abundance within a stage, and this likely influences other studies as well. We only allowed factors to influence density-independent survival, either before or after density dependence; however, the factors could also influence the strength or form of the density dependence (Walters 1987). For example, Ciannelli et al. (2004) found that high wind speed induced negative density dependence in the survival of walleye pollock eggs. Our analysis is one of the few, but expanding, applications investigating both density-dependent and density-independent factors in a rigorous statistical framework that integrates multiple data sets within a life cycle model. The framework amalgamates the density and the mechanistic paradigms of investigating population regula-

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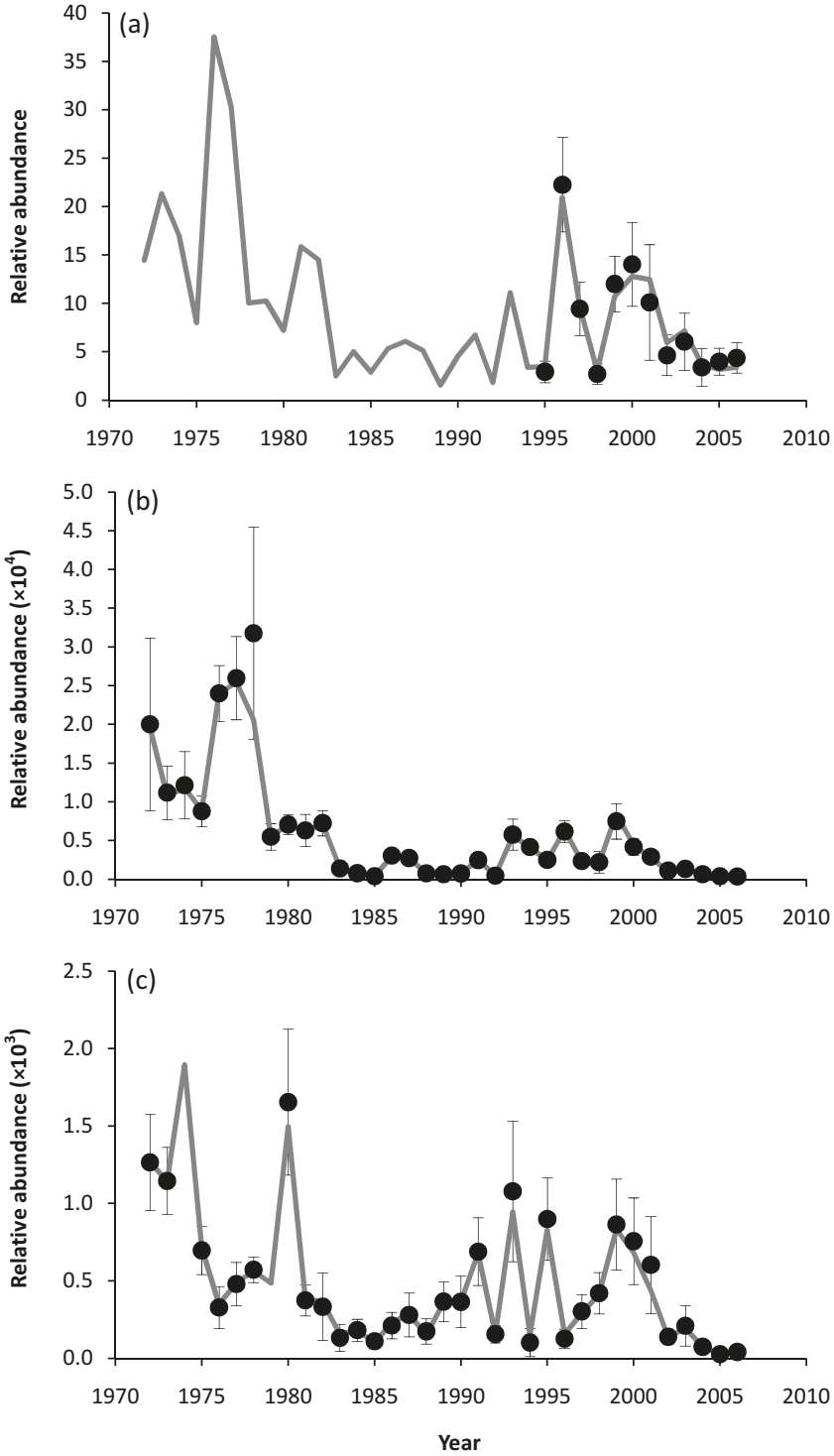
Fig. 5. Fit (line) to the survey abundance data (circles) for the alternative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model) that includes Ricker survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.



tion outlined by Krebs (2002) while accommodating the fact that most available data is observational rather than experimental. More detailed mechanistic processes could be included in the model if the appropriate observational or experimental data are available.

One factor is often erroneously singled out as the only major cause of population decline (e.g., overfishing; Sibert et al. 2006). However, there is a substantial accumulation of evidence that multiple factors interact to cause population declines. Our analysis found support for a variety of factors that influence delta smelt population dynamics. We also showed that together these factors explain the decline in the

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Fig. 6. Estimates of the realizations of the process variation random effects ($\exp\left(\sigma_s \varepsilon_{t,s} - 0.5\sigma_s^2\right)$) for the lowest AIC_c model that includes Ricker survival between juveniles and adults and a Beverton–Holt stock–recruitment relationship (*a*) and the alternative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model) (*b*).

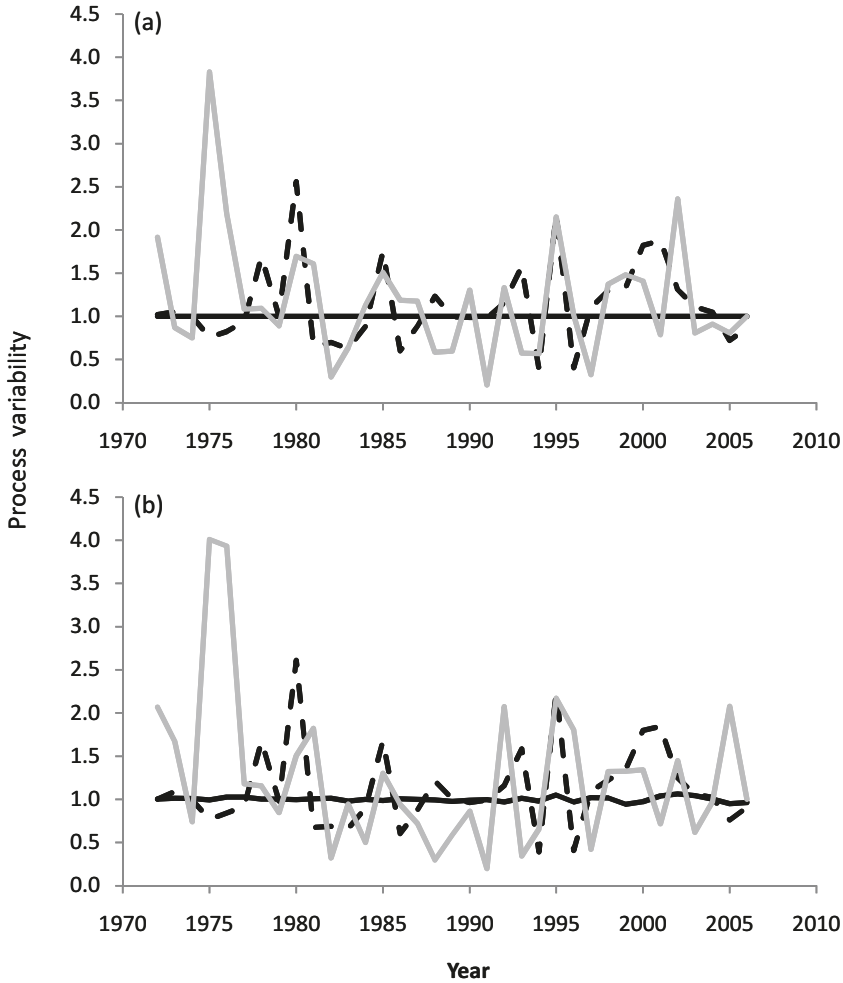

Table 7. Estimates of standard deviation of the process variation and the percentage of the process variation explained by the covariates for the lowest AIC_c model.

	Standard deviation		
	Without covariates	With covariates	% variation explained
Larvae	0.72	0.00	100
Juvenile	0.63	0.48	43
Adult	0.71	0.62	24

delta smelt population. Deriso et al. (2008) also found support that multiple factors influenced the decline and suppression of the Prince William Sound herring (*Clupea pallasii*) population, including one or more unidentified factors related to a particular year.

Three of the first four factors included in the delta smelt application acted on the survival between larvae and juveniles. This is also the period where no density dependence in survival occurred. The final model estimates that the factors explain all the variability in survival from larvae to juveniles. The 20 mm trawl survey, which provides information on juvenile abundance, only starts in 1995 so there is less data to explain, and this may be partly why the unexplained process variability variance goes to zero. The process variability for the other stages may partly absorb the variability in survival from larvae to juveniles.

Deriso et al. (2008) showed that multiple factors influence populations and that analysis of factors in isolation can be misleading. We also found that multiple factors influence the dynamics of delta smelt and that evaluating factors in isolation can produce different results than evaluating them in combination. The type of density dependence assumed also impacted what factors were selected. Specifically, one predator covariate (Pred2) would be the first selected covariate based simply on AIC_c for two of the density-dependent assumptions, but was not selected by the two-factor stepwise procedure (see supplementary material[1]). However, this covariate was selected in the first step of the two-factor stepwise procedure for another density-dependent assumption, which happened to be the final model with the lowest AIC_c. In the final model the confidence intervals on the coefficient indicate that this factor should not be included in the model. Exploratory analysis showed that this covariate had about a 0.6 correlation with a temperature (TpAJ) and a prey (EPAJ) covariate that were consistently selected in the first or seconds steps, which operated on the same stage (larvae), when these

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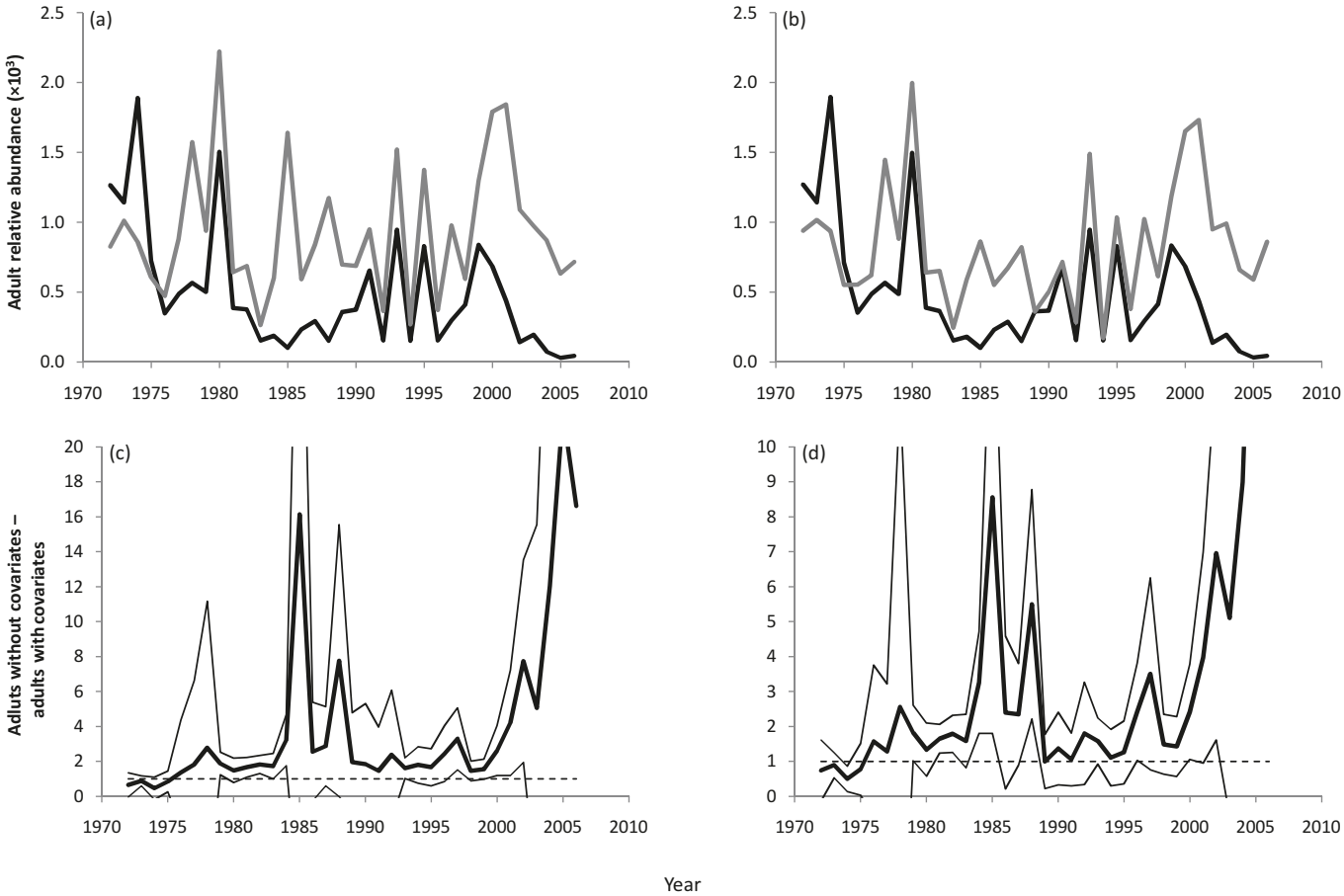
Fig. 7. Estimates of abundance with and without covariates (coefficients of the covariates set to zero) (top panels) and ratio of the two with 95% confidence intervals (bottom panels, *y* axis limited to show details) from the lowest AIC_c (left panels) model that has Ricker survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship and the alternative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model) (right panels).



covariates were combined together. The covariate was also highly correlated with time (see supplementary material[1]). We did find, to some extent, which other covariates were included in the model, and the order in which they were included changed depending on the density dependence assumptions. However, apart from the one predator covariate, the four density dependence assumptions tended to select the same factors in the first few steps of the model selection procedure, although the order of selection differed.

Several of the model parameters show moderate to strong correlations. The three covariates included in the lowest AIC model, but not in the alternative model (EPJul, Secchi, and Aent), are highly correlated with other model parameters. The only coefficients that show strong correlation with each other in the alternative model are EPAJ and TPJul. These covariates have a moderate negative correlation, while the coefficients have a positive correlation and therefore offset each other. High correlation may indicate that the data do not provide enough information to separate the effects represented by the two parameters. However, hypothesis tests and the confidence intervals of the coefficients are used to judge if a particular hypothesis (covariate) is supported by the data. If there is not enough information in the data to separate two hypotheses, the hypothesis tests will fail to include one of the covariates or the confidence interval of the covariate's coefficient will contain zero. The parameters of the density dependence function were highly positively correlated as previously observed for stock–recruitment relationships (Quinn and Deriso 1999), and reparameterization might improve the estimation algorithm. The inclusion of several covariates (TpAJ, EPAJ, EPJA, TpJul, Pred1) were robust to the form of density dependence and only showed low to moderate correlation among their coefficients. The predator covariate coefficient was highly correlated with the juvenile survival density dependence parameters, making the inclusion of this covariate less convincing. The predator covariate was also positively correlated with year. The coefficients for water clarity and adult entrainment, which were included in the lowest AIC model but excluded from the alternative model, were highly confounded with density dependence and required constraining the density dependence to reasonable parameter space. This may indicate that the effect of adult entrainment only shows up when abundance is very low. A model within two AIC units of the lowest AIC model did not contain either adult entrainment or water clarity, but did include all the robust factors. The coefficient for adult entrainment is also unrealistically large, suggesting that the model including water clarity and adult entrainment is unreliable.

The covariates were included in the model as simple log-

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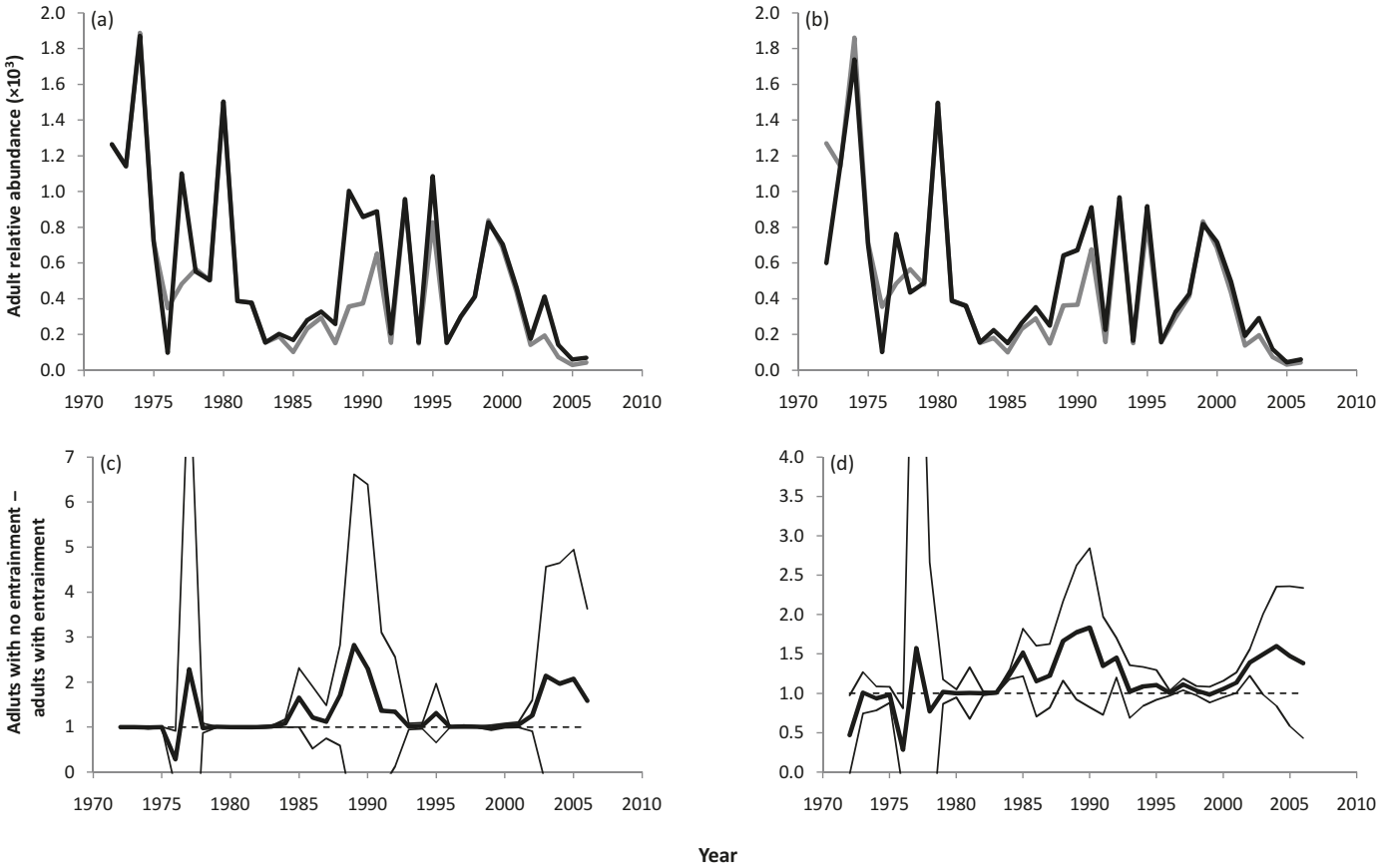
Fig. 8. Estimates of the adult abundance with and without adult entrainment (top panels) and the ratio of adult abundance without adult entrainment to that with adult entrainment (bottom panels, *y* axis limited to show details) from the lowest AIC_c model (left panels) with Ricker survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship and the alterative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model) (right panels).



linear terms. There may be more appropriate relationships between survival and the covariates. For example, good survival may be limited to a range of covariate values, so a polynomial that describes a dome-shaped curve may be more appropriate. There may also be interactions among the covariates. Neither of these was considered in the delta smelt application, although some of the covariates were developed based on combining different factors such as water clarity and predator abundance. Some of the covariates were highly correlated (see supplementary material[1]), but those with the highest correlations were either for different stages or not selected in the final models.

Density dependence and environmental factors could influence other population processes (e.g., growth rates) or the ability (catchability) of the survey to catch delta smelt. Modeling of catchability has been extensively researched for indices of abundance based on commercial catch data (Maunder and Punt 2004), and results have shown that the relationship between catch per unit effort and abundance can be nonlinear (Harley et al. 2001; Walters 2003). Rigorous statistical methods have been developed to account for habitat quality in the development of indices of abundance from catch and effort data (Maunder et al. 2006). Methods have been developed to integrate the modeling of catchability within population dynamics models as a random walk (Fournier et al. 1998) or as a function of covariates (Maunder 2001; Maunder and Langley 2004). Surveys are less likely to be effected by systematic changes in catchability because sampling effort and survey design tend to be more consistent over time than effort conducted by commercial fishing fleets. Most fisheries stock assessments assume that there are no systematic changes in survey catchability unless there is an obvious change (e.g., change in survey vessel). Previous studies using the data in this study have also assumed that catchability is constant over time (Mac Nally et al. 2010; Thomson et al. 2010). However, catchability may change because of factors such as changes in the spatial distribution of the species or population density. Similar methods as used for survival can be used to model catchability as a function of density or environmental factors. The standard deviations used in the likelihood functions are based on bootstrap analysis that takes the within-year sampling variability into consideration, but does not account for between-year variation in catchability. Random influences on catchability beyond those caused by simple random sampling can be accommodated by estimating the standard deviation of the likelihood function used to fit the model to the survey data (Maunder and Starr 2003). However, the fit to the delta smelt data appears better than expected from the bootstrap confidence intervals, suggesting that the observation error is smaller than estimated by the bootstrap procedure. Systematic and additional random variation in catchability could bias the evaluation of strength and statistical significance of density dependence and environmental factors (Deriso et al. 2007).

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The estimates of the *b* parameter of the Beverton–Holt stock–recruitment relationship between adults and larvae produced density dependence that was unrealistically strong in a few models. Consequently, this caused estimates of some coefficients that were also unrealistic (e.g., the coefficient for adult entrainment was nearly two orders of magnitude higher than expected). Even when a model was selected for which the *b* parameter was considered reasonable, the coefficient for adult entrainment was still an order of magnitude greater than expected. This illustrates that naively following AIC_c model selection without use of professional judgment is not recommended. We could have included all models in the sum of the AIC_c weights by bounding the *b* parameter in the parameter estimation process (the parameter would probably be at the bound), but we considered inference based on models with a parameter at the bound inappropriate. An alternative approach would be to use an informative prior for *b* (Punt and Hilborn 1997) to pull it away from unrealistic values, but we did not have any prior information that was considered appropriate.

Anderson et al. (2000) warn against data dredging as a method to test factors that influence population dynamics. In their definition of data dredging, they include the testing of all possible models, unless, perhaps, if model averaging is used. This provides somewhat of a dilemma when using a multistage life cycle model because there are often multiple candidate factors for each life stage and they may only be detectable if included in the model together. For this reason, we use an approximation to all possible models and rely on AIC_c and AIC_c weights to rank models and provide an idea of the strength of evidence in the data about the models and do not apply strict hypothesis tests. Some form of model averaging using AIC_c weights might be applicable to the impact analysis, although the estimates of uncertainty would have to include both model and parameter uncertainty. The estimates of uncertainty in our impact analysis underestimate uncertainty because they do not include model selection uncertainty, and use of model averaging might provide better estimates of uncertainty (Burnham and Anderson 2002). In addition, we use symmetric confidence intervals and approaches that provide asymmetric confidence intervals may be more appropriate (e.g., based on profile likelihood or Bayesian posterior distribution).

Our results suggest that of all the factors that we tested, food abundance, temperature, predator abundance, and density dependence are the most important factors controlling the population dynamics of delta smelt. Survival is positively related to food abundance and negatively related to temperature and predator abundance. There was also some support for a negative relationship with water clarity and adult entrainment and a positive relationship with the number of days where the water temperature was appropriate for spawning. The first variables to be included in the model were those related to survival from larvae to juveniles, followed by survival from juveniles to adults, and finally the stock–recruitment relationship. Mac Nally et al. (2010) also found that high summer water temperatures had an inverse relationship with delta smelt abundance. Thomson et al. (2010) found exports and water clarity as important factors. We did not include exports, but included explicit estimates of entrainment. We found some support for adult entrainment, but it was not one of the main factors, and the coefficient was unrealistically high and highly correlated with the coefficient for water clarity. Mac Nally et al. (2010) and Thomson et al. (2010) only used the FMWT data and did not look at the different life stages, which probably explains why the factors supported by their analyses differ from what we found.

We found strong evidence for density dependence in survival from juveniles to adults, some evidence for density dependence for the stock–recruitment relationship from adults to larvae, and evidence against density dependence in survival from larvae to juveniles. This might be surprising since the population is of conservation concern owing to low abundance levels. However, the available data covers years, particularly in the 1970s, where the abundance was high, and data for these years provide information on the form and strength of the density dependence. At the recent levels of abundance, density dependence is probably not having a substantial impact on the population, and survival is impacted mainly by density-independent factors. Previous studies only found weak evidence for a stock–recruitment relationship and suggested that density-independent factors regulate the delta smelt population (e.g., Moyle et al. 1992). Bennett (2005) found that the strongest evidence for density dependence was between juveniles and pre-adults. Mac Nally et al. (2010) found strong support for density dependence, but Thomson et al. (2010) did not.

Several pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Thomson et al. (2010) used Bayesian change point analysis to determine when the declines occurred and included covariates to investigate what caused the declines. They were unable to fully explain the decline, and unexplained declines were still apparent in the early 2000s. The impact analysis we applied to delta smelt suggests that the factors included in the model explain the low levels of delta smelt from 2002 to 2006. However, there is still substantial annual variation in the delta smelt abundance and uncertainty in the estimates of abundance for these years.

The theory for state–space stage-structured life cycle models is well developed (Newman 1998; de Valpine 2002; Maunder 2004), they have been promoted (Thomson et al. 2010; Mac Nally et al. 2010), they facilitate the use of multiple data sets (Maunder 2003), they provide more detailed information about how factors impact a population, they encompass all the statistical modeling advances advocated by Rose et al. 2001, and we have shown that they can be implemented. Therefore, we recommend that they are an essential tool for evaluating factors impacting species of concern such as delta smelt.

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Appendix A. Calculating realistic values for the *b* parameter of the Beverton–Holt and Ricker versions of the Deriso–Schnute stock–recruitment model

The third parameter (γ) of the Deriso–Schnute stock–recruitment model (Deriso 1980; Schnute 1985)

$$f(N) = aN(1 - b\gamma N)^{\frac{1}{\gamma}}$$

can be set to represent the Beverton–Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) models (Quinn and Deriso 1999, page 95), which correspond to

$$f(N) = \frac{aN}{1 + bN} \quad \text{and} \quad f(N) = aN\exp(-bN)$$

The recruitment at a given reference abundance level (e.g., the carrying capacity N_0) can be calculated as

$$R_0 = \frac{aN_0}{1 + bN_0} \quad \text{and} \quad R_0 = aN_0\exp(-bN_0)$$

The recruitment when the abundance is at a certain fraction (p) of this reference level can be calculated as

$$R_p = \frac{apN_0}{1 + bpN_0} \quad \text{and} \quad R_p = aN_0\exp(-bpN_0)$$

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A standard reference in fisheries is the recruitment as a fraction of the recruitment in the absence of fishing (the carrying capacity) that is achieved when the abundance is 20% of the abundance in the absence of fishing (steepness).

$$h = \frac{R_{0.2}}{R_0} = \frac{\frac{1}{N_0} + b}{\frac{5}{N_0} + b} \quad \text{and} \quad h = \frac{R_{0.2}}{R_0} = 0.2\exp(0.8bN_0)$$

To set b for a given steepness

$$b = \frac{5h - 1}{N_0 - hN_0} \quad \text{and} \quad b = \frac{\ln(5h)}{0.8N_0}$$

The 20% reference level was probably chosen because the objective of fisheries management has traditionally been to maximize yield, and it is generally considered that when a population falls below 20% of its unexploited level, the stock cannot sustain that level of yield. In the delta smelt application, the concern is about low levels of population abundance and we do not estimate the unexploited population size. Therefore, a more appropriate reference level might be 5% of the average level observed in the surveys.

$$h_{0.05} = \frac{R_{0.05}}{R_{\text{avg}}} = \frac{\frac{1}{N_{\text{avg}}} + b}{\frac{20}{N_{\text{avg}}} + b} \quad \text{and} \quad h_{0.05} = \frac{R_{0.05}}{R_{\text{avg}}} = 0.05\exp(0.95bN_{\text{avg}})$$

$$b = \frac{20h_{0.05} - 1}{N_{\text{avg}} - h_{0.05}N_{\text{avg}}} \quad \text{and} \quad b = \frac{\ln(20h_{0.05})}{0.95N_{0.05}}$$

This specification is also more appropriate when considering both the Beverton–Holt and Ricker models because the Ricker model reduces at high abundance levels, and the recruitment at an abundance level that is 20% of the carrying capacity could be higher than the recruitment at carrying capacity. We restrict the models to those that have b estimates such that the expected recruitment when the population is at 5% of its average level (over the survey period) is equal to or less than 80% of the recruitment expected when the population is at its average level (Table A1). This is equivalent to a Beverton–Holt $h_{0.2} = 0.95$ based on the abundance reference level being the average abundance from the surveys, which is probably conservative in the sense of not rejecting high values of b.

Table A1. Maximum values of the parameter b for inclusion of models in the model selection process.

		Maximum b	
	Average abundance	Beverton–Holt	Ricker
20 mm (larvae)	7.99	9.3867	0.3653
STN (juveniles)	6140	0.0122	0.0005
FMWT (adults)	459	0.1634	0.0064

Note: STN, summer tow net; FMWT, fall midwater tow.

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Update of Results for the Maunder and Deriso Delta Smelt Life-cycle Model

Rick Deriso, Mark Maunder, Dave Fullerton, BJ Miller, and Bryan Manly

November 2011

An update was made to the covariates and abundance indices in the model version described in Maunder and Deriso (2011) as the lowest AICc model. The update is intended to extend the analysis through 2010 so that now the variables used span the years 1972-2010. The model version applied contained the eight candidate environmental covariates in Miller (2011): two temperature variables TPAJ and TPJul, three prey variables EPAJ, EPJul, and EPJA, one predation variable PRED1, one sechi depth Sechi, and one adult entrainment Aent. A description of the covariates is given in table 1. Both the fall FMWT abundance index and the summer STN abundance index as well as variance estimates were updated through 2010 (Manly 2011a, Manly 2011b), but the 20mm index has not yet been updated. There are some differences in some of the covariates compared to the ones used in Deriso and Maunder (2011); namely, the new PRED1 index omits inland silverside data and the Sechi variable was reconstructed because the original calculations could not be located (the new Sechi is highly correlated ($R^2 = 0.91$) with the Sechi data used in the publication. The prey variable EPAJ value for 2010 was not available so one was constructed based on the historically high correlation ($R^2 = 0.84$) between EPAJ and a prey index based on the minimum over the spring months of zooplankton estimates from monthly trawl zooplankton densities for all stations in the lower Rivers through Suisun Bay for April, May and June.

The model selection procedure applied here is similar to the one employed in our earlier December 2010 report; namely it is a forward step-wise process involving the following steps.

1. Fit the model using the state space approach to abundance indices only.
2. Record the AIC score from the model fit,
3. Calculate a correlation matrix between all covariates in Table 1 and process errors calculated from the model fit.
4. Choose the covariate which has the highest correlation with any of the process errors.
5. Rerun the model with the additional covariate added.
6. If the AIC score is improved then retain the additional covariate.
7. Iterate again starting at step 2 with the additional covariate retained.

AIC scores from the iterations and covariates added to the model are listed in Table 2. The final model (highlighted in yellow) contained the same set of covariates as listed in Deriso and Maunder (2011) for what they define as the "alternative model." The alternative model

also excludes the covariates entrainment Aent and sechi depth (Sechi). As seen in Table 2 adding those covariates produces a worse (higher) AICc score.

Table 1. The variables used as candidates to account for the changes in delta smelt abundance.

Factor	Name	Description
1	TpAJ	Average water temperature Apr-Jun in delta smelt habitat
2	TpJul	Average water temperature July in delta smelt habitat
3	EPAJ	Minimum eurytemora and pseudodiaptomus density April-June
4	EPJA	Sum of eurytemora and pseudodiaptomus densities over sub-regions in July-August, with each sub-region density weighted by the fraction of delta smelt in the sub-region in July, based on the July abundance estimates
5	EPJul	Sum of eurytemora and pseudodiaptomus densities over sub-regions in July, with each sub-region density weighted by the fraction of delta smelt in the sub-region in July, based on the July abundance estimates
6	Pred1	Sum of relative densities of largemouth bass, Pomixis, and Lepomis, based on beach seine data averaged over all months of the year, and excludes striped bass and inland silverside. The sum of abundances was weighted with the square of Secchi depth averaged over Sep-Dec.
7	Secchi	Secchi depth in Jan-Feb averaged over subregions typically occupied by most delta smelt based on Kodiak Trawl abundance estimates
8	Aent	Adult winter entrainment as described in Maunder and Deriso 2011

Table 2: Stepwise results of updated analysis. EPJul was not selected through the 7th selection step.

Number Covariates	none	1	2	3	4	5	6	7
Covariate		TPAJ	EPAJ	EPJA	TpJul	Pred1	Aent	Sechi
Stage from		L	L	J	L	J	A	A
AICc	905.53	897.14	876.68	868.19	861.94	858.82	860.30	862.09
AICc-min AICc	46.71	38.32	17.86	9.37	3.12	0.00	1.48	3.27

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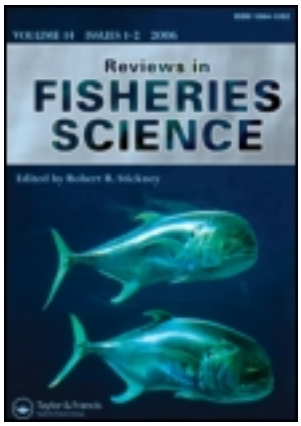

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An Investigation of Factors Affecting the Decline of Delta Smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary

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An Investigation of Factors Affecting the Decline of Delta Smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary

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The delta smelt is an annual fish that is endemic to the Sacramento-San Joaquin Estuary and is protected under federal and California Endangered Species Acts. Record low abundances have occurred since 2004. Three questions are addressed here: What is the relative importance of environmental factors with direct effects on abundance? Do factors that may have indirect effects provide an explanation of abundance changes? Are effects of environmental factors better accounted for individually or as criteria defining the volume of water with suitable abiotic attributes? Strong evidence was found of density-dependent population regulation. The density of prey was the most important environmental factor explaining variations in delta smelt abundance from 1972 to 2006 and over the recent period of decline in the abundance of the fish. Predation and water temperature showed possible effects. Entrainment of delta smelt at south Delta pumping plants showed statistically significant effects on adult-to-juvenile survival but not over the fish's life cycle. Neither the volume of water with suitable abiotic attributes nor other factors with indirect effects, including the location of the 2 ppt isohaline in the Delta in the previous fall ("fall X2"), explained delta smelt population trends beyond those accounted for by prey density.

[Supplementary materials are available for this article. Go to the publisher's online edition of *Reviews in Fisheries Science* for the following free supplemental resources: information on factor selection and specification; and estimating the volume of abiotic habitat.]

Keywords delta smelt, life-cycle model, multiple regression, effects hierarchy, pelagic organism decline

INTRODUCTION

It is a terrible juxtaposition of superlatives for the delta smelt. No other species currently protected under the federal Endangered Species Act has declined so dramatically since its listing. The index of abundance of delta smelt in the Sacramento-San Joaquin Delta has fallen almost three orders of magnitude since the fish was afforded protection in 1993 (California Department of Fish and Game [CDFG], 2010a). The need for immediate conservation responses is acute, but that need confronts another unfortunate delta smelt reality—perhaps less is known about the habitat of delta smelt, resources essential to its persistence, and the environmental stressors causing its low population numbers than is known about any other listed species. The life cycle of the tiny estuarine fish takes place in turbid, open waters, making it impossible to observe its behavior and

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account for many of its vital ecological relationships. Several candidate factors have plausible mechanisms of effect on delta smelt numbers, but previous attempts to relate environmental stressors to the decline of this fish were not able to identify the factors responsible for the recent declines in the abundance index to near-extinction levels. It might be fairly argued that no other federally listed species needs more immediate conservation attention, but a lack of reliable scientific guidance has hampered focused actions in support of delta smelt recovery.

The delta smelt is predominantly an annual species, with few individuals surviving to two years (Bennett, 2005). They are endemic to the San Francisco Bay-Delta Estuary. Delta smelt rear as juveniles and sub-adults upstream and downstream of the confluence of the Sacramento and San Joaquin Rivers for about seven months of the year, from late spring until the following winter (Bennett, 2005). Moyle (2002) described delta smelt as fish that "hang out in the water column and rely on their small size and transparency to hide them from predators in turbid water" (p. 228). Some delta smelt reside upstream in low salinity and fresh waters year around (Sommer et al., 2009). In winter, adults disperse into turbid waters that are necessary for efficient feeding of larvae on zooplankton (Baskerville-Bridges et al., 2004; Mager et al., 2004), with much of the population entering the Sacramento-San Joaquin Delta (Moyle, 2002). Spawning, triggered by increasing water temperature, begins as early as late February and can continue into June (Bennett, 2005). The environmental changes that have accompanied settlement and exploitation of the Delta have forced major adjustments in resources and conditions essential to survival and persistence of delta smelt.

No field data have been derived from experiments that directly relate delta smelt population responses to variation in physical and biotic conditions; however, general agreement exists both on the environmental features that seem to determine the location of delta smelt in the estuary and on stressors that could be contributing to decline of the fish. A conceptual model that describes and relates essential resources and suspected threat factors affecting population dynamics of delta smelt and other declining pelagic organisms in the Delta was developed by a multi-agency working group (Armor et al., 2005; Baxter et al., 2008; Baxter, 2010); however, no quantitative model has been available. Several recent studies have attempted to relate delta smelt population index data to suspected environmental stressors, but those studies had deficiencies that rendered their results uninformative (Feyrer et al., 2007; Mac Nally et al., 2010; Thomson et al., 2010).

Relating delta smelt population trends to changes in environmental factors that affect survival and reproduction of the fish, both directly (for example, predation, food supply, and entrainment) and indirectly (for example, flow and phytoplankton density), risks producing uninformative or confusing results. To maximize the likelihood of identifying actual causative relationships, the analysis presented here is initiated by developing an effects hierarchy that differentiates between those environmental covariates that act directly on the survival, reproduction, or recruitment of the delta smelt and those that act indirectly through one or more factors that act directly. This article focuses primarily on environmental factors with direct effects on survival or reproduction, leaving a rigorous attempt to identify indirect factors with important effects on direct factors for subsequent analyses (see Glibert et al., 2011, for example). This approach has three advantages. First, focusing on the limited number of variables with direct effects on delta smelt reduces the confounding effects of multi-collinearity and differential measurement error. When candidate causation factors are related to or interact with one another, the factor with lower measurement error may displace factors that have greater measurement error, even when those latter factors can be demonstrated to have greater effects signals (Zidek et al., 1996). Second, it reduces the possibility that identification of important environmental factors will be uninformative to decisions about resource management. This problem can arise if a factor with indirect effects is identified as itself important, but that factor acts through other factors that have direct or indirect effects. The best management response may involve controlling, or otherwise mitigating, not the environmental factor with an indirect effect identified as important, but rather, other factors. Third, arrangement of factors according to their hierarchy of effects provides information important in choosing the analytical method. Because pathways of effects can be delineated from knowledge of the mechanisms of ecological effects, a straightforward succession of multiple regression analyses, proceeding down each vertical path of the hierarchy, is suggested as the appropriate analytical approach to identifying the factors that best predict delta smelt population dynamics.

Several analysts have previously used measures of the volume of water with suitable attributes of conductivity, Secchi depth (as a measure of turbidity), and water temperature, which have been termed "abiotic habitat," to account for changes in abundance of delta smelt (e.g., Feyrer et al., 2007). In a subsequent biological opinion on delta smelt developed by the U.S. Fish and Wildlife Service (USFWS), inferences from those analyses were used to assert that a range of suitability in the extent of those abiotic factors limits abundance of delta smelt, and that increasing that extent is important to the recovery of delta smelt (USFWS, 2008). The hypothesis was tested that the volume of water within ranges of conductivity, Secchi depth, and water temperature at which most delta smelt occur explained variations in survival and reproduction. Several measures of that volume were developed and their effects on survival and reproduction were analyzed.

Index values for relative abundance of delta smelt were derived from standard trawler-generated data, specifically, the Fall Midwater Trawl (FMWT; CDFG, 2010a) and the Summer Townet Survey (STN; CDFG, 2010b). From relative abundance estimates, annual estimates of survival from juvenile to sub-adult life stages were developed, as well as survival and reproduction (hereinafter, referred to as "survival") across generations from sub-adult to juvenile life stages. Those estimates

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were used as response variables. Annual values for a variety of environmental variables were then developed, each of which could plausibly affect delta smelt population size and persistence. In doing so, the resource requirements and distribution of delta smelt at different sizes and in different stages in their life cycle were considered. From those candidate factors, a limited number were selected that offer the most plausible mechanism(s) of direct effect on delta smelt survival and abundance. In so doing, well-considered direct factors were differentiated from factors that may indirectly affect the size of and trend in delta smelt numbers through their effects on direct factors. From the abiotic and biotic factors in the Delta that appear to have direct effects on delta smelt, those that may be most important were selected, based on inferences drawn from available data and analyses. Multiple regression was used with three criteria to identify environmental factors that may be most important to survival and to evaluate the relative importance of those factors: goodness of fit of equations measured by the Akaike Information Criterion (AICc), the proportion of variation accounted for, and the significance of the regression coefficients. Using this general method, analyses were conducted to address three fundamental questions with important management implications: What is the relative importance of environmental factors that have direct effects on delta smelt abundance? Do environmental factors with indirect effects further explain abundance changes once effects of factors with direct effect are accounted for? Are the effects of environmental factors best accounted for independently or as criteria by which the volume of water with suitable attributes can be measured?

Based on the availability of data, these questions were directed at three periods in the annual life cycle of delta smelt—sub-adult (fall) to juvenile (summer), juvenile (summer) to sub-adult (fall), and sub-adult (fall) to sub-adult (fall). Because delta smelt has an annual life cycle, the last period is one version of a life-cycle model. Such a model has been identified as critically important in the development of a program to encourage recovery of delta smelt and to prevent jeopardizing its existence (Wanger, 2010). Analysis of the two within-year periods was carried out to better understand the factors that affect delta smelt survival between intermediate life stages during the year.

METHODS

Period of Analysis

The period of analysis covered the years 1972 through 2006. The initial year was selected because it was the first year of comprehensive surveys for zooplankton density throughout regions of the estuary occupied by delta smelt. The year 2006 was chosen because at the time this analysis began, comprehensive environmental data were only available through that year, and the period 2000 to 2006 includes the sharp decline in abundance of delta smelt that has persisted with little change since 2006.

Abundance and Survival

Two trawler-based surveys provide time-series population data from which long-term measures of annual delta smelt abundance can be estimated—the FMWT (1967–present), which samples sub-adult delta smelt, and the STN (1959–present), which samples for juveniles. Those data were used to provide the response variables representing delta smelt population size through time. An index of relative abundance has been calculated from both surveys by the CDFG since before 1970 (http://www.dfg.ca.gov/delta/). The indices are calculated by averaging catch per unit effort (for FMWT) or catch (for STN), assuming that volumes of water passing through the net are approximately the same for all STN tows over each Delta sub-region, then weighting the resulting averages by the estimated volume of water in the respective sub-region and summing sub-region estimates of abundance over all sub-regions. The FMWT index was used as calculated by the CDFG (http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT); this index is generally assumed to be the most accurate long-term index of delta smelt abundance, because it samples larger fish at approximately the same times each year over more stations than the STN. FMWT surveys were not conducted in 1974 and 1979, so those years were eliminated from the analysis.

There were concerns about the STN index. It is based on data from the first two surveys each year, and starting dates for the first survey can vary from year to year by as much as six weeks. Furthermore, more than one tow typically is made at each station, and catch is summed over all tow samples rather than averaged. It could not be confirmed that volumes of water in each sub-region used for the STN index were as accurate as those derived by detailed analysis of NOAA navigation charts. Therefore, despite the decades-long use of the STN index by analysts in this estuary, it was concluded that its flaws were too serious to justify its use as one of the two abundance variables in the present analyses, so an alternative estimate of summer juvenile delta smelt abundance was derived to overcome these problems. This estimate is referred to as "July abundance." It is based only on STN surveys that occur all or in part in July (the only month in which surveys occur each year), uses average rather than summed catch per tow, and uses updated volumes for each sub-region of the Bay Delta system.

Delta smelt survival is the response variable in the statistical analyses in this study. In these analyses, survival, as measured by index values, includes reproduction that occurs during the fall-to-summer period (that is, from pre-spawning adults in the fall to the next generation's juveniles in the July) and the fall-to-fall period (that is, a complete life cycle from pre-spawning adults in the fall to the next generation's pre-spawning adults the following fall). Three measures of delta smelt survival can be derived from the two abundance indices—fall-to-summer

survival, summer-to-fall survival, and fall-to-fall survival. Environmental factors that can reasonably be surmised to affect each of these three measures of survival were analyzed. Analyses of the former two measures provided insight into more important factors affecting fall-to-fall survival.

Environmental Factors and Their Hierarchy of Effects

Drawing on agency reports, several dozen biotic and abiotic factors were specified, that is, identified and quantified, along with variations of those factors, that have plausible mechanisms of effect on the abundance of delta smelt (Armor et al., 2005; Baxter et al., 2008; USFWS, 2009; Baxter, 2010) and for which data were available. Each factor was carefully specified, with consideration of the distribution of delta smelt and ranges of factor variation at different times of the year. Data on delta smelt distribution and environmental factors were segregated into sub-regions of the estuary, shown in Figure 1. Based on their mechanisms of effects, environmental factors were segregated into those with direct effects on delta smelt abundance and those with indirect effects, that is, effects that act through other factors that have direct effects. Factors that have direct effects on survival of delta smelt were grouped into categories (for example, water temperature, prey densities, entrainment at water export pumps); the same was done for factors with indirect effects on the smelt. Descriptions of each factor are in supplemental material to this article, along with the rationale for the selection of each factor and method used for its quantification. Figure 2 illustrates the general categories of factors, arranged as an "effects hierarchy." Apparent in the diagram is that certain factors—such as turbidity, water temperature, and flows through the Delta—appear at several locations in the hierarchy and may act indirectly on delta smelt, often in combination with other indirect factors. Data were available for all direct factors except disease and contaminants; however, effects of disease and contaminants on factors with indirect effect would be manifested as changes in factors with direct effect.

A Sawtooth Pattern in Survival

A pronounced inter-year "sawtooth" pattern in the survival of delta smelt was identified, that is, a persistent pattern of alternating years with higher and lower survival. This pattern was nearly identical in fall-to-summer and fall-to-fall index sequences, as shown in Figure 3. The probability was simulated that alternating peaks and troughs for 13 years would occur, as they did for years 1987 to 2000, if survival were random from year to year. This probability was estimated as 0.025—likely an overestimate because of the actual decreasing trend in delta smelt abundance over that period. Based on this analysis, it was concluded that there was a very low probability that this pattern occurred by chance. Two possible causes of the pattern were considered, one being the effect on delta smelt numbers of an environmental factor or combination of factors that exhibit corresponding, year-to-year sawtooth variation, and the other being an inherent aspect of the physiological ecology and/or

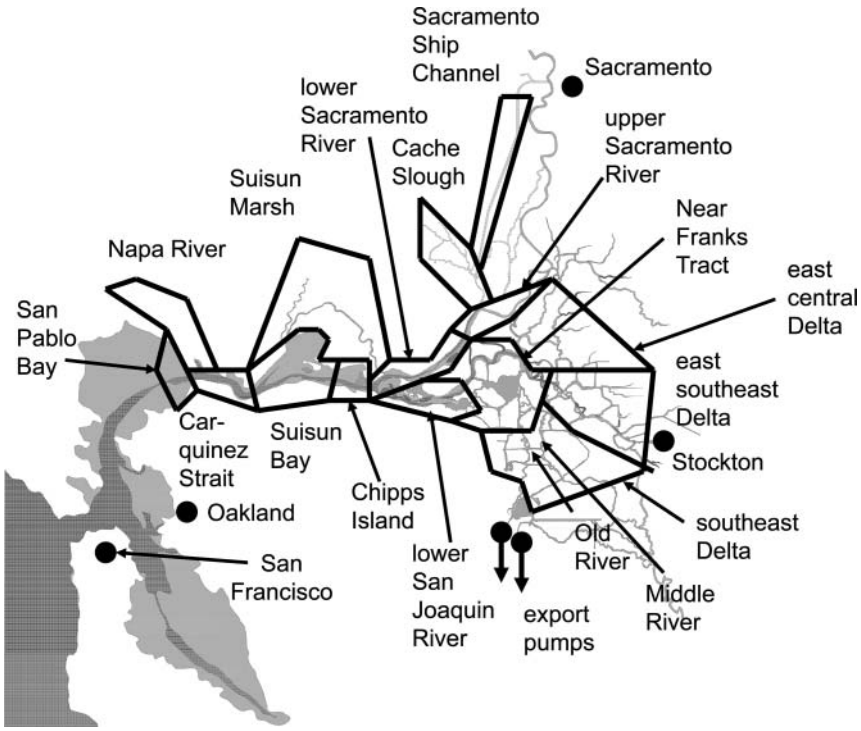

Figure 1 Sub-regions of the Bay-Delta Estuary.

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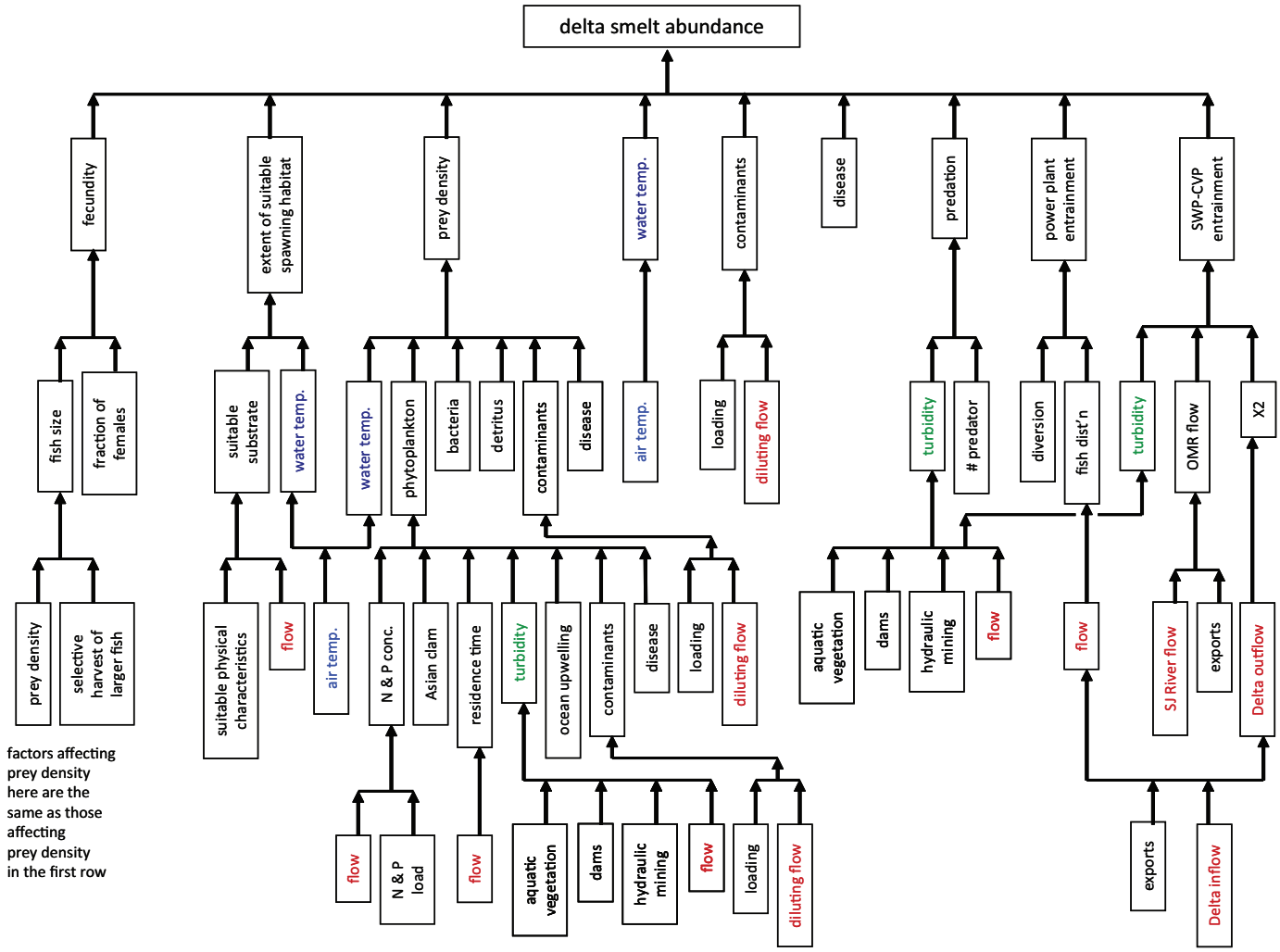

Figure 2 A simplified effects hierarchy of factors affecting delta smelt abundance. Row one, below delta smelt abundance, shows the factor categories that act directly to affect delta smelt. Row two includes factors that act indirectly on the fish. Rows three and four represent second-order and third-order indirect factors. Factors appearing in several locations are colored (color figure available online).

behavior of delta smelt. Relationships were examined between the sawtooth pattern and environmental factors with both direct and indirect effects on delta smelt. No factor or factors could be identified that explained the sawtooth pattern for more than a few sequential years, so it was concluded that an inherent cause seems more tenable. This effect was captured by including abundance from the year previous to that over which survival was estimated, a term referred to herein as "previous-previous fall abundance."

Identifying Best Regression Equations Using Factors with Direct Effect

General Approach

From each category of environmental factors with direct effects, represented as the factors in the first row in Figure 2, one or two initial factor quantifications were selected that, based on available knowledge of delta smelt biology, were likely to be most important in determining delta smelt survival. Values of those environmental factors are shown in Table 1. The reasons for their selection are presented in supplemental material. Then the effect of each of these factors was analyzed, along with previous delta smelt abundance (to capture effects of density dependence) and previous-previous fall abundance (to capture effects of the sawtooth pattern in survival). Statistical methods for this analysis are described below and are based on two key assumptions: that the FMWT and July abundance indices are approximately proportional to delta smelt abundance, and that the abundance index at one point in time is proportional to the abundance index at a previous time, apart from the effects of measured variables, sampling errors, process error variation, and density-dependent effects.

The analysis was initiated using the Ricker model (Ricker, 1958). This model assumes that the population abundance at

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Table 1 Factors with direct effect on delta smelt selected as most important to fall-to-summer, summer-to-fall, and fall-to-fall survival

	July abundance	FMWT index	Previous FMWT index	Spawning period, days of water temperature 11–20°C	Average water temperature Apr–Jun (°C)	Average water temperature July (°C)	Maximum two-week average water temperature Jul–Sep (°C)	Minimum *Eurytemora* + *Pseudodiaptomus* Apr–Jun (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* July (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Jul–Aug (#/m^3)	Secchi depth Apr–Jun (cm)	Adjusted Kimmerer proportional entrainment	Previous Sep–Dec striped bass adult abundance and Secchi depth	Previous Sep–Dec abundance other predators and Secchi depth	Apr–Jun abundance of other predators and Secchi depth	Sep–Dec striped bass adult abundance and Secchi depth	Sep–Dec abundance other predators and Secchi depth	Average length of delta smelt in December (mm)
Year	*Jab*	*Fab*	*PFAb*	*SpDys*	*TpAJ*	*TpJul*	*TpJS*	*EPAJ*	*EPJul*	*EPJA*	*SecAJ*	*Entrain*	*PStBass*	*PPreds1*	*Preds2*	*StBass*	*Preds1*	*DSLth*
1972	20,005	1,265	1,303	110	17.8	21.3	21.8	1,244	4,725	4,303	30	0.229	24,855	490	354	36,498	586	65.3
1973	11,185	1,145	1,265	104	18.6	21.3	21.9	754	1,547	2,082	32	0.110	36,498	586	793	27,596	1,041	65.3
1974	12,147		1,145	85	17.7	21.0	22.5	614	4,202	3,799	30	0.091	27,596	1,041	446	32,314	850	65.3
1975	8,786	697		92	17.2	20.1	21.5	480	1,520	1,545	26	0.094	32,314	850	280	41,650	735	65.1
1976	24,000	328	697	130	17.6	21.4	21.9	666	4,125	2,895	31	0.262	41,650	735	6,118	65,427	19,410	65.3
1977	25,965	480	328	118	17.0	21.1	21.5	581	4,194	3,972	33	0.256	65,427	19,410	7,095	40,655	22,324	65.6
1978	31,758	572	480	110	17.8	21.1	22.4	1,458	2,082	1,391	30	0.077	40,655	22,324	8,423	28,399	14,726	65.3
1979	5,484		572	90	18.0	21.0	22.1	517	947	722	28	0.160	28,399	14,726	18,631	25,761	37,712	67.8
1980	7,068	1,654	137	137	16.8	20.5	22.5	428	548	647	34	0.038	25,761	37,712	15,120	20,254	20,360	70.3
1981	6,300	374	1,654	108	18.7	21.8	22.8	788	922	724	37	0.199	20,254	20,360	17,070	20,621	22,248	67.2
1982	7,242	333	374	105	17.0	20.6	21.4	19	636	670	37	0.069	20,621	22,248	23,570	21,560	30,605	66.2
1983	1,390	132	333	102	17.3	20.7	22.2	271	530	544	34	0.020	21,560	30,605	13,957	31,059	28,422	62.2
1984	779	182	132	100	18.3	22.4	22.8	251	1,560	1,545	41	0.144	31,059	28,422	20,444	35,459	29,082	69.5
1985	387	110	182	105	18.5	22.0	22.5	135	548	543	43	0.231	35,459	29,082	30,364	46,997	62,483	69.1
1986	3,057	212	110	122	18.1	21.2	21.5	649	626	534	36	0.019	46,997	62,483	22,921	22,752	30,255	68.1
1987	2,743	280	212	102	19.0	20.6	21.3	534	392	519	44	0.199	22,752	30,255	26,771	41,144	42,089	64.8
1988	764	174	280	125	17.8	22.4	23.1	119	364	360	43	0.282	41,144	42,089	26,668	30,207	36,828	69.5
1989	647	366	174	108	17.9	21.1	21.7	384	2,558	3,641	42	0.222	30,207	36,828	24,067	29,441	38,551	67.8
1990	747	364	366	100	18.4	22.0	22.7	200	3,616	3,837	43	0.274	29,441	38,551	26,671	32,336	57,128	63.9
1991	2,486	689	364	108	17.2	21.3	21.8	151	2,542	3,059	38	0.231	32,336	57,128	23,754	39,881	63,209	62.5
1992	471	156	689	99	19.2	21.3	22.5	532	2,733	2,828	44	0.201	39,881	63,209	42,138	44,102	89,736	57.9
1993	5,763	1,078	156	112	17.8	21.5	22.2	603	1,184	1,425	42	0.119	44,102	89,736	25,301	27,938	48,487	54.7
1994	4,156	102	1,078	102	17.8	21.1	21.4	1,112	965	856	56	0.139	27,938	48,487	53,729	32,635	61,942	62.9
1995	2,490	899	102	142	17.0	21.5	22.0	574	2,366	1,431	44	0.064	32,635	61,942	38,412	34,966	59,091	58.5
1996	6,162	127	899	115	18.3	21.4	22.6	381	533	731	49	0.016	34,966	59,091	52,547	44,927	72,056	55.1
1997	2,362	303	127	104	19.3	21.2	21.8	369	590	800	44	0.093	44,927	72,056	33,056	56,551	64,436	57.6
1998	2,209	420	303	117	16.3	21.3	22.6	272	1,002	842	40	0.003	56,551	64,436	21,106	32,979	25,623	59.3
1999	7,478	864	420	112	17.3	21.3	22.0	752	1,308	1,091	41	0.052	32,979	25,623	21,961	42,465	29,853	59.1
2000	4,178	756	864	118	18.9	20.8	22.2	411	825	1,007	44	0.097	42,465	29,853	50,114	60,639	74,907	59.3
2001	2,897	603	756	73	19.5	21.3	22.0	424	758	484	42	0.133	60,639	74,907	50,992	48,811	81,186	63.5
2002	1,115	139	603	108	18.6	21.8	22.2	105	641	462	45	0.206	48,811	81,186	59,540	32,632	75,565	62.2
2003	1,329	210	139	106	18.0	22.2	23.2	136	787	1,525	47	0.175	32,632	75,565	56,424	40,081	86,509	58.6
2004	649	74	210	108	19.1	21.3	22.3	154	354	1,012	44	0.187	40,081	86,509	50,151	82,253	109,036	62
2005	393	27	74	123	18.1	22.0	22.8	57	849	466	51	0.049	82,253	109,036	68,310	58,943	119,419	59.6
2006	352	41	27	95	17.8	22.6	23.7	122	1,321	884	43	0.012	58,943	119,419	53,328	41,977	116,848	58
Fall-to-summer	■		■	■	■	■		■	■		■	■	■	■	■			■
Summer-to-fall	■	■					■			■						■	■	
Fall-to-fall	■		■	■	■		■	■		■	■	■			■			■

The last three rows are shaded to indicate the survival period to which each factor is relevant.

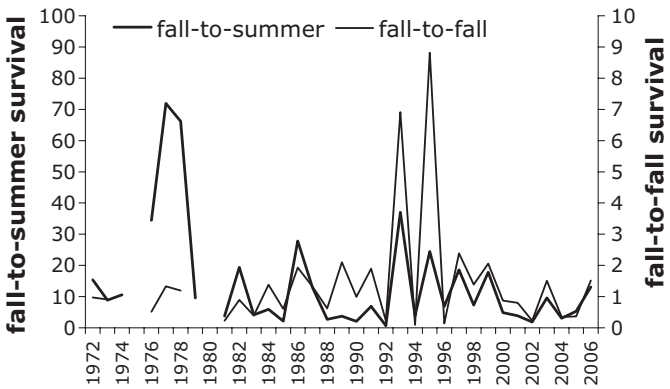

Figure 3 Delta smelt survival values from fall to summer and from fall to fall, which are derived from survey index values.

time $t + 1$ is related to the abundance at time t by an equation of the form

$$N_{t+1} = N_t \mathrm{Exp}\{r(1 - N_t/k)\}, \quad (1)$$

where r is the intrinsic growth rate, and k is the carrying capacity for the population. Taking natural logarithms gives

$$\mathrm{Ln}(N_{t+1}/N_t) = r - (r/k)N_t$$

and a linear relationship of the form

$$\mathrm{Ln}(N_{t+1}/N_t) = A + BN_t \quad (2)$$

relating the change ratio N_{t+1}/N_t to the density-dependent term BN_t. A generalization of this model assumes that the right-hand side of equation 1 also includes multiplicative effects of p variables $X_1, X_2, \ldots, X_p$, so that

$$N_{t+1} = N_t \mathrm{Exp}\{r(1 - N_t/k)\} \times \mathrm{Exp}(\alpha + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p), \quad (3)$$

where α is a constant. Equation 2 then becomes

$$\mathrm{Ln}(N_{t+1}/N_t) = \beta_0 + BN_t + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \quad (4)$$

where $\beta_0 = A + \alpha$ is a constant.

A further generalization of the Ricker model includes a term for delta smelt abundance two years before a given population year, allowing characterization of the sawtooth pattern in survival, so that it becomes

$$\mathrm{Ln}(N_{t+1}/N_t) = \beta_0 + BN_t + CN_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \quad (5)$$

where C is another regression coefficient. This equation applies when the change in abundance from time t to time $t + 1$ depends to some extent on population abundance both at time t and at time $t - 1$.

Abundance Changes from Fall to Summer

For changes in abundance from fall to summer, the equivalent to equation 5 is

$$\mathrm{Ln}(JAb_{t+1}/FAb_t) = \beta_0 + BFAb_t + CFAb_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \quad (6)$$

where JAb_{t+1} is the July abundance in year $t + 1$, and FAb_t is the fall abundance in year t.

In practice, equation 6 will have a process error; the value of the dependent variable will be the value predicted by the right-hand side of the equation plus an error e_t. Also, observed values of $\mathrm{Ln}(JAb_{t+1})$ and $\mathrm{Ln}(PFAb_t)$ and FAb_t and FAb_{t-1} will have sampling errors. This raises the possibility of biases in the estimated values of coefficients on the right-hand side of the equation, if these are estimated by ordinary multiple linear regression.

For this reason, the Solow (1998) method for fitting population models with sampling errors in abundance estimates was initially considered for the estimation of equation 6 and the models below for summer-to-fall and fall-to-fall changes in delta smelt abundance. Essentially, this method uses the principle of simulation and extrapolation (SIMEX) to first simulate an increase in the level of sampling errors in abundance estimates, then it extrapolates to estimate outputs with no sampling errors in the abundance estimates. Use of the Solow method indicated that any biases in the estimated coefficients of X variables are quite small due to sampling errors in the delta smelt abundance indices. Therefore, it was concluded that ordinary multiple regression is appropriate for estimating equation 6 and the equations for summer-to-fall and fall-to-fall changes in the abundance of delta smelt.

Nevertheless, the extent of possible biases was investigated further by simulating data based on fitted versions of equation 6. First, the value of $\mathrm{Ln}(JAb_{t+1}/FAb_t)$ was set equal to the right-hand side of the estimated equation 6 plus a normally distributed process error with a mean of zero. Normally distributed sampling errors were then added to the values of $\mathrm{Ln}(JAb)$ and $\mathrm{Ln}(FAb)$ with means of zero and standard deviations obtained by bootstrap resampling of the FMWT and STN data as described by Manly (2010a, 2010b). The simulated data with process errors and sampling errors were then used to obtain multiple regression estimates of the parameters β_0, B, C, and β_1 to β_p of equation 6. The generation of simulated data was repeated 10,000 times. Mean values of the estimated parameters were compared with the values used to generate the data to establish whether sampling errors in abundance indices introduce important biases in the estimates. Standard deviations in the simulated parameter estimates were also compared with the standard errors obtained from the original regression to estimate equation 6 using the observed data to see if any biases are introduced by sampling errors in the abundance indices. This simulation confirmed that the estimates and standard errors obtained by ordinary regression have negligible biases due to

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sampling errors in the abundance indices, as was expected from the Solow (1998) analysis.

Abundance Changes from Summer to Fall

For summer-to-fall abundance changes, the equivalent to equation 5 becomes

$$\mathrm{Ln}(FAb_t/JAb_t) = \beta_0 + BJAb_t + CJAb_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p.$$

In this case, it is not clear why the abundance of delta smelt in the fall of a given year should depend on the abundance in July in the previous year. There was no evidence of a sawtooth pattern in survival from summer to fall, the effect of which might be captured by this abundance measure, and initial analyses gave no evidence for this type of effect. Therefore, the equation was modified to

$$\mathrm{Ln}(FAb_t/JAb_t) = \beta_0 + BJAb_t + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p. \quad (7)$$

As for abundance changes from fall to summer, there will be process errors in the results from equation 7 and sampling errors in the abundance indices; simulation was used to ensure that these errors do not introduce large biases in the estimated parameters for the equation when they are estimated by ordinary multiple regression. The simulations were carried out in a similar fashion to the simulations used with equation 6. As for the fall-to-summer analysis, this showed negligible bias in estimates and standard errors obtained using ordinary regression due to sampling errors in abundance indices.

Abundance Changes from Fall to Fall

For the fall-to-fall changes in the FMWT abundance index, the equivalent to equation 5 becomes

$$\mathrm{Ln}(FAb_{t+1}/FAb_t) = \beta_0 + BFAb_t + CFAb_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \quad (8)$$

where the terms $B\ FAb_t$ and $C\ FAb_{t-1}$ imply that the change in delta smelt abundance from one fall to the next depends on the initial abundance and also the abundance in the fall of the previous year.

As for fall-to-summer and summer-to-fall changes, the use of equation 8 will be affected by process errors and sampling errors in the estimated abundance indices. However, the sampling errors in abundances are particularly likely to introduce biases in estimated parameters for equation 8 when using ordinary multiple regression because of the estimated value of FAb_t residing on both sides of the equation. Simulation was again used to ensure that these biases are relatively small using similar methods to those used with equations 6 and 7. This simulation showed negligible biases in the estimated constant term and in the coefficients of the X variables in equation 8 and negligible biases in the estimated standard errors of these parameters. The simulation indicated that the coefficient of FAb_t has a negligible bias, but the coefficient of FAb_{t-1} has a negative bias of about 10%; at the same time, the standard errors of these estimated density-dependent effects tend to be slightly higher than the estimates from ordinary regression. Using regression to estimate the effects of factors on delta smelt abundance seems to work well, but it should be noted that there may be small bias in estimated density-dependent effects.

This initial analysis used the factors in Table 1 and was carried out as follows. Multiple regression was used to estimate the corrected AICc, to account for the proportion of variation, and to estimate the significance and sign of the regression coefficients for all possible equations using all or some of the initial-analyses factors. From among those equations selected as exhibiting explanatory importance, equations with the lowest AICc and equations with AICc values that were within two units of the lowest AICc were selected (following Burnham and Anderson, 1998). In all cases, equations were restricted to those for which each environmental factor had a level of significance less than 0.10 and coefficients with signs consistent with their hypothesized effect. This analysis identified the abundance and environmental factors that produced the best regression equations for the initial analyses.

Adding Other Factors with Direct Effect to the Best Equations from the Initial Analysis

Using the methods described above, further analyses were carried out to see if the addition of other factors with presumed direct effect, or other ways of quantifying factors from among those not selected for initial analyses, showed important effects. These factors are shown in Table 2. Factors were added sequentially to the best regression equations to assess what portion of the variation in Ln(*Survival*) was explained by each factor. If any of these "secondary" direct factors proved to be important according to the above criteria, it reflected imperfect *a priori* understanding of the relationship between delta smelt and the specific environmental variables. In subsequent analyses, regression equations were used that contained factors with direct effect that can be identified as important from the combined results of these two analyses; these are herein referred to as the best regression equations based on factors that have direct effect.

It should be noted that this method—adding factors to regression equations—cannot completely eliminate problems arising from collinearity among factors; however, because the analysis is restricted to factors that have direct effects on delta smelt, the effects of collinearity are diminished relative to those that would have occurred had all factors that may have indirect effects on delta smelt been included.

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Table 2 Factors with direct effect not selected as most important in initial analyses of fall-to-summer, summer-to-fall, and fall-to-fall survival

Year	July abundance *Jab*	FMWT index *Fab*	Previous FMWT index *PFAb*	Deviation of water temperature from 16°C Mar–May degree-days *TpMM*	Deviation of water temperature from 17°C Apr–July degree-days *TpAJ*	Average *Eurytemora* April 30 (#/m^3) *EuApr*	Average *Eurytemora* + *Pseudodiaptomus* Apr–June (#/m^3) *EPAJ1*	Minimum total calanoid copepod biomass Apr–June (mg C/m^3) *CCAJ*	Average *Limnoithona* April–June (#/m^3) *LimAJ*	Average *Limnoithona* July (#/m^3) *LimJuly*	Average *Limnoithona* July–August (#/m^3) *LimJA*	Average *Eurytemora* + *Pseudodiaptomus* Sep–Dec (#/m^3) *EPSD*	Average *Limnoithona* Sep–Dec (#/m^3) *LimSD*	Average *Eurytemora* + *Pseudodiaptomus* Jan–Mar (#/m^3) *EPJM*	Average *Limnoithona* Jan–Mar (#/m^3) *LimJM*
1972	20,005	1,265	1,303	121	323	2,552	2,298	2,681	0	0	0	2,826	0	346	0
1973	11,185	1,145	1,265	232	354	2,914	1,997	2,220	0	0	0	2,042	0	767	0
1974	12,147		1,145	191	329	1,522	2,606	446	0	0	0	1,659	0	1,586	0
1975	8,786	697		274	376	734	998	711	0	0	0	666	0	184	0
1976	24,000	328	697	238	356	1,144	1,021	876	0	0	0	718	0	570	0
1977	25,965	480	328	201	300	1,071	1,022	872	0	0	0	680	0	1,193	0
1978	31,758	572	480	156	328	1,765	3,341	1,445	0	0	0	1,250	0	465	0
1979	5,484		572	207	369	893	1,140	1,494	0	0	0	907	0	513	0
1980	7,068	1,654		161	218	305	713	4,632	0	0	0	760	353	573	0
1981	6,300	374	1,654	233	415	845	1,006	2,610	5	15	824	588	1,084	516	5
1982	7,242	333	374	266	324	307	1,065	266	5	207	495	246	1,211	530	20
1983	1,390	132	333	232	377	11	594	138	0	184	757	20	2,037	25	0
1984	779	182	132	158	379	248	581	1,823	19	62	636	446	1,762	116	0
1985	387	110	182	192	337	175	327	3,496	106	1,271	2,008	494	1,490	193	0
1986	3,057	212	110	110	315	1,134	1,511	2,404	3	81	157	512	241	0	0
1987	2,743	280	212	264	326	2,015	1,184	2,466	114	633	1,056	228	998	449	0
1988	764	174	280	132	320	2,261	1,068	947	53	266	398	1,045	276	24	0
1989	647	366	174	151	266	632	2,909	1,621	48	192	134	2,255	128	117	0
1990	747	364	366	191	311	574	3,645	1,188	61	17	68	2,019	107	234	0
1991	2,486	689	364	205	315	470	1,513	162	6	27	44	1,480	91	47	0
1992	471	156	689	185	363	1,343	6,219	3,237	5	14	39	1,312	30	63	0
1993	5,763	1,078	156	153	320	776	4,074	1,783	0	218	751	1,047	5,466	125	28
1994	4,156	102	1,078	128	286	5,716	2,888	3,277	913	21,679	25,613	458	11,179	28	202
1995	2,490	899	102	168	309	560	2,046	985	894	9,070	14,901	648	4,344	52	54
1996	6,162	127	899	185	340	470	1,684	1,197	343	10,455	13,451	365	5,331	62	561
1997	2,362	303	127	192	359	650	1,924	1,494	1,917	20,440	21,622	466	17,468	66	185
1998	2,209	420	303	191	301	160	3,971	402	6,788	7,749	9,663	1,155	4,873	82	617
1999	7,478	864	420	246	323	1,740	1,710	987	1,378	17,586	18,700	540	30,340	101	1,231
2000	4,178	756	864	166	311	540	2,842	834	2,850	19,624	12,580	817	24,404	76	2,530
2001	2,897	603	756	240	433	520	1,838	1,045	4,165	37,284	33,272	222	19,672	46	1,765
2002	1,115	139	603	143	326	340	578	845	3,676	37,266	32,897	398	23,642	86	3,617
2003	1,329	210	139	167	404	80	1,411	1,996	2,137	43,190	21,778	363	18,635	94	4,197
2004	649	74	210	162	328	100	824	1,482	4,396	27,296	26,731	266	18,747	59	600
2005	393	27	74	151	361	220	726	1,233	815	19,423	26,595	295	14,849	49	395
2006	352	41	27	292	437	161	3,264	200	1,703	32,331	36,409	356	14,789	153	1,249
Fall-to-summer															
Summer-to-fall															
Fall-to-fall															

The last three rows are shaded to indicate the survival period to which each factor is relevant.

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Comparing the Relative Contribution of Each Factor to the Explained Variation in Ln (Survival)

Using the best equations for fall-to-summer, summer-to-fall, and fall-to-fall survival, based on factors with direct effect, the relative contribution of each factor to the percentage of variation in Ln(*Survival*) was assessed.

Testing of Selected Factors with Potential Indirect Effect on Survival

Although the present approach to identifying the dominant environmental stressors acting on delta smelt is based on the effects hierarchy displayed in Figure 2, the analysis was extended to see if addition of selected indirect factors to equations that are based on factors with direct effects on delta smelt might further contribute to explaining variation in survival. This was done by focusing on the fall-to-fall model, both because that period of analysis represents a complete life cycle and because it limits the number of correlations that can be attempted and, therefore, limits the possibility of spurious correlations arising by chance. The selection criteria, described above for analysis of direct factors were used to test the importance of six indirect factors when added to the best fall-to-fall equation based on the direct factors. The number of indirect factors was restricted to avoid producing uninformative, multiple-factor equations by chance. Six indirect factors were selected from those identified as important to survival in other studies of pelagic fishes in the Delta (Kimmerer, 2002; Feyrer et al., 2007; Grimaldo et al., 2009; Mac Nally et al., 2010; Thomson et al., 2010). The selected factors are presence/absence of the Asian clam (*Corbula amurensis*), the value of X2 (the distance along the main channel from the Golden Gate Bridge to the 2 ppt isohaline, a measure of estuary salinity) averaged over the previous fall ("fall X2"), average Secchi depth in January–March, average ammonium concentration in the Chipps Island and Suisun Bay sub-regions (see Figure 2) in April–June, and Old and Middle Rivers (OMR) flow (that is, flows steered to the south Delta water export pumps) averaged over December–March and April–June. Values of these six indirect factors are shown in Table 3.

Testing Effects of Measures of Abiotic Habitat Volume on the Best Fall-to-Fall Regression Equation

The importance of a combination of conductivity, Secchi depth, and water temperature—deemed abiotic habitat in a previous study (Feyrer et al., 2007)—were analyzed both alone and weighted by prey density. Estimates were made of the volume of water with levels of conductivity, Secchi depth, and water temperature at which virtually all delta smelt occur. These ranges of suitable values were compared with actual values of conductivity, Secchi depth, and water temperature for each month and sub-region (see Figure 1) for the period 1972–2006. Based on estimated volumes of water in each sub-region, the volume of water with suitable abiotic (physical) characteristics available to delta smelt in each month was estimated. These estimated volumes alone were used, and they were weighted with the sum of densities of the prey species *Eurytemora* and *Pseudodiaptomus*. Seasonal average and minimum monthly values of these volumes and prey-weighted volumes were used in the best regression equations based on factors having direct effect on delta smelt abundance to establish whether volume or prey-weighted volume measures met criteria for inclusion in the best regression equation for fall-to-fall survival, either as an addition to or, in the case of prey density, replacement for factors with direct effect.

RESULTS

Statistical Analysis to Identify the Best Regression Equations Using Factors with Direct Effect

Initial analyses were carried out using the factors in Table 1—those environmental factors with direct effect on delta smelt—that were selected as most likely to be important in determining delta smelt abundances based on biological considerations. From among those factors, the most important affecting survival from fall to summer, summer to fall, and fall to fall were identified based on the above-described criteria. Results are shown in Table 4.

From the factors considered in these initial analyses, the most important to fall-to-summer survival (by virtue of their appearance in the best regression equation) are previous-previous fall abundance, previous fall abundance, minimum *Eurytemora* + *Pseudodiaptomus* in April–June, and proportional entrainment of adult and larval-juvenile delta smelt, with some indication that average water temperature in April–June is also important. For survival from summer to fall, the most important factors are July abundance and average *Eurytemora* + *Pseudodiaptomus* density in July–August. For survival from fall to fall, the most important factors are previous-previous fall abundance, previous fall abundance, and minimum *Eurytemora* + *Pseudodiaptomus* in April–June, with some indication that predation in April–June by predators other than striped bass (inland silverside, largemouth bass, crappie, and sunfish) is also important.

Among the factors with direct effects selected for the initial analysis, the number of days of spawning, July water temperature, *Eurytemora* + *Pseudodiaptomus* in July, Secchi depth (turbidity) in April–June, predation by striped bass, and delta smelt fecundity did not appear in the best regression equations for fall-to-summer survival. Maximum two-week average water temperature in July–September and predation did not appear in the best regression equations for summer-to-fall survival. The number of days of spawning, average water temperature in April–June, maximum two-week average water temperature in July-September, average *Eurytemora* + *Pseudodiaptomus* availability in July–August, Secchi depth (turbidity) in April–June, entrainment, predation by striped bass, and delta smelt fecundity did not appear in the best regression equations for fall-to-fall survival.

Table 3 Factors with indirect effect on delta smelt abundance, selected for analysis based on results of other studies

Year	Presence (1) or absence (0) of Asian clam	Previous Oct–Dec avg X2, km of 2 ppt line from Golden Gate	Previous Sept–Dec Secchi depth in sub-regions occupied by delta smelt habitat (cm)	Secchi depth Jan-Mar (cm)	Average ammonium in Chipps Island and Suisun Bay sub-regions, Apr–June (mg/L)	Average December–March flow in Old and Middle Rivers (cfs)	Average April–June flow in Old and Middle Rivers (cfs)
	AsClam	*PODX2*	*PFSec*	*JMSec*	*AJAm1*	*DMOMR*	*AJOMR*
1972	0	71	35	41	0.046	−2,260	−6,606
1973	0	71	38	26	0.034	953	−4,790
1974	0	66	37	35	0.024	−940	−4,955
1975	0	68	41	36	0.045	−2,093	−3,736
1976	0	70	42	51	0.047	−6,033	−5,491
1977	0	89	56	48	0.059	−4,054	−3,037
1978	0	92	58	17	0.027	−4,231	3,827
1979	0	77	40	34	0.027	−686	−5,487
1980	0	79	40	27	0.040	3,887	−1,142
1981	0	79	39	33	0.037	−4,678	−5,342
1982	0	75	42	31	0.035	−3,736	2,769
1983	0	63	42	25	0.040	9,124	14,610
1984	0	58	49	53	0.038	6,026	−5,623
1985	0	70	49	66	0.065	−5,023	−6,424
1986	0	88	61	45	0.039	−732	413
1987	1	78	41	50	0.047	−4,474	−5,471
1988	1	88	55	41	0.073	−8,006	−6,765
1989	1	90	51	44	0.058	−7,645	−7,198
1990	1	88	54	47	0.080	−9,086	−5,858
1991	1	89	62	58	0.083	−5,356	−4,752
1992	1	88	62	60	0.065	−5,561	−3,073
1993	1	87	64	29	0.034	−5,765	−2,304
1994	1	82	58	58	0.093	−4,742	−1,613
1995	1	86	60	31	0.033	−3,145	4,721
1996	1	75	55	37	0.036	−1,281	−2,848
1997	1	78	57	29	0.087	10,376	−3,972
1998	1	81	61	29	0.043	2,103	6,536
1999	1	69	45	51	0.060	−760	−2,155
2000	1	83	47	48	0.065	−5,282	−4,338
2001	1	85	53	45	0.089	−5,681	−2,919
2002	1	82	53	36	0.070	−7,731	−3,857
2003	1	84	50	36	0.055	−8,185	−5,374
2004	1	83	58	34	0.080	−8,080	−4,851
2005	1	82	65	48	0.055	−5,525	−1,055
2006	1	82	68	39	0.040	−3,214	10,026

Additional analyses were carried out using factors with direct effects that were not selected for the initial analyses. These were added to the best equations from the initial analyses to see whether they made a significant improvement. Results of this analysis, shown in Table 5, indicate that average *Eurytemora* + *Pseudodiaptomus* density in January–March should be added as an important factor that explains survival from fall to summer. Average *Eurytemora* + *Pseudodiaptomus* density in September–December should replace average *Eurytemora* + *Pseudodiaptomus* density in July–August as an important factor explaining survival from summer to fall and should be added to the regression equation for fall-to-fall survival.

Of the factors with direct effect on delta smelt population dynamics that was used for the additional analyses, the number of degree-days of deviation of water temperature from optimum in March–May or April–July; average *Eurytemora* density in late April; average *Eurytemora* + *Pseudodiaptomus* density in April–June; and average *Limnoithona* density in April–June, July, or January–March did not appear in the best regression equations for fall-to-summer survival. Average *Limnoithona* density in July–August and September–December did not appear in the best regression equation for summer-to-fall. None of these factors appeared in the best regression equations for fall-to-fall. There was some evidence that minimum calanoid copepod biomass in April–June was important for fall-to-summer survival but not survival from fall-to-fall.

The best regression equations based on factors with direct effects on delta smelt abundance were derived from the best regression equations from the initial analyses, as adjusted by results from the additional analyses using factors with direct effect that were not selected for the initial analyses.

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Table 4 Summary of results of initial analyses of factors with direct effect that were selected as important based on the most reliable knowledge of delta smelt biology

			Initial analyses factors with direct effect on delta smelt survival																	
			Previous previous fall abundance	Previous fall abundance	July abundance	Spawning period, days of water temperature 11–20°C	Average water temperature Apr–Jun (°C)	Average water temperature July (°C)	Maximum two-week average water temperature Jul–Sep (°C)	Minimum *Eurytemora + Pseudodiaptomus* Apr–Jun (#/m^3)	Average *Eurytemora + Pseudodiaptomus* July (#/m^3)	Average *Eurytemora + Pseudodiaptomus* Jul–Aug (#/m^3)	Secchi depth Apr–Jun (cm)	Adjusted Kimmerer proportional entrainment	Previous Sep–Dec striped bass adult abundance and Secchi depth	Previous Sep–Dec abundance other predators and Secchi depth	Apr–Jun abundance of other predators and Secchi depth	Sep–Dec striped bass adult abundance and Secchi depth	Sep–Dec abundance other predators and Secchi depth	Average length of delta smelt in December (mm)
Period	AICc value	Adjusted R^2	*PFAb* 1	*PFAb*	*Jab*	*SpDys*	*TpAJ*	*TpJul*	*TpJS*	*EPAJ*	*EPJul*	*EPJA*	*SecAJ*	*Entrain*	*PStBass*	*PPreds1*	*Preds2*	*StBass*	*Preds*1	*DSLth*
Fall-to-summer	**36.4**	**59%**	**0.001**	**0.000**	Not relevant to this period	–	–	–	Not relevant to this period	**0.000**	–	Not relevant to this period	–	**0.035**	–	–	–	Not relevant to this period		–
	36.9	**58%**	**0.004**	**0.000**		–	**0.048**	–		**0.000**	–		–	–	–	–	–			–
	37.0	62%	0.002	0.000		–	0.104	–		0.000	–		–	0.077	–	–	–			–
	37.4	61%	0.011	0.000		–	–	–		0.000	–		0.136	0.028	–	–	–			–
	37.7	60%	0.007	0.000		–	–	–		0.001	–		–	0.020	–	–	0.172			–
	38.1	**53%**	**0.002**	**0.000**		–	–	–		**0.000**	–		–	–	–	–	–			–
	38.1	60%	0.002	0.001		–	0.035	–		0.000	–		–	–	0.162	–	–			–
	38.5	59%	Not estimated			–	–	–		0.000	–		–	0.023	–	0.315	–			–
	38.8	58%				–	–	–		0.000	–		–	0.056	0.413	–	–			–
	39.1	54%				–	–	–		0.000	–		0.189	–	–	–	–			–
Summer-to-fall	**38.1**	**60%**	Not relevant to this period		**0.000**	Not relevant to this period			–	Not relevant to this period		**0.002**	Not relevant to this period					–	–	Not relevant to this period
	38.6	61%			0.000				–			0.003						–	0.153	
	39.2	63%			0.000				0.147			0.002						–	0.066	
	39.3	60%			0.000				–			0.002						0.239	–	
	40.0	60%			0.000				0.397			0.002						–	–	
	41.2	60%			Not estimated				0.371			0.002						0.229	–	
	41.2	60%							–			0.003						0.707	0.378	
	42.2	62%							0.169			0.002						0.969	0.172	
	46.9	49%							–			–						–	0.174	
	48.2	49%							0.322			–						–	0.109	
Fall-to-fall	30.8	59%	0.016	0.000	Not relevant to this period	–	–	Not relevant to this period	–	–	Not relevant to this period	–	–	–	Not relevant to this period		0.002	–	–	0.034
	30.9	**53%**	**0.001**	**0.000**		–	–		–	**0.009**		–	–	–			–	–	–	–
	31.7	**52%**	**0.014**	**0.000**		–	–		–	–		–	–	–			**0.015**	–	–	–
	31.8	56%	0.017	0.000		–	–		–	–		–	–	–			–	–	0.003	0.036
	31.9	56%	0.006	0.000		–	–		–	0.073		–	–	–			0.125	–	–	–
	32.1	56%	0.002	0.000		–	–		–	0.016		0.149	–	–			–	–	–	–
	32.3	61%	0.008	0.000		–	–		–	0.133		–	–	–			0.022	–	–	0.061
	32.6	54%	0.005	0.000		–	–		–	0.065		–	–	–			–	–	0.229	–
	32.8	**49%**	**0.014**	**0.000**		–	–		–	–		–	–	–			–	–	**0.029**	–
	32.9	54%	Not estimated			–	–		–	0.034		–	–	–			–	–	–	–

Entries in the last 18 columns are significance levels for regression coefficients from two-sided tests. Gray shading shows instances of AICc greater than two units above the best equation, a level of significance above 0.10, or, in the case of delta smelt length (a measure of fecundity), a negative coefficient in the regression equation, which is contrary to the hypothesized effect. Boldface indicates factors in equations meeting all selection criteria. Tick marks indicate that the factor was not among those used in the equation that was tested.

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Table 5 Results of analyses of factors with direct effect, not selected for the initial analyses, added to the best regression equations for each period, from the initial analyses

			Direct factors not selected for initial analyses											
			Deviation of water temperature from 16° C Mar--May (degree-days)	Deviation of water temperature from 17° C Apr–July (degree-days)	Average *Eurytemora* April 30 (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Apr–June (#/m^3)	Minimum total calanoid copepod biomass Apr--June (mg C/m^3)	Average *Limnoithona* April–June (#/m^3)	Average *Limnoithona* July (#/m^3)	Average *Limnoithona* July--August (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Sep–Dec (#/m^3)	Average *Limnoithona* Sep–Dec (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Jan–Mar (#/m^3)	Average *Limnoithona* Jan–Mar (#/m^3)
Period	AICc value	Adjusted R^2	*TpMM*	*TpAJ*	*EuApr*	*EPAJ*1	*CCAJ*	*LimAJ*	*LimJuly*	*LimJA*	*EPSD*	*LimSD*	*EPJM*	*LimJM*
Fall-to-summer	**38.9**	**70%**	–	–	–	–	–	–	–	Not relevant to this period			**0.003**	–
	39.5	**73%**	–	–	–	–	0.080	–	–				**0.010**	–
	40.1	72%	–	–	–	0.127	–	–	–				0.004	–
	40.8	75%	–	–	–	0.101	0.066	–	–				0.012	–
	41.4	70%	–	–	–	–	–	–	–				0.002	0.331
	42.0	69%	–	–	–	–	–	–	0.578				0.003	–
	42.1	69%	–	0.611	–	–	–	–	–				0.004	–
	42.3	69%	0.835	–	–	–	–	–	–				0.007	–
	42.3	69%	–	–	–	–	–	0.907	–				0.004	–
	42.3	69%	–	–	0.929	–	–	–	–				0.004	–
Summer-to-fall	**39.50**	**67%**	Not relevant to this period							–	**0.012**	–	Not relevant to this period	
	41.55	66%								0.406	0.026	–		
	42.23	66%								–	0.013	0.805		
	42.23	68%								0.095	0.023	0.139		
	44.58	61%								0.169	–	–		
	45.02	62%								0.056	–	0.167		
	46.89	59%								–	–	0.783		
Fall-to-fall	**32.2**	**62%**	–	–	–	–	–	–	Not relevant to this period	–	**0.020**	–	–	–
	33.4	64%	0.120	–	–	–	–	–		–	0.010	–	–	–
	33.8	63%	–	–	–	–	0.160	–		–	0.020	–	–	–
	34.0	63%	–	–	–	–	–	–		–	0.010	0.190	–	–
	34.5	62%	–	–	–	–	–	–		–	0.010	–	–	0.300
	34.6	62%	–	–	–	–	–	0.310		–	0.010	–	–	–
	34.8	61%	–	–	0.370	–	–	–		–	0.020	–	–	–
	35.2	60%	–	–	–	0.580	–	–		–	0.060	–	–	–
	35.3	66%	0.090	–	–	–	–	–		–	0.000	0.150	–	–
	35.3	56%	–	–	–	0.160	–	–		–	---	–	–	–

Entries in the last 12 columns are significance levels for regression coefficients from two-sided tests. Gray shading shows instances of AICc greater than two units above best equation or a level of significance above 0.10. Boldface indicates factors in equations meeting both selection criteria. Tick marks indicate that the factor was not among those used in the equation that was tested.

The best regression equation for the fall-to-summer survival of delta smelt is

$$\mathrm{Ln}(Survival) = 2.003 - 2.197*PFAb + 0.781*PFAb1 + 1.988*EPAJ - 3.826*Entrain + 1.143*EPJM, \quad (9)$$

where survival is the ratio of July abundance, a measure of juvenile abundance in July, to the previous year's FMWT index, a measure of sub-adult abundance; *PFAb* is the FMWT index of the previous year divided by 1,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June divided by 1,000; *Entrain* is the proportional entrainment of delta smelt, as a fraction; and *EPJM* is the average *Eurytemora* + *Pseudodiaptomus* density in January–March divided by 1,000.

The best regression equation found for summer-to-fall survival of delta smelt is

$$\mathrm{Ln}(Survival) = -2.176 - 1.003*JAb + 0.698*EPSD, \quad (10)$$

where *Survival* is the ratio of the FMWT index, a measure of sub-adult abundance, to July abundance, a measure of juvenile abundance in July, in the same year; *JAb* is July abundance, a measure of juvenile abundance in summer divided by 10,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; and *EPSD* is the average *Eurytemora* + *Pseudodiaptomus* density in September–December divided by 1,000. Note that *EPSD*, the average *Eurytemora* + *Pseudodiaptomus* in September–December, replaced *EPJA*, the average *Eurytemora* + *Pseudodiaptomus* in July–August in the best regression equation from the initial analysis because *EPJA* was no longer significant in the equation for summer-to-fall survival when other factors with direct effects were considered.

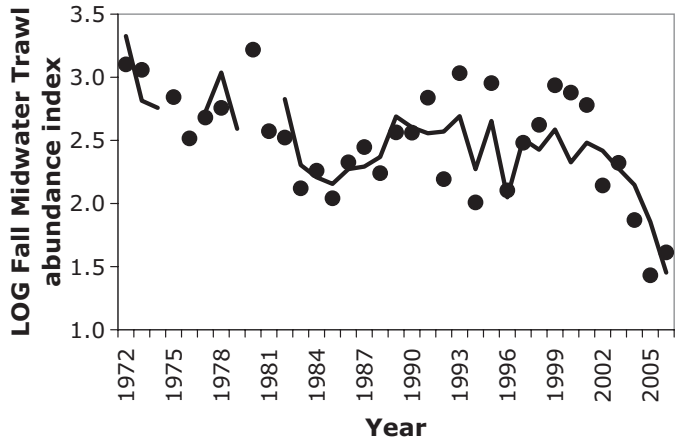

Figure 4 Actual and predicted values of the Fall Midwater Trawl index of abundance of sub-adult delta smelt. Circles are actual values. The line shows predicted values.

The best regression equation found for the fall-to-fall survival of delta smelt is

$$\mathrm{Ln}(Survival) = -0.246 - 2.781*PFAb + 1.048*PFAb1 + 0.997*EPAJ + 0.482*EPSD, \quad (11)$$

where survival is the ratio of the FMWT index, a measure of sub-adult abundance in the fall, to the previous year's FMWT index; *PFAb* is the FMWT index of the previous year divided by 1,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June divided by 1,000; and *EPSD* is average *Eurytemora* + *Pseudodiaptomus* density in September–December divided by 1,000. Figure 4 shows actual abundance of sub-adult delta smelt (the FMWT index) and values predicted by equation 11.

These three equations each reflect a stock-recruitment relationship in which end-of-period abundance is proportional to

Table 6 Percentage of variation in Ln(*Survival*) explained and the contribution of each factor to that percentage

Period	% Ln(*Survival*)[a] variation explained	Important factors	Percent of variation explained[b]	Percent of variation explained[c]
Fall-to-summer	70.2%	*PFAb* = previous fall abundance/1,000	0.0%	38.3%
		*PFAb*1 = previous previous fall abundance/1,000	14.0%	7.7%
		EPAJ = minimum *Eury* + *Pseu*, Apr–Jun/1,000	39.0%	32.8%
		Entrain = proportional entrainment at export pumping plants, %/100	6.0%	9.1%
		EPJM = average *Eury* + *Pseu*, Jan–Mar/1,000	11.2%	11.2%
Summer-to-fall	67.6%	*JAb* = July abundance/10,000	47.0%	64.1%
		EPSD = average *Eury* + *Pseu*, Sep–Dec/1,000	20.6%	20.6%
Fall-to-fall	61.6%	*PFAb* = previous fall abundance/1,000	25.8%	61.6%
		*PFAb*1 = previous-previous fall abundance/1,000	15.2%	18.6%
		EPAJ = minimum *Eury* + *Pseu*, Apr–Jun/1,000	12.5%	8.0%
		EPSD = average *Eury* + *Pseu*, Sep–Dec/1,000	8.1%	8.1%

[a]For fall-to-summer and fall-to-fall analyses, "survival" means survival and reproduction.
[b]Percent of variation explained by the variables when added one at a time in order shown.
[c]Percent of variation explained when variable is added last into the equation.

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beginning-of-period abundance. However, this proportional relationship is adjusted by a density-dependence term that causes abundance to be reduced when beginning-of-period abundance is high and is further adjusted by prey-density terms that cause delta smelt abundance to increase with availability of prey. In addition, summer abundance relative to previous fall abundance is reduced by entrainment. Both summer abundance and fall abundance, relative to previous fall abundance, are higher than expected when the abundance two-years previous is high.

Comparing the Relative Contribution of Each Factor to the Explained Variation in Ln(Survival)

Table 6 shows the percentage of variation in Ln(*Survival*) that is explained by each equation and the contribution of each factor to that percentage. The density-dependence terms, *PFAb* or *JAb*, have relatively important contributions to variation in Ln(*Survival*) for all three periods, and, while *PFAb* is not important as an individual factor for fall-to-summer survival, its inclusion renders important the contribution of other factors once it is added to the equation. Prey-density terms have a relatively important contribution to variation in Ln(*Survival*), as does the previous-previous fall abundance, which accounts for the sawtooth survival pattern. The contribution of entrainment to variation in Ln(*Survival*) is not as important as the contribution of prey densities to fall-to-summer survival. Entrainment was not chosen for inclusion in the fall-to-fall equation because it did not meet the criteria for inclusion.

Testing Selected Factors with Indirect Effects on Survival

There was no evidence that any of six environmental factors with indirect effects, which were identified in previous studies, further explained changes in fall-to-fall delta smelt survival beyond those accounted for by factors with direct effects shown in equations 9, 10, and 11. It is noted that this does not necessarily mean that these or other factors with indirect effects might not have important effects on one or more factors that have direct effects.

Testing Effects of Measures of "Abiotic Habitat" Volume on the Best Fall-to-Fall Regression Equation

This study attempted to add estimates of the volume of water within the suitable range of conductivity, Secchi depth, and water temperature to the best regression equation, as well as suitable volumes weighted with prey density (densities of *Eurytemora* + *Pseudodiaptomus*), the values of which are in the supplemental material to this article. When adding volume weighted by prey density, prey density terms were first removed from the best regression equations. None of those measures met the criteria above for inclusion in the best regression equation for fall-to-fall survival.

DISCUSSION

The analyses presented here focused on environmental factors that have plausible mechanisms for direct effects on the survival of delta smelt, leaving identification of factors having important, indirect effects—that is, the factors that have important effects on important factors with direct effects—for subsequent analyses. Effects on delta smelt survival were analyzed from fall (when delta smelt are sub-adult or pre-spawning adults) to summer (when delta smelt are next-generation juveniles) and from fall to fall (addressing the life cycle across a single generation). The regression equations resulting from this latter analysis serve as a life-cycle model. Effects on survival from summer to fall were also analyzed, thereby allowing insight into sources of mortality during this delta smelt growth stage. Analyses indicate that prey density is the most important environmental factor affecting abundance and population trends in delta smelt over the period 1972 through 2006 and also that changes in prey density appear to best explain the sharp drop in delta smelt abundance in this century. Entrainment of delta smelt at state and federal export pumping plants in the Sacramento-San Joaquin Delta appears to contribute to survival rates from fall to summer and, therefore, to juvenile abundance in summer, but entrainment was not a statistically significant factor in survival from fall to fall—that is, to inter-annual changes in the size of the delta smelt population. Density dependence was an important factor affecting survival from fall to summer, summer to fall, and fall to fall. Its inclusion in the best regression equations was also important in revealing the effects of prey density and entrainment on delta smelt abundance. This finding indicates that density dependence must be accounted for in analyses directed at identifying factors that are important to the abundance of delta smelt. Delta smelt survival from fall to summer and fall to fall showed a persistent sawtooth pattern over much of the period analyzed, and this effect was captured by inclusion of a term for delta smelt abundance in fall of the year prior to beginning-of-period abundance in fall-to-summer and fall-to-fall survival analyses. It is noted that the best regression equations may not apply for values of factors outside the range of values actually observed.

The regression equations can be interpreted as follows, using the fall-to-fall equation as an example. Delta smelt survival is the ratio *FMWT*/*PFAb*, where *PFAb* is the previous year's FMWT index. So, equation 11 can be written as

$$\frac{FAb}{PFAb} = e^{-0.246-(2.781\times10^{-3}PFAb)+(1.048\times10^{-3}PFAb1)+(0.997\times10^{-3}EPAJ)+(0.482\times10^{-3}EPSD)}$$

or

$$FAb = 0.782PFAb\, e^{-(2.781\times10^{-3}PFAb)} e^{(1.048\times10^{-3}PFAb1)} e^{(0.997\times10^{-3}EPAJ)} e^{(0.482\times10^{-3}EPSD)},$$

where *PFAb1* is the previous-previous FMWT index, *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June, and *EPSD* is the average *Eurytemora* + *Pseudodiaptomus* density in September–December. Assuming that the

number of delta smelt eggs in spring is proportional to the previous abundance index derived from the FMWT, this equation can be interpreted as follows:

$$
\begin{aligned}
&FMWT = [\text{eggs in spring} = 0.782PFAb] \\
&\times[\text{survival reduction related to density dependence} \\
&\text{from previous FMWT} = e^{-(2.781\times10^{-3}PFAb)}] \\
&\times[\text{survival increase from contribution of previous}- \\
&\text{previous abundance} = e^{(1.048\times10^{-3}PFAb1)}] \\
&\times[\text{survival increase from high minimum food density in} \\
&\text{April} - \text{June} = e^{(0.997\times10^{-3}EPAJ)}] \\
&\times[\text{survival increase from high September}- \\
&\text{December food density} = e^{(0.482\times10^{-3}EPSD)}],
\end{aligned}
$$

with the negative constant term in equation 11 indicating that survival (that is, the combined effects of survival and reproduction) from fall to fall is less than one—typical of a species experiencing an extended decline in abundance.

There was some indication that average water temperature and calanoid copepod biomass (a general measure of prey density) in April–June were important contributors to survival of delta smelt from fall to summer. Furthermore, predation in April–June, representing the combined effects of water clarity and abundance of the predators, inland silversides, largemouth bass, crappie, and sunfish, was important to delta smelt survival from fall to fall. Numerous factors with direct effects on delta smelt survival did not have statistically significant effects on the subsequent abundance of delta smelt, including the length of the spawning period as determined by water temperature; turbidity as an individual factor affecting larval feeding success in spring as measured by Secchi depth; average or maximum water temperature in summer; deviations of water temperature from optimum values in spring; predation in summer and fall by predators other than striped bass and predation in all seasons by striped bass; delta smelt fecundity, as measured by the size (average length) of delta smelt in December; and the average density of *Limnoithona*, an invasive zooplankton that has become the most abundant potential prey species in the estuary.

The effects of factors that might have indirect effects on survival were analyzed using factors that were identified by previous studies as potentially important in determining delta smelt population trends. These factors are the average value of X2 (a measure of western Delta salinity) in the previous fall ("fall X2"), turbidity in winter as measured by Secchi depth, ammonium concentration in spring in downstream sub-regions of the Delta, and flows that feed the Delta's export pumps in winter and spring. None of these factors met the criteria for inclusion in the best regression equations based on factors with direct effects on delta smelt survival. It is noted that these factors and other factors with indirect effects could have important effects on factors that have direct effects on delta smelt, as suggested in Figure 2, but there was no attempt to identify those relationships here, although it is noted that Delta water flows to the export pumps were incorporated in estimates of proportional entrainment.

Results indicate that delta smelt survival was more sensitive to measures of the effects of individually specified factors with direct effects on fish than to measures of the volume of water within suitable ranges of conductivity, Secchi depth, and temperature (abiotic habitat, the term used in Feyrer et al. [2007]). Once the effects of individually specified factors were accounted for, with attention to their co-occurrence with delta smelt, the volume of water with conductivity, Secchi depth, and temperature in the suitable ranges for each of those three variables did not meet the criteria for inclusion in the best regression equation for fall-to-fall survival, nor did such volumes weighted with prey density, even after prey density terms were removed from the best regression equations for fall-to-fall survival based on factors with direct effect.

Some caution should be taken in interpreting results pertaining to entrainment of delta smelt at state and federal Delta export pumping plants. Estimates of delta smelt entrainment are based on those used in a previous modeling exercise (Kimmerer, 2008). Those methods of estimating proportional entrainment provide a more rational conceptual framework than other methods that have been used (see Grimaldo et al. [2009], for example), because Kimmerer estimated entrainment relative to population size, attempted to estimate the standing crop of delta smelt at the time of entrainment (rather than using abundance estimates derived from samples collected several months earlier), and attempted to overcome uncertainties associated with the fact that larval delta smelt are not actually incorporated in fish salvage data from pumping plants. However, Kimmerer's model estimates are based on a number of assumptions. Of 18 assumptions underlying estimates, Miller (2011) concluded that at least 12 of these assumptions introduced bias, and 11 of those 12 introduced an upward bias in the putative effects of export pumps on delta smelt mortality. This study attempted to correct Kimmerer's estimates to account for that bias, but could do so for just three of the 12 assumptions. The corrections reduced Kimmerer's annual estimates of proportional entrainment by about half, and Miller (2011) concluded that further reductions would be appropriate if other assumptions could be quantified. Furthermore, Kimmerer did not estimate proportional entrainment prior to 1995; however, his estimates were extended back to 1972 using correlations with X2, flow, and Secchi depth measures for those years (as described in supplemental material) and Kimmerer's 1995–2006 estimates and those hind-cast estimates were adjusted to account for bias that could be quantified. Therefore, the role of entrainment as a contributing factor to population trends from fall to summer that are largely determined by density-dependence factors and availability of the preferred foods used by delta smelt is uncertain and likely (still) biased upward.

Ascertaining the importance of prey density in determining population trends in delta smelt in part resulted from attentive specification of factor values. The densities of the two prey species, *Eurytemora* and *Pseudodiaptomus*, were used, summed as the measure of prey density, reflecting findings in several

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previous studies that explicitly reference consumption of these zooplankton by delta smelt (see supplemental material). There was also an attempt to account for the location of delta smelt when estimating prey density, because prey densities in subregions that are not occupied by delta smelt cannot be relevant to delta smelt survival. Moreover, there was an attempt to measure the seasonal low point in prey density in the spring of recent years, when the favored prey *Eurytemora* rises from near zero in late winter and then declines to near zero in May or June, at approximately the same time that other suitable prey species *Pseudodiaptomus* increases in numbers from essentially zero and persists at greater numbers until the following winter (see supplemental material).

It is noted that the importance of the factor, minimum *Eurytemora* plus *Pseudodiaptomus* in April–June, which measures the low point in the food availability for young delta smelt, provides a plausible mechanism for Bennett's observation that almost no early-hatch larvae of delta smelt have survived until later life stages in recent years (Bennett, 2005; USFWS 2009). That spring low point appeared in the mid 1980s; since then, if larval delta smelt hatch prior to the occurrence of this low point in densities of the two zooplankton species, larval survival might exhibit a pattern of low returns.

This study's findings are consistent with recent assertions that contaminant-mediated prey availability shows dominant effects on patterns of the abundance of delta smelt and several other fish in the Delta (Glibert, 2010), although the analysis did not attempt to identify the causes of the substantial changes in prey densities in recent years. Furthermore, the analyses address an observation by Feyrer et al. (2007), who concluded that their analyses of just several physical factors as determinants of delta smelt abundance would have been improved by consideration of other factors, particularly prey density. Without carrying out analyses that accounted for density dependence and included such essential variables as prey availability and predation on delta smelt, they concluded that the average value of X2 in the previous fall was the essential causative agent of subsequent summer juvenile abundance (see Feyrer et al., 2007, and USFWS, 2009). The analyses of this study considered the effects of density dependence and prey density, as well as numerous other factors in addition to average X2 position in the previous fall, and once the effects of prey density were accounted for, no evidence was found of effects of average X2 value in the previous fall on delta smelt population dynamics. Thomson et al. (2009) found that water clarity, position of X2 in winter–spring, and the volume of water exports were important to long-term abundance of delta smelt and other fish but could not explain the recent decline in abundance of delta smelt to record low levels. Mac Nally et al. (2010) found that the position of X2 in the spring in the estuary and increased water clarity were important to delta smelt abundance. Differences between the present findings and those of Thomson et al. and Mac Nally et al. are attributed to this study's focus on those factors that specifically should have direct effects on abundance and to a more precise quantification of environmental factors—including explicitly considering spatial and temporal aspects of prey availability, integrating the specific locations of different life stages of delta smelt in average values of variables, and expressing prey availabilities in terms of densities of zooplankton species known to be preferred by delta smelt. Grimaldo et al. (2009) attributed demographic trend effects to entrainment of delta smelt at the export pumping plants (measured as the number of fish salvaged there) and to export volumes by virtue of the relationship of those flows to rates of fish salvage. While some effect of entrainment (which incorporated effects of export flows) was found on delta smelt survival from fall to summer, entrainment of fish at the export pumps did not exhibit a significant relationship with the population dynamics of the fish over its entire life cycle. Assessment of the relative importance of entrainment in determining delta smelt survival, as well as that of several other factors, during various periods in the past and for various future management actions, awaits further analysis.

It is believed that this study's analysis is the first to combine careful quantification of variables, based on publicly available agency data, with wildlife agency-derived conceptual models transformed to represent the hierarchical manner in which environmental factors interact to affect abundance and survival of delta smelt. The benefits of this approach included a reduction in the occurrence of correlations that might arise by chance, due to the inclusion of many variables relative to the number of years of data, and identification of environmental factors on which future studies can focus in order to elucidate the ecological mechanisms as a basis for management actions, thereby providing a sound basis for agency determinations and policy decisions.

Nonetheless, limitations in the presented analyses are acknowledged. Time-series index values of delta smelt abundance are based on data from surveys that were not explicitly designed to sample that fish species, and more recently initiated surveys that are designed to sample delta smelt more efficiently suffer from lack of longer time series and from the challenges of sampling for a species that now is scarce. In addition there are no data on disease, a factor with a potentially important, direct effect on delta smelt abundance and, with the exception of ammonia, almost no data on contaminants that act directly on delta smelt. Some comfort can be taken in findings that 60 to 70% of the variation in delta smelt survival can be explained by factors included in the analyses, but that finding cannot rule out the importance of disease and contaminants. Further limitations to clearer resolution of the causative factors in the decline of delta smelt include the infrequency with which some environmental factors are being measured. For example, zooplankton samples were taken once or twice per month beginning in 1972 and in the separate, 20-mm survey (CDFG, http://www.dfg.ca.gov/delta/projects.asp?ProjectID=20mm), every two weeks in spring beginning in 1995. Hourly water temperature data are not available prior to the mid 1990s, requiring reliance on correlations with air temperature, which, fortunately, is highly related to water temperature. These limitations are offset somewhat by the large variations in delta smelt abundance from year to year, and the 95% decline in

abundance from 1999 to 2006, suggesting that the signals of environmental effects that have been identified are not subtle and that the current lack of desired levels of precision in and frequency of sampling for underlying data for environmental variables can be tolerated.

The present results, indicating that the importance of prey density as measured by the sum of *Eurytemora* + *Pseudodiaptomus* densities, are supported by observed recent sharp declines in the abundance of two other pelagic fish that share at least partial reliance on the same prey—longfin smelt and young striped bass (Armor et al., 2005; Baxter et al., 2008). Slater (2008) concluded from diet studies that young longfin smelt rely heavily on *Eurytemora* in spring, and Moyle (2002) reported that striped bass larvae frequently feed on *Eurytemora*.

The results presented here suggest several areas for further study. Identification of the environmental factors that determine prey density leads the list. There is a need to elucidate and quantify that part of the effects hierarchy related to prey density. Strong inference can be drawn from this study—if the densities of the favored prey species consumed by delta smelt were to increase substantially, delta smelt abundance should increase. Under that circumstance, whatever the effects of entrainment from fall to summer, those effects would become less important because of density dependence. It would appear, therefore, that the key to recovery of delta smelt to levels of abundance that would reduce conservation concern is increased prey density.

Another area for further study relates to the cause of density dependence. Bennett (2005) suggested that density dependence was important based on his observation that, when comparing two poor stock-recruitment relationships—one with and one without density dependence—the one with density dependence appeared to be a better predictor. The present analysis, incorporating effects of many other factors, provides more convincing evidence that density-dependence effects act on delta smelt from fall to summer, summer to fall, and fall to fall, and it has demonstrated effects at low levels of abundance and reveals effects of other factors. Density dependence from summer to fall, as represented by terms for previous abundance in regression equations for survival, is one reason, along with variation in prey density, why entrainment, while contributing to the best regression equation that describes delta smelt survival from fall to summer, did not meet the criteria for inclusion in the best regression equation that explains survival from fall to fall, that is, from one generation to the next. The cause of density dependence in delta smelt deserves further study. This analysis suggests that it arises from some factor that was not considered here, or from a factor that was considered but was not specified adequately, such that its effects would be revealed. Delta smelt spawn most successfully on cobble or clean sand (J. Lindberg, University of California at Davis, personal communication), and meager sediment data (see http://www.water.ca.gov/bdma/meta/benthic.cfm) suggest that few stations in areas occupied by delta smelt show evidence of cobble or clean sand substrate. Nor was the possibility considered that the contemporary relatively small numbers of fish have led to stochastic demographic phenomena, such as difficulty in finding mates or some other manifestation of Allee effects (Allee et al., 1949). Identifying the cause of density dependence on delta smelt could provide a basis for actions to lessen its effects.

Further study is recommended of the inter-year sawtooth pattern in the abundance of delta smelt. This, too, is an important factor in these regression equations. Failure to identify an environmental factor or factors causing this pattern suggests that its cause may be inherent in the reproductive biology of delta smelt. Approximately 5% of delta smelt live for two years and spawn in the second year, producing a large number of eggs because of their larger size (Bennett, 2005). The existence of distinct demographic units of delta smelt that spawn every two years could explain the sawtooth pattern, but the absence of larger fish in the FMWT and STN argues against this possible explanation.

Predation also deserves more study. The identification of predation as a factor of some importance must be confirmed by more careful studies to overcome the general conclusion drawn by Moyle (2002) that there was little evidence of important predation effects, even when delta smelt were abundant relative to other prey fish many years ago. It is possible that the arrival and proliferation of invasive predators alters Moyle's conclusion.

There was some indication that water temperature is important, but water temperature, depending almost entirely on air temperature, cannot be controlled. However, the increasing trend in water temperature could affect various factors that are important to the abundance of delta smelt, including prey density, and such effects deserve study.

Results also indicate that the development of an effects hierarchy can provide an important framework on which to base analyses designed to assess the relative importance of multiple factors affecting the population dynamics of at-risk species. The findings presented here suggest that multiple environmental factors were responsible for the decline in abundance of delta smelt to record low levels, but that multiplicity is vertical with respect to the effects hierarchy, primarily extending down the hierarchy below prey density rather than horizontally across the hierarchy, as others have surmised (Baxter et al., 2010).

Furthermore, in the case of delta smelt, not only does an effects hierarchy suggest the use of simple linear regression models, but the low sampling errors in abundance relative to process errors indicates that this simple and transparent method of analysis is an appropriate method for identifying environmental factors with direct effects. Therefore, at least for delta smelt and perhaps for other fish for which sampling errors in abundance are relatively low, simple linear regression, as an alternative to more complex life-cycle models, can produce informative results.

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6

Assessment of the RPAs

INTRODUCTION

The RPAs include many specific actions that fall into several categories for each species. The RPA in the FWS biological opinion for delta smelt focuses on limiting OMR negative flows in winter to protect migrating adults (Actions 1 and 2) and to protect larval smelt (Action 3) from entrainment at the export pumps. It also aims to protect estuarine habitat for smelt during the fall by managing the position of X2 (Action 4). Action 5 is to protect larval and juvenile smelt from entrainments by refraining from installing the Head of Old River Barrier (HORB) depending on conditions; if the HORB is installed, then the Temporary Barrier Project's gates would remain open. Finally, Action 6 calls for restoration and construction of 8,000 acres of intertidal and tidal habitat.

The RPA in the NMFS biological opinion for Chinook salmon, Central Valley steelhead, and green sturgeon is divided into far too many specific actions (72) to summarize here, but the biological opinion describes 10 major effects of the RPA on the listed species. They include management of storage and releases to manage temperature in the Sacramento River for steelhead and salmon; maintaining flows and temperatures in Clear Creek for spring-run Chinook salmon; opening gates at the Red Bluff Diversion Dam (RBDD) at critical times to promote passage for salmon and sturgeon; improving rearing habitat for salmon in the lower Sacramento River and in the northern delta; closure of the gates of the Delta Cross Channel (DCC) at critical times to keep juvenile salmon and steelhead out of the interior delta and instead allowing them to migrate out to sea; limiting OMR negative flows to avoid entrainment of juvenile salmon; increased flows in the San Joaquin River and curtailment of water exports to improve survival of San Joaquin steelhead smolts, along with an acoustic tagging program to evaluate the effectiveness of this action; flow and temperature management on the American River for steelhead; a year-round flow regime on the Stanislaus River to benefit steelhead; and the development of Hatchery Genetics Manage-

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ment Plans at the Nimbus (American River) and Trinity River hatcheries to benefit steelhead and fall-run Chinook salmon.

Rather than review every action and every detail, the committee comments on the broader concepts at issue and general categories of actions. Three important goals are to consider how well the RPAs are based on available scientific information; whether there are any potential RPAs not adopted that would have lesser impacts to other water uses as compared to those adopted in the biological opinions, and would provide equal or greater protection for the listed fishes; and whether there are provisions in the FWS and NMFS biological opinions to resolve potential incompatibilities between them. In addition we assess the integration of the RPAs within and across species and across all actions.

Addressing these goals requires explicitly recognizing the fundamental differences in the main conflicting arguments. There is concern, on one hand, that the increasing diversions of water from the delta over a period of many decades and the alteration of the seasonal flow regime have contributed to direct effects on populations of native species through mortality at the pumps, changes in habitat quality, and changes in water quality; and to indirect, long-term effects from alterations of food webs, biological communities, and delta-wide habitat changes. The RPAs propose that their collective effects will offset the impacts of the proposed operations of the SVP and the CWP by manipulating river flows and diversions, along with other actions. An alternative argument is that the effects of water diversions on the listed fishes are marginal. It is argued that the changes imposed by the RPAs would result, therefore, only in marginal benefits to the species, especially now that the delta environment and its biota have been altered (to a new ecological baseline) by multiple stressors. Those stressors obviously include water exports, but this argument suggests a smaller role for water exports in causing the fish declines and hence a smaller role for managing the exports to reduce or halt those declines. However, even with the copious amounts of data available, it is difficult to draw conclusions about what variable or variables are most important among the pervasive, irregular, multivariate changes in the system that have occurred over the past century.

The committee's charge was to provide a scientific evaluation, not a legal one, and that is what is presented below. Nothing in this report should be interpreted as a legal judgment as to whether the agencies have met their legal requirements under the ESA. The committee's report is intended to provide a scientific evaluation of agency actions, to help refine them, and to help the general attempt to better understand the dynamics of the delta ecosystem, including the listed fishes.

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DELTA SMELT

Actions Related to Limiting Flow Reversal on the Old and Middle Rivers (OMR)

The general purpose of this set of actions is to limit the size of the zone of influence around the water-diversion points at critical times. The actions would limit negative OMR flows (i.e., toward the pumps) by controlling water exports during crucial periods in winter (December through March) when delta smelt are expected to be in the central delta (FWS, 2008). The data supporting this approach show an increase in salvage of delta smelt as OMR flows become more negative. However, there are important disagreements about how to express salvage and the choice of the trigger point or threshold in negative flows above which diversions should be limited.

An important issue is whether and how salvage numbers should be normalized to account for delta smelt population size. An increase in salvage could be due to an increase in the number of smelt at risk for entrainment, an increase in negative flows that bring smelt within range of the pumps, or both. Thus, an increase in salvage could reflect a recovery of the smelt population or it could reflect increasingly adverse flows toward the pumps for the remaining smelt population. The biological opinion (FWS, 2008) recognizes this relationship, and that is why salvage is used to calculate the percentage of the population entrained, rather than absolute numbers (FWS, 2008, Figures E-4 and E-5). However, the historical distribution of smelt on which the relationship with OMR flows was established no longer exists. Delta smelt are now sparsely distributed in the central and southern delta (*www.dfg.ca.gov/delta/data*), and pump salvage also has been extremely low, less than four percent of the 50-year average index. Since 2005, a significant portion of the remaining smelt population, 42 percent (Sommer et al., 2009), is in the Cache Slough complex to the north and is therefore largely isolated from the central delta. These changes in the distribution of delta smelt increase the uncertainty surrounding current estimates of the population and its likely response to alterations in delta hydraulics, and until the numbers of smelt rise closer towards the pre-2005 levels, they do not provide a reliable index for incorporation into models for the effects of pumping on smelt salvage.

Different authors have taken different statistical approaches to analyzing the data to interpret the relationship between OMR flows and effects on smelt, and thus chose different thresholds at which OMR flows should be limited. The choice of the limit to negative flows in the RPA gives the benefit of the doubt to the species. But there are important uncertainties in the choice. The different

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trigger points suggested by the different analyses have important implications for water users. The committee concludes that until better monitoring data and comprehensive life-cycle and fish-movement models are available, it is scientifically reasonable to conclude that high negative OMR flows in winter probably adversely affect smelt. We note as well that actions 1 and 2 of the FWS RPA are adaptive in that they depend for their implementation on a trigger related to measured turbidity and measured salvage numbers; they also may be suspended during three-day average flows of 90,000 cfs or greater in the Sacramento River at Rio Vista and 10,000 cfs or greater in the San Joaquin River at Vernalis. However, the portion of the existing smelt population in the Cache Slough complex appears not to move downstream towards the brackish areas (Sommer et al., 2009) and thus they should be largely insulated from the effects of the OMR flows and actions 1 and 2.

The biological benefits and the water requirements of this action are likely to be sensitive to the precise values of trigger and threshold values. There clearly is a relationship between OMR flows and salvage rates, but the available data do not permit a confident identification of the threshold values to use in the action, and they do not permit a confident assessment of the benefits to the population of the action. As a result, the implementation of this action needs to be accompanied by careful monitoring, adaptive management, and additional analyses.

Some monitoring and reporting is required in RPA component 5 (monitoring and reporting). However, more should be required, recognizing limits to the agencies' and operators' human and fiscal resources. Given the uncertainties in any choice of a trigger point, a carefully designed study that directly addresses measures of the performance (effectiveness) of the action is essential. This could include monitoring of variables like salvage at the pumps and numbers of delta smelt adults and larvae at the south ends of OMR channels during pumping actions, but it should also include other variables that might affect both salvage and populations. History shows that salvage and delta smelt indices have been insufficient for such an analysis alone, partly because the populations are small and partly because of the uncertainties in the salvage numbers (e.g., to what degree do they accurately reflect mortality, and to what degree are they affected by sampling error?). This deficiency in the data needs to be remedied. But other "proximate" measures such as monitoring of flows over the tidal cycle between and during the pumping limitations could help to understand the driving mechanism for the predicted entrainment mortality associated with pumping. Measuring mean daily discharges also is not sufficient. Temperature, salinity, turbidity, and possibly other environmental factors should also be monitored at appropriate scales as this action is implemented, to determine the availability of suitable

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A Scientific Assessment of Alternatives for Reducing Water Management Effects on Threatened and Endangered Fishes in California's Bay Delta

habitat in the south delta during periods of reduced pumping. Information also is needed on how fish movement is affected by the immediate water-quality and hydraulic environment they experience. Because the effectiveness of the pumping needs to be expressed in terms of the population, the influence of pumping needs to be identified in more life-stage and area specific measures, In particular, the relevance of the Cache Slough complex needs to be resolved in assessing the effectiveness of pumping restrictions. In addition, because uncertainty is high regarding several aspects of this action, it would be helpful to include an accounting of the water requirements. Ongoing evaluation of performance measures could ultimately reduce the water requirements of actions and increase the benefits to the species. Addressing the effectiveness of the proposed actions on a long-term basis could also support consensus conclusions about the effectiveness of specific actions and increase public trust. To the degree that such studies could be jointly planned and conducted by the agencies and other interested parties, transparency and public trust would be enhanced.

X2 Management for Delta Smelt

Although the mean position of X2, the isohaline (contour line of equal salinity) of total salinity 2, is a measure of the location of a single salinity characteristic, it is used in this system to indicate the position and nature of the salinity gradient between the Sacramento River and San Francisco Bay. The position of X2 is measured in kilometers from the Golden Gate Bridge. In the RPA, it has been used by the agencies as a measure of the amount of smelt habitat—influenced by salinity as well as temperature and turbidity, which are also driven by the river-estuary interaction—and thus to approximate the seasonal extent and shifting of that habitat within the ecosystem. By this reasoning, the position of X2 affects the size of delta smelt habitat (Feyrer et al., 2007; Kimmerer, 2008a).

The RPA's action 4 (FWS, 2008, page 369) proposes to maintain X2 in the fall of wet years at 74 km east of the Golden Gate Bridge and in above-normal years at 81 km east. (The action was restricted to wetter years in response to consultation with the NMFS, which expressed concern that in drier years, this action could adversely affect salmon and steelhead [memorandum from FWS and NMFS to this committee on coordination, January 15, 2010].) The action is to be achieved primarily by releases from reservoirs. The objective of the component is to manage X2 to increase the quality and quantity of habitat for delta smelt growth and rearing.

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The relationship between the position of X2 and habitat area for delta smelt, as defined by smelt presence, turbidity, temperature, and salinity (Nobriga et al, 2008; Feyrer et al., in review), is critical in designing this action. A habitat-area index was derived from the probability of occurrence estimates for delta smelt (fall mid-water trawl survey, FMT) when individuals are recruiting to the adult population. Presence/absence data were used because populations are so small that quantitative estimates of populations probably are unreliable. The authors show a broad relationship between the FMT index and salinity and turbidity, supporting the choice of these variables as habitat indicators. The statistical relationship is complex. When the area of highly suitable habitat as defined by the indicators is low, either high or low FMT indices can occur. In other words, delta smelt can be successful even when habitat is restricted. More important, however, is that the lowest abundances all occurred when the habitat-area index was less than 6,000 ha. This could mean that reduced habitat area is a necessary condition for the worst population collapses, but it is not the only cause of the collapse. Thus, the relationship between the habitat and FMT indexes is not strong or simple. Above a threshold on the x-axis it allows a response on the y-axis (allows very low FMT indices).

The controversy about the action arises from the poor and sometimes confounding relationship between indirect measures of delta smelt populations (indices) and X2. The weak statistical relationship between the location of X2 and the size of smelt populations makes the justification for this action difficult to understand. In addition, although the position of X2 is correlated with the distribution of salinity and turbidity regimes (Feyrer et al., 2007), the relationship of that distribution and smelt abundance indices is unclear. The X2 action is conceptually sound in that to the degree that habitat for smelt limits their abundance, the provision of more or better habitat would be helpful. However, the examination of uncertainty in the derivation of the details of this action lacks rigor. The action is based on a series of linked statistical analyses (e.g., the relationship of presence/absence data to environmental variables, the relationship of environmental variables to habitat, the relationship of habitat to X2, the relationship of X2 to smelt abundance), with each step being uncertain. The relationships are correlative with substantial variance being left unexplained at each step. The action also may have high water requirements and may adversely affect salmon and steelhead under some conditions (memorandum from FWS and NMFS, January 15, 2010). As a result, how specific X2 targets were chosen and their likely beneficial effects need further clarification.

The X2 action for delta smelt includes a requirement for an adaptive management process that includes evaluation of other possible means of achieving the RPA's goal and it requires the establishment and peer review of performance

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measures and performance evaluation. It also requires "additional studies addressing elements of the habitat conceptual model" to be formulated as soon as possible and to be implemented promptly. Finally, it requires the FWS to "conduct a comprehensive review of the outcomes of the Action and the effectiveness of the adaptive management program ten years from the signing of the biological opinion, or sooner if circumstances warrant." This review is to include an independent peer review; the overall aim is to decide whether the action should be continued, modified, or terminated. It is critical that these requirements be implemented in light of the uncertainty about the biological effectiveness of the action and its high water requirements.

Tidal Habitat Action

The proposed RPA calls for the creation or restoration of 8,000 acres of intertidal and associated subtidal habitat in the delta and in Suisun Marsh. A separate planning effort also is under way for Suisun Marsh. The justification provided in the biological opinion is that the original amount of approximately 350,000 acres of tidal wetland has been reduced to less than 10,000 acres today, that the near-complete loss of tidal wetlands threatens delta smelt by reducing productivity at the base of the food web, and that delta smelt appear to benefit from the intertidal and subtidal habitat in Liberty Island, which includes tidal wetlands. This action has been less controversial than the others because it does not directly affect other water users.

However, although the concept of increasing and improving habitat to help offset other risks to smelt is conceptually sound, the scientific justification provided in the biological opinion is weak, because the relationship between tidal habitat and food availability for smelt is poorly understood, and it is inadequate to support the details of the implementation of this action. The opinion notes the importance of high-quality food sources to delta smelt and the association of these food resources with tidal habitats (including wetlands), and it references recent monitoring data from Liberty Island showing that such freshwater tidal habitats can be a source of high-quality phytoplankton that contribute to the pelagic food web downstream (p. 380). However, the specifics of which attributes of tidal habitat are essential to providing these food sources are not addressed.

In addition, the California Department of Fish and Game has raised questions about the details of this action (Wilcox, 2010). They include questions about the relative benefits of vegetated tidal marsh as opposed to open water; the extent to which invasive clams may divert new primary production; the amount of suitable productivity exported from restoration areas; the potential effect of

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the restored habitat on predation; the importance of productivity from vegetated tidal marsh directly or indirectly to the smelt; and the degree to which other fish species might use the habitat, possibly to the detriment of the smelt In briefings to the panel, the importance of ongoing studies in resolving these issues was identified. Identifying the characteristics of the "intertidal and associated subtidal habitat" that the action is expected to produce is needed to ensure that expectations of the outcomes, in terms of both habitat type and species benefits, are clear to all. The relative roles of areas of emergent vegetation, unvegetated intertidal and shallow, highly turbid subtidal habitat must be identified for the action to be effectively implemented.

The committee recommends that this action be implemented in phases, with the first phase to include the development of an implementation and adaptive management plan (similar to the approach used for the floodplain habitat action in the NMFS biological opinion), but also to explicitly consider the sustainability of the resulting habitats, especially those dependent on emergent vegetation, in the face of expected sea-level rise. In addition, there should be consideration of the types and amounts of tidal habitats necessary to produce the expected outcomes and how they can be achieved and sustained in the long term. More justification for the extent of the restoration is needed. The committee supports the monitoring program referred to in Action 6, and appropriate adaptive management triggers and actions.

SALMONIDS AND STURGEON

The NMFS RPA for salmon, steelhead, and green sturgeon is a broad complex of diverse actions spanning three habitat realms: tributary watersheds, the mainstem Sacramento and San Joaquin Rivers, and the delta. On balance, the actions are primarily crafted to improve life-stage-specific survival rates for salmon and steelhead, with the recognition that the benefits also will accrue to sturgeon. The committee agrees with this approach. The conceptual bases of the strategies underpinning many of the individual actions are generally well-founded, although the extent to which the intended responses are likely to be realized is not always clear. Given the absence of a clear, quantitative framework for analyzing the effects of individual and collective actions, it is difficult to make definitive statements regarding the merits of such a complex RPA. Indeed, absent such an analysis, the controversial aspects of some of the RPA actions could detract from the merits of the rest of the RPA.

The assortment of actions among the three habitat realms (watersheds, mainstem rivers, and delta) is designed to improve survival and to enhance con-

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nectivity throughout this system. This approach is consistent with the contemporary scientific consensus on improving ecosystem functioning as a means to improve productivity of anadromous and other migratory species (e.g., NRC 1996, 2004a, 2004b; Williams 2005). Watershed actions would be pointless if mainstem passage conditions connecting the tributaries to, and through, the delta were not made satisfactory.

Watershed and Mainstem River Actions

Watershed-level actions that are implemented in the tributaries are organized and formulated to meet the needs of specific listed populations in that system. The actions target limiting factors specific to those locales and populations. In general, the rationale for conducting the actions appears to be well-founded. However, it is difficult to ascertain to what extent, or even whether, the collective actions will appreciably reduce the risk to the fishes within the watershed or throughout the entire river system. We suggest that inclusion of some type of quantitative analysis using a tool like Ecosystem Diagnosis and Treatment (EDT) model during the planning process may have provided an even stronger justification for the set of actions selected (*http://jonesandstokes.com/*). We understand there is a recent application of EDT in the lower San Joaquin River, by Jones & Stokes, thus providing a precedent for its use in California's Central Valley. EDT is presented here as an example of a quantitative modeling approach that integrates the effects of various actions to produce relative changes in productivity and abundance. The committee emphasizes the need for a quantitative assessment framework, and does not necessarily specifically advocate the use of EDT.

The RPA also prescribes actions to improve mainstem passage conditions, most notably at the Red Bluff Diversion Dam (RBDD). The objective is to provide unobstructed upstream passage at the RBDD, to ensure more efficient access of adult salmonids to restored watersheds, and access for adult sturgeon to spawning grounds. Without such actions connectivity could not be fully realized. Furthermore, the passage improvement at the diversion dam, in combination with increased water delivery from storage reservoirs, is expected to improve smolt survival during downstream migration. This component is well justified scientifically, although the absence of a system-wide salmon survival model limits our ability to evaluate the extent to which this action contributes to improved survival for the populations in question.

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Smolt Survival Near and Through the Delta

The net survival of salmonid smolts though the mainstem rivers and the delta under different water-management operations is of keen interest. Several RPA actions are intended to improve survival of the juveniles as they migrate seaward. Some of these actions have significant water requirements, and so they are controversial. The common goal of these actions is improve smolt survival by retaining a high proportion of the migrating smolt population in the mainstem Sacramento and San Joaquin Rivers. This involves two general approaches: block entrances to the interior delta, or manipulate currents in major channels to reduce the transport of smolt towards the pump facilities and possible entrainment or locations where they may be lost to predation, starvation, or disease. Here we focus on three pivotal actions: the closure of the Delta Cross Channel, the manipulation of OMR flows, and water-management actions in the lower San Joaquin River.

Delta Cross Channel (DCC)

As smolts migrate seaward from the upper Sacramento River they encounter the DCC near Walnut Grove. The DCC can at times draw large volumes of water from the Sacramento River, and some of the smolts follow that current toward the interior delta, where salmon mortality is high.

The objective of this action is to physically block the entrance of the DCC at strategic times during the smolt migration, thereby preventing access to the interior delta. This is a long-standing action that appears to be scientifically justified. However, Burau et al. (2007) estimated that when the DCC gates are open, approximately 45 percent of the Sacramento River flow measured at Freeport is redirected into the delta interior through the DCC and Georgiana Slough. The salmon action (Action Suite IV.1), which under certain triggers requires prolonged closure of the DCC gates from October 1 through June 15, must also consider the effects on delta smelt. The Smelt Working Group (notes from June 4, 2007 meeting) concluded that there could be a small beneficial effect on delta smelt from having the DCC gates open from late May until mid-June.

Although this action does not appear to constitute an important conflict between the needs of smelt and salmon, it illustrates the potential for conflict among the two opinions and the need for closer integration of the actions within the delta that have consequences for more than one of the listed species. This is an example where a systematic analysis of the implications for both species of actions would seem to be a scientific requirement.

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Managing OMR Flows for Salmonids

This RPA action (IV.2.3, Old and Middle River Flow Management) also seeks to limit smolt excursion into part of the delta associated with high smolt mortality, but it does so by manipulating current direction and intensity within the Old and Middle River (OMR) drainages. The objective is to reduce current velocity toward the SWP and CVP facilities, thereby exposing fewer smolts to pump entrainment and being drawn into other unfavorable environments.

To accomplish the objective, the action calls for, reducing exports from January 1 through June 15, as necessary, to limit negative OMR flows to -2,500 to -5,000 cfs, depending on the presence of salmonids. The reverse flow will be managed within this range to reduce flows toward the pumps during periods of increased salmonid presence. The flow range was established through correlations of OMR flow and salmon entrainment indices at the pumps, and from entrainment proportions derived using the particle-tracking model (PTM). While the flow management strategy is conceptually sound, the threshold levels needed to protect fish is not definitively established. The response of loss at the pumps to OMR flow (e.g. figure 6-65 from NMFS, 2009) does not suggest a significant change in the vicinity of the flow triggers, but it does suggest that the loss rate increases exponentially above the triggers. The PTM suggests a gradual linear response in the vicinity of the trigger. However, no analysis was presented for the entrainment rate above the trigger (Figure 6-68 from NMFS, 2009), and it is not clear whether the salvage *rates* as well as salvage numbers were modeled. Therefore, the committee is unable to evaluate the validity of the exponential increase in loss rate above the trigger. Uncertainty in the effect of the flow triggers needs to be reduced, and more flexible triggers that might require less water should be evaluated.

The committee concludes that the strategy of limiting net tidal flows toward the pump facilities is sound, but the support for the specific flows targets is less certain. In the near-term telemetry-based smolt migration and survival studies (e.g, Perry and Skalski, 2008) should be used to improve our understanding of smolt responses to OMR flow levels. Reliance on salvage indices or the PTM results alone is not sufficient.

Additionally, there is little direct evidence to support the position that this action alone will benefit the San Joaquin salmon, unless it is combined with an increase in San Joaquin River flows. Furthermore, we understand this and other flow management actions are coordinated with the delta smelt actions. But we found no quantitative analysis that integrates across the actions to systematically evaluate their aggregate effects on both salmonids and smelt. Understanding

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those interactions will benefit from the development and use of multiple single-species models, including movement models.

Managing Exports and Flows in the San Joaquin River

The objective of this action (IV.2.1) is to reduce the vulnerability of emigrating Central Valley steelhead within the lower San Joaquin River to entrainment into the channels of the south delta and at the pumps by increasing the inflow-to-export ratio. It seeks to enhance the likelihood of salmonids' successfully exiting the delta at Chipps Island by creating more suitable hydraulic conditions in the mainstem of the San Joaquin River for emigrating fish, including greater net downstream flows.

The action has two components: reducing exports, and augmenting San Joaquin River flows at Vernalis. The rationale that increasing San Joaquin inflows to the delta will benefit smolt survival through this region of the delta is based on data from coded-wire tags on smolts. This statistical evidence provides only a coarse assessment of the action, but it indicates that increasing San Joaquin River flows can explain observed increases in escapement. Historical data indicate that high San Joaquin River flows in the spring result in higher survival of outmigrating Chinook salmon smolts and greater adult returns 2.5 years later (Kjelson et al., 1981; Kjelson and Brandes, 1989), and that when the ratio between spring flows and exports increase, Chinook salmon production increases (CDFG, 2005; SJRGA, 2007). In its biological opinion, NMFS therefore concludes that San Joaquin River Basin and Calaveras River steelhead would likewise benefit under higher spring flows in the San Joaquin River in much the same way as fall-run Chinook do. NMFS recognizes this assumption is critical, and thus the biological opinion calls for implementation of a six-year smolt-survival study (acoustic tags) (Action IV.2.2), using hatchery steelhead and fall Chinook.

The controversy lies in the effectiveness of the component of this action that reduces water exports from the delta. The effectiveness of reducing exports to improve steelhead smolt survival is less certain, in part because within the VAMP (Vernalis Adaptive Management Plan) increased flows and reduced exports are combined, and in part because steelhead smolts are larger and stronger swimmers than Chinook salmon smolts. Furthermore, it is not clear in the biological opinion how managing exports for this purpose would be integrated with export management for other actions. The choice of a 4:1 ratio of net flows to exports appears to be the result of coordinated discussions among the interested parties. Given the weak influence of exports in all survival relationships (New-

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man, 2008), continued negotiation offers opportunities to reduce water use in this specific action without great risk to steelhead. Further analysis of VAMP data also offers an opportunity to help clarify the issue.

The committee concludes that the rationale for increasing San Joaquin River flows has a stronger foundation than the prescribed action of concurrently managing inflows and exports. We further conclude that the implementation of the six-year steelhead smolt survival study (action IV.2.2) could provide useful insight as to the actual effectiveness of the proposed flow management actions as a long-term solution.

Increase Passage through Yolo Bypass

This action would reduce migratory delays and loss of adult and juvenile salmon and green sturgeon at structures in the Yolo Bypass. For sturgeon there is substantial evidence that improved upstream passage at Yolo will be beneficial. For salmon, the purpose is to route salmon away from the interior delta and through a habitat that is favorable for growth. This action is scientifically justified and prudent, but its implications for the routing of flows through the system as a whole were not transparently evaluated. For example, moving water through the Yolo Bypass results in less water coming through the Sacramento River. Were the effects of less flow in the Sacramento River considered in the design of the action? Similarly, how were the possible negative consequences of increased flooding of the Yolo Bypass on mercury cycling considered? This exemplifies a general tendency throughout the discussion of the actions to focus on the biologically beneficial aspects but to not fully present how any conflicting consequences or potential for such consequences were considered.

Floodplain Habitat

The floodplain habitat actions (Actions I.6.1-4) involve increasing the inundation of private and public lands within the Sacramento River basin to increase the amount and quality of rearing habitat for juvenile salmon. This action suite appears scientifically justified on the basis of a number of studies (e.g., Moyle et al., 2007; Sommer et al., 2001; Whitener and Kennedy, 1999). Given the strong basis, the committee recommends early implementation of these actions providing the implications for releases and routing of flows on other actions, and any potential negative consequences, e.g., mobilization of mercury, are adequately considered. In addition, the committee suggests detailed studies of the outcome

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of these actions to provide important data for improved life cycle models for these species.

INTEGRATION OF RPAs

The RPAs lack a quantitative analytical framework that ties them together within species, between smelt and salmonid species, and across the watershed. This type of systematic, formalized analysis is necessary to provide an objective determination of the net effect of the actions on the listed species and on water users.

An additional overall, systematic, coordinated analysis of the effect of all actions taken together and a process for implementing the optimized, combined set of actions would help to establish the credibility of the effort overall. Instances of coordination certainly exist. For example, the analysis done by NMFS for the Action IV.2.1 (Appendix 5), is an example of coordination, where the water needs for the 4-to-1 flow-to-export ratio for steelhead were determined and used to refine the action. But coordination is not integration. The lack of a systematic, well framed overall analysis is a serious deficiency. The interagency effort to transparently reach consensus on implications of the combined RPAs for their effects on all the species and on water quality and quantity within the delta and on water operations and deliveries should use scientific principles and methods in a collaborative and integrative manner. Full documentation of decisions is an essential part of such an effort, as is inclusion of the environmental water needs of specific actions and for the entire RPA.

It is clear that integrative tools that, for example, combine the effect over life stages into a population-level response would greatly help the development and evaluation of the combined actions. This was acknowledged by the FWS and NMFS, as well by many of the other presenters during the two days of public session of the committee meeting. There has been significant investment in operations and hydrodynamic models for the system, which have been invaluable for understanding and managing the system. An investment in ecological models that complement the operations and hydrodynamics models is sorely needed. This issue has been raised repeatedly in peer reviews, but still has not been incorporated in the NMFS and FWS analyses. Without a quantitative integration tool, the expected effects of individual actions on the listed species will remain a matter of judgment based on the interpretation of many disparate studies. The NMFS and FWS had to therefore determine the cumulative effects of the multiple actions in each RPA in a qualitative manner. This leads to arguments and disputes that are extremely difficult to resolve and that can undermine

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the credibility of the biological opinions. Commitment to a long-term effort to develop a quantitative tool (or tools) should be part of the RPA, with the explicit goal of formalizing and focusing the sources of disagreement and allowing for the clear testing of alternative arguments.

Transparent consideration of the implications of water requirements also would seem well advised because some of the actions have significant water requirements. DWR and NMFS used CalSim-II and Calite to simulate a collection of actions to determine water needs associated with the NMFS RPA, and concluded that they would amount to 5-7 percent of total water allocations (NMFS, 2009). (Because the actions involving negative OMR flows were similar in timing and magnitude in both the NMFS and the FWS RPAs, all OMR flow management was included in this estimate.) Those, and complementary efforts, should be extended to as many of the actions in combination as feasible, recognizing that the adaptive nature of many aspects of the RPAs, along with variations in environmental conditions and in water demands, limit the degree of certainty associated with such estimates. Credible documentation of the water needed to implement each action and the combined actions, would enable an even clearer and more logical formulation of how the suite of actions might be coordinated to simultaneously benefit the species and ensure water efficiency.

OTHER POSSIBLE RPAs

The committee's charge included the task that the committee should identify, if possible, additional potential RPAs that would provide the potential to provide equal or greater protection to the fishes than the current RPAs while costing less in terms of water availability for other uses. The committee considered RPAs that had been considered and rejected by the agencies or that were recommended to the committee for its consideration (Hamilton, 2010). They included using bubble-curtain technology instead of hard barriers to direct migration of salmon and steelhead smolts, use of weirs to protect wild steelhead from interbreeding and competition, use of weirs to reduce spring-run Chinook from inbreeding and competition with fall-run Chinook, habitat restoration and food-web enhancement, restoration of a more-natural hydrograph, reducing mortality caused by nonnative predators, reducing contaminants, reducing other sources of 'take," implementation of actions to reduce adverse effects of hatcheries, and ferrying San Joaquin River steelhead smolts through the delta.

Some of these are already included to some degree in the RPAs (e.g., reduction of adverse hatchery effects, habitat restoration), and some might not be within the agencies' authorities as RPA actions under the ESA (e.g., contami-

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nant reduction and reduction of other sources of "take"). The committee did not attempt to evaluate whether these suggestions represent good actions to help reduce risks to the listed species in a general attempt at restoration, as that will be addressed in the committee's second report. The committee concludes that none of the above suggested alternative RPAs has received sufficient documentation or evaluation to be confident at present that any of them would have the potential to provide equal or greater protection for the listed species while requiring less disruption of delta water diversions.

Several long-term actions described above have the potential to increase protections for the species while requiring the use of less water for that purpose, because they will result in a better understanding of the system. That better understanding should allow for a better matching of water for species needs, thus potentially reducing the amount of water used in less-effective actions. However, no short-term measure was identified that would provide equal protection to the fishes while reducing restrictions on water diversions.

RESOLVING INCOMPATIBILITIES BETWEEN THE RPAs

The committee noted in its discussion of the Delta Cross Channel action for salmon that it has a small potential for conflict with the requirements for smelt, although the action itself includes a consideration of the effects on smelt. In addition, the agencies have coordinated, and in some cases changed, their actions to avoid or reduce such conflicts, including actions concerning the installation of a "non-physical" barrier at the Head of Old River and the possibility of constructing a barrier across Georgiana Slough (NMFS and FWS, 2010). However, as the committee has noted elsewhere, coordination is not integration, and while it commends the agencies for working together to avoid incompatibilities between the RPAs, it concludes that this coordination is not sufficient to achieve the best results or full evaluation of incompatibilities. To achieve those goals requires an integrated analysis, because without such an analysis it is difficult or impossible to properly evaluate potential conflicts among RPA actions. More important, such an analysis would help to produce more-effective actions. The lack of an integrated analysis also prevented the committee from a fuller evaluation of potential incompatibilities between the RPAs.

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EXPECTATIONS AND PROXIMATE MEASURES

The committee heard several times at the public sessions that the RPA actions for delta smelt are not working as there has been no response in the standard annual abundance indices during the last three years when action-related restrictions have been imposed. Such comments are appropriate, but only if realistic expectations are used to judge effectiveness. In this case, it is unrealistic to expect immediate and proportional responses to actions in annual indices of delta smelt, especially within the first few years of implementation. There are several reasons for this. First, fish abundances are influenced by many factors not affected by the actions. This is true in all estuarine and marine systems, and is simply inherent in fish population dynamics. For example, in the case of the species here, three drought years coincided with the implementation of the actions. Other factors have also varied that would further mask any response in the annual indices.

Second, delta smelt populations are very small. The ability of the annual indices to show changes in response to actions is compromised due to the inherent lack of precision in sampling and constructing indices of abundance when populations are very small. Unlike salmon and steelhead, the adults of which can be counted with great precision as they migrate upstream, delta smelt are more difficult to count as well as being rare. While this is frustrating, little change in the annual indices over a few years neither invalidates the utility of the actions nor do they demonstrate that the actions are effective. Finally, there were no prior quantified estimates of response to calibrate expectations. Expectations would be better established if the RPA proposals more explicitly quantified the nature and the expected timescale of responses in the target species, and detailed exactly what would be done to assess the validity of those predictions.

RPA RECOMMENDATIONS

The committee concluded that the uncertainties and disagreements surrounding some of the RPA actions could be reduced by some additional activities. In general, the committee recommends that, within the limits the agencies face with respect to human and financial resources, a more-integrated approach to analyzing adverse effects of water operations and potential actions to reduce those effects would be helpful. The approach would include a broader examination of the life cycles of each fish species and where possible, integrating analyses across species. Although there is much general evidence that the profound reduction and altered timing of the delta water supply has been part of the reason

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for the degradation of these species' habitats, the marginal benefits of beginning to reverse the damage will be difficult to recognize for some time and there is much uncertainty about how to design attempts at the reversal. At this time, the best that can be done is to design a strategy of pumping limitations that uses the best available monitoring data and the best methods of statistical analysis to design an exploratory approach that could include enhanced field measurements to manage the pumping limitations adaptively while minimizing impacts on water users. Such an approach would include a more explicit and transparent consideration of water requirements, despite the variability in environmental conditions and water demand; and population models to evaluate the combined effects of the individual actions.

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An evaluation of four Sacramento-San Joaquin River Delta juvenile salmon survival studies

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Executive Summary:

An evaluation of four Sacramento-San Joaquin River Delta juvenile salmon survival studies

Background.
The US Fish and Wildlife Service, Stockton Fish and Wildlife Office, has since the mid-1980s conducted several multi-year release-recovery experiments with coded-wire-tagged juvenile Chinook salmon. The objectives of the studies were (1) to estimate survival through the lower portions of the Sacramento and San Joaquin river systems, the California Delta, and (2) to quantify the factors affecting survival. Four of these studies, listed more or less by their historical start dates, are the *Delta Cross Channel*, *Interior*, *Delta Action 8*, and *VAMP* experiments.

Delta Cross Channel: These studies focused on how the position of the Delta cross-channel (DCC) gate affected survival of out-migrating juvenile salmon. When the gate(s) is open, water flow from the Sacramento river into the central Delta increases. The *a priori* hypothesis for these studies was that survival would be lowered with the gate open since the probability of entering the interior Delta would increase and the fish would thereby be more vulnerable to the water export pumps at the state water project (SWP) and at the federal Central Valley project (CVP). Temporally paired releases were made above the DCC (near Courtland) and below the DCC (at Ryde) and recoveries were made at Chipps Island and in the ocean fisheries.

Interior: These studies were somewhat of a follow-up to the *Delta Cross Channel* studies that aimed to more directly compare the survival of fish already in the interior Delta to the survival of fish remaining in the Sacramento River. Temporally paired releases were made, one in the interior Delta (in Georgiana Slough) and one in the Sacramento River (at Ryde), and recoveries were made at Chipps Island and in the ocean fisheries.

Delta Action 8: These studies were essentially an alternative analysis of the *Interior* studies in that the relative survival of interior Delta releases (compared to Sacramento River releases) was to be modeled as a function of water exports. However, with *Delta Action 8* objectives in mind, export levels were deliberately manipulated to increase the scope of inference.

VAMP: In contrast to the other three studies which examined survival for fish out-migrating from the Sacramento River, VAMP focused on the survival of salmon out-migrating from the San Joaquin River. The primary factors of interest were

water export and flow levels. Of additional interest was the effect on survival of placing a barrier at the head of Old River (HORB). When the HORB is in place the chance that a fish will enter Old River from the San Joaquin River is decreased, and presumably the influence of the CVP and SWP, which are located adjacent to Old River, is lessened. Temporally paired releases were made at two or three locations, though a total of five release locations were at one time or another used, and recoveries were made at Chipps Island and in the ocean fisheries, and in more recent years at Antioch.

A positive design feature of all four release-recovery studies was the temporal pairing of releases made at different locations in the river system, i.e., for each upstream release (or releases), a concurrent release was made downstream. The temporal pairing aimed to control for the effect of potentially confounding factors and thereby increase precision.

USFWS staff have previously analyzed these studies at various stages of completion. These analyses utilized the temporal pairing but an underlying probability framework for the release-recovery data was not explicitly specified. The analyses did not account for unequal sampling variation (due to, for example, differing release numbers) nor between release pair variation (e.g., unaccounted-for environmental variation in underlying survival or capture probabilities). Analyses of recoveries at different locations were typically carried out separately on a location-specific basis; e.g., results for recoveries at Chipps Island were analyzed and then the analysis was repeated for recoveries from the ocean fishery.

Bayesian hierarchical models.
In this report, Bayesian hierarchical models (BHMs) were used to reanalyze the data from these studies. The BHM framework explicitly defined probability models for the release-recovery data and accounted for unequal sampling variation and between release pair variation. Recoveries from multiple locations were analyzed in combination. Such a framework is more statistically efficient and coherent than previous analyses in that several levels of uncertainty are explicitly accounted for, using recoveries from multiple locations simultaneously increases precision, and the effect of sample size on precision can be readily examined. However, the costs of the BHM approach include increased model complexity and more technically difficult model fitting procedures, in this case, Markov chain Monte Carlo.

Some assumptions of the BHMs as applied to these studies are worth highlighting. One is that for temporally paired releases the capture probabilities at recovery locations were identical; e.g., for a temporally paired Courtland and Ryde release, the probability that a fish alive at Chipps Island is then caught at Chipps Island is the same for fish from either release location. A related assumption is that the ocean recovery probabilities, which includes survival, spatial distribution, and maturation probabilities, are the same for temporally paired releases. Finally for the *VAMP* studies, where releases at two or three locations were made more or less upstream of one another, and *absolute* survival, as contrasted to *relative* survival is estimated, the survival of fish through in-common downstream sections was assumed the same. For example, given a paired release at Dos Reis and at Jersey Point, fish from Dos Reis that have survived to Jersey Point have the same survival probability from there on as do the Jersey Point releases. Thus, it is assumed that there is no temperature shock, due to differences in truck water temperature and river water temperature, which increases mortality for Jersey Point releases over and above the mortality that will be experienced by Dos Reis fish that have reached Jersey Point. To estimate relative survival, however, between release groups, such shock is acceptable so long as it is the same for both release groups.

Results.
For the most part, the substantive conclusions from the BHM analyses, summarized below, were consistent with previous USFWS analyses.

Delta Cross Channel: There was modest evidence, 64 to 70% probability, that survival of Courtland releases, relative to the survival of Ryde releases, increased when the gate was closed.

Interior: Survival for the interior Delta releases was estimated to be about 44% of the survival for the Sacramento River releases.

Delta Action 8: There was a negative association between export volume and relative survival, i.e., a 98% chance that as exports increased, relative survival decreased. Environmental variation in the relative survival was very large, however; e.g., for one paired release the actual relative survival at a low export export level could with high probability be lower than relative survival at a high export level for another paired release.

VAMP: (a) The expected probability of surviving to Jersey Point was consistently larger for fish staying in the San Joaquin River (say passing Dos Reis) than fish entering Old River, but the magnitude of the difference varied between models somewhat; (b) thus if the HORB effectively keeps fish from entering Old River, survival of

out-migrants should increase; (c) there was a positive association between flow at Dos Reis and subsequent survival from Dos Reis and Jersey Point, and if data from 2003 and later were eliminated from analysis the strength of the association increased and a positive association between flow in Old River and survival in Old River appeared; (d) associations between water export levels and survival probabilities were weak to negligible. Given complexity and number of potential models for the VAMP data, however, a more thorough model selection procedure using Reversible Jump MCMC is recommended.

Discussion.
The resulting BHM analyses are not the ultimate, definitive explanations for what affects juvenile salmon survival through the Delta, particularly for out-migrants from the San Joaquin River. In general data limitations inherent to release-recovery data, i.e., that only one capture is possible, relatively low capture probabilities, relatively high environmental variation, and in the case of *VAMP* the lack of balance in the release strategy, affect the accuracy of estimates of effects on survival.

The BHM framework, however, which allowed for between release variation in survival and capture probabilities, is arguably an improvement over previous analyses. For example, models without such random effects in the survival and capture probabilities, for example, did not fit the data nearly as well as models with random effects. The variation in recoveries was greater than what would be explained by standard, non-random effects logistic regression.

Given the apparently high environmental variation, it may take many replications of temporally paired releases to more accurately quantify the effects of DCC gate position, exports, flow, and HORB on survival. Regarding future work, if CWT release-recovery data continue to be the primary source of information, then (a) making releases below the in-river recovery locations, such as Chipps Island, is recommended to allow separate estimation of capture and survival probabilities and (b) more detailed analysis of ocean recovery patterns for temporally paired releases may be useful. A promising alternative to CWT data is the use of acoustic tags and in-river receivers. Fish must be sacrificed to read CWTs while acoustic tags can be detected, and read, remotely, thus allowing repeated recaptures and increased precision in estimates of survival. Additionally, by judicious placement of receivers, acoustic tags can provide information about migration paths much more readily than CWT data.

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1. Introduction

Throughout the Sacramento and San Joaquin river systems abundances of native Chinook salmon runs are far below historical levels. The declines in abundances of some runs have been drastic enough to result in endangered species listings; e.g., Sacramento winter run Chinook salmon were put on the federal endangered species list in 1994. Reasons for the declines include man induced losses of and changes in adult spawning and juvenile rearing habitat such as the building of dams and various water diversions. To attempt to estimate the survival probabilities for juvenile salmon during the out-migration period, and to understand how survival may be associated with various water conditions and man-made structures, the US Fish and Wildlife Service (USFWS), Stockton Fish and Wildlife Office, has been carrying out various survival studies, more or less annually, for over twenty years.

Many of these studies have focused on survival through and near the California Delta (hereafter the Delta), which is located in the lower reaches of the Sacramento and San Joaquin rivers, including their confluence. The general design of the studies is to release hatchery-reared juvenile Chinook salmon at two or more locations in the river, catch fish downstream using a trawl, typically over a two to three week period, and then, over a two to four year period, recover others in samples taken from ocean fishery catches. At the hatchery the fish are tagged internally with coded-wire-tags and externally marked by excising the adipose fin.

The release and recovery locations and duration of four of the studies are summarized in Table 1. The locations of the various release locations for the studies and the downstream recovery locations (Antioch and Chipps Island) are shown in Figure 1. Schematics of the release-recovery design for each of the studies are shown in Figure 2.

The primary objectives of each study are listed below.

(1) *Delta Cross Channel studies (DCC)*: To determine whether survival of out-migrating juvenile salmon from Courtland, located on the Sacramento River just above the Delta Cross Channel, to Chipps Island is higher when the Delta Cross Channel Gates are closed than when they are open.
(2) *Interior Delta vs mainstem Sacramento studies (Interior)*: To determine whether survival of out-migrating juvenile salmon from Georgiana Slough, located in the north (interior) Delta, to Chipps Island is lower than the survival from Ryde, located in the Sacramento River, to Chipps Island.

(3) *Delta Action 8 studies (DA 8)*: To determine whether survival of Georgiana Slough releases relative to Ryde releases is associated with water project exports (see the Central Valley Project (CVP) and State Water Project (SWP) in Figure 1). (Note: this is an extension of the Interior study.)

(4) *Vernalis Adaptive Management Plan studies (VAMP)*: To determine if survival of out-migrating juvenile salmon from various locations on the San Joaquin River (Durham Ferry, Mossdale, Dos Reis, and Jersey Point) to Antioch and Chipps Island is related to water project exports and San Joaquin River flows.

There are three main purposes of this paper: (1) to evaluate the four studies, some of which are still ongoing, in terms of how well the studies did (or can) achieve their stated objectives, (2) to demonstrate alternative analysis procedures, and (3) to make recommendations for alternative study designs.

Section 2 reviews the data generation and analysis procedures of the USFWS for each study. A general probability framework, hierarchical models, for viewing all four studies is described in Section 3, particular models for each of the studies are given in Section 4, and the framework is applied, with a reanalysis, to each of the studies in Section 5. Sample size determination for some of the studies is discussed in Section 6 and the last section includes recommendations and conclusions. Appendices include technical details of some of the analysis procedures along with computer code.

2. Background: Data Summary and Previous Analyses

2.1. **Data.** In all four studies releases were made in temporally matched pairs or sets, where one release served as a control group in some regard. The term paired release-recovery experiment will be used to describe these studies, even when more than two temporally-matched releases were made. Table 2 summarizes the release-recovery notation used in this report,with more explanation below, along with some of the notation used for models. The release numbers and recoveries for the paired releases in each of the four studies are shown in Tables 3-5.

Notation. Number of fish released is denoted by R and y is the number recovered. Release locations Courtland, Georgiana Slough, Ryde, Durham Ferry, Mossdale, Dos Reis, and Jersey Point are abbreviated Ct, GS, Ry, DF, MD, DR, and JP, respectively. Similarly, recovery locations Chipps Island, Antioch, and the ocean fishery samples are abbreviated by CI, Ant, and Oc. The release and recovery abbreviations are used as subscripts for R and y; for example, recoveries at Chipps Island of releases made from Courtland are represented by $y_{Ct \to CI}$. The ocean recoveries used for analysis are estimated, not observed, values and are shown with a hat, e.g., $\hat{y}_{Ry \to Oc}$. Recovery fractions, numbers recovered divided by number released, are denoted $\hat{r}$; e.g., $\hat{r}_{Ry \to Oc} = \hat{y}_{Ry \to Oc}/R$. The fraction of total recoveries relative to number release are called combined recovery fractions and denoted, for example, $\hat{r}_{Ry \to CI+Oc}$.

In-river smolt recoveries. For all four studies a midwater trawl operating at Chipps Island has been used to capture the released salmon. The trawl is part of a longterm USFWS monitoring program to collect information on the abundance of salmon and other species. A single tow is usually of 20 minute duration and is made either along the north shore, in the middle of the river, or along the south shore. During the period when fish from the studies are out-migrating past Chipps Island, the trawl sampling effort is often increased. For example, sampling during May and June (which is when DCC fish and VAMP fish pass by) and during December and January (when Interior/Delta Action 8 fish pass by) has usually been on a daily basis. For a given sample day at least 10 tows are made, and for some days in May and June the number of tows is doubled.

For the VAMP study (since year 2000) additional trawling has been done using a Kodiak trawl at Antioch in a fashion similar to that at Chipps Island. However, the number of tows made in a sampled day has been more variable than that at Chipps Island; e.g., in year 2005, the number of tows made at Antioch on a given sample day ranged from 5 to 30.

Ocean adult recoveries. The estimated number of ocean recoveries are expansions of observed recoveries taken from samples of landed ocean catches. Spatially and temporally stratified random samples are taken of the catches landed by the commercial troll and sport fisheries at various ports along the Pacific coast throughout the fishing season. Recoveries from a given release can occur at ages 2, 3, 4 or 5; i.e., if out-migrating in year t (age 1), it could be caught in years t+1, t+2, t+3, or t+4. The expanded recoveries from a given release can be written approximately as follows, ignoring the distinction between samples taken of commercial and of sport fisheries. Within stratum h (a particular year-week-area combination), letting N_h be the total number of sample units, n_h be the number selected (within stratum h), and $obs_{x \to h}$ be the number of sample recoveries from release x, the estimated number of recoveries is

$$\hat{y}_{x \to Oc} \approx \sum_{year} \sum_{week} \sum_{area} \frac{N_{year,week,area}}{n_{year,week,area}} obs_{x \to year,week,area}.$$

These estimates will be referred to as *expanded* ocean recoveries. The overall sampling rate is around 20 to 25%, i.e., $n/N \approx 0.20$ to 0.25, and the precision of the estimates is likely relatively high.

Salvaged fish. Out-migrating smolts are also recovered or collected at salvage facilities at the water export locations (one near the state water project, SWP, and one near the federal water project, CVP). The collection facilities are sampled on a regular, fairly systematic basis, and salmon in the sample with a missing adipose fin are sacrificed to read the coded-wire tag. Based on these samples, the total number of tagged fish in the collection facility are estimated. This total, including sacrificed fish, is the estimated salvage. All the collected fish (excluding those sacrificed during sampling) are then trucked from the facilities to locations about 8 to 11 miles upstream of Chipps Island. Fish from the state facility are released either in the Sacramento River, at Horseshoe Bend and, or in the San Joaquin River, at Curtis Landing near Antioch Bridge; from federal facilities releases are either in the San Joaquin River at Antioch, near Antioch Bridge, or in the Sacramento River at Emmanton, near Sherman Island. Salvaged fish are potentially being recovered at Chipps Island and in the ocean fisheries, thus using estimated salvaged fish as a response variable along with recoveries at Chipps Island and elsewhere would potentially lead to double-counting. However, Newman (2003) estimated that the probability of recovery at Chipps Island is in the range of 0.001 to 0.002. Thus the number of fish salvaged and caught at Chipps Island may be relatively small.

Inland recoveries. Returning adult fish are also recovered in freshwater areas, in samples taken to estimate escapement and at hatcheries, sometimes referred to as inland recoveries.

Similar to ocean recoveries, observed and expanded numbers are calculated. Escapement sampling procedures vary considerably throughout the Central Valley, and coverage is uneven. Hatchery fish released away from the hatchery they were reared in are quite likely to stray, with straying probabilities generally increasing with increasing distance from the hatchery. If the straying pattern differs between releases within the same release set, and if the sampling effort differs between return locations, then estimates of adult freshwater returns need to be adjusted accordingly, otherwise bias will result. Such adjustments, however, would be a considerable undertaking, and has not been attempted for the work described herein.

Trawl efficiency measure. For some of the USFWS analyses, a survival "index" was calculated using a measure of the trawl gear efficiency. The idea behind the trawl efficiency measure was to adjust for possible differences in the capture probabilities between releases in a paired release. The measure is based on duration of sampling and the channel width sampled relative to the the length of out-migration time and total channel width at Chipps Island (or Antioch) during that time. The relative width of channel sampled is calculated by dividing the net width by the estimated channel width; e.g., at Chipps Island the channel width is 3900 feet, the midwater trawl net is 30 feet wide, thus the fraction sampled is 30/3900 = 0.00769. The fraction of out-migration time sampled is calculated by dividing the total minutes the net was towed by the number of minutes elapsed between the first and last days of recovery; e.g., if the first recovery was on May 5 and the last on May 11, and the net was towed for 2608 minutes, the fraction is 2608/(7*24*60) = 0.259. Trawl efficiency is then the product of these two fractions, e.g., 0.259*0.00769 = 0.00199. More generically, letting f denote the trawl efficiency measure:

$$f = \left[\frac{\text{Sampling duration}}{\text{Out-migration duration}}\right] \times \left[\frac{\text{Trawl net width}}{\text{Channel width}}\right]$$

Since the calculated out-migration duration is tied to the recovery dates, efficiency estimates can differ between paired releases if the dates of first and last capture do not coincide. Problems with this measure are discussed later.

2.2. **DCC studies.** The Delta Cross Channel (DCC) was built in 1951 by the US Bureau of Reclamation to increase the amount of water transferred from the Sacramento River across the Delta to the federal pumping plant at Tracy (the CVP), which in turns pumps water into the Delta Mendota Canal. There are two movable gates, the DCC gate, which can be opened to let water from the Sacramento River enter the Delta or closed to stop such transfer. Just below the entrance to the DCC on the Sacramento River is the entrance to the Georgiana Slough, which is another way for water, and fish, to enter the Delta. Once

fish enter the Delta, because of the stream geometry and the relative proximity of the SWP and CVP, they are presumably more vulnerable to mortality induced by the pumps.

To understand how the position of the Delta Cross Channel gate, as well as release location relative to the entrance to Georgiana Slough, affected the survival of fish out-migrating down the mainstem of the Sacramento River, a total of thirteen paired releases were made during the spring months (usually May) between 1983 and 1989 at Courtland and at Ryde (Figure 1). All of the releases were juvenile *fall run* Chinook salmon that had been raised at the California Department of Fish and Game's Feather River fish hatchery. The Courtland site is on the mainstem of the Sacramento River just above the entrances to the Delta Cross Channel and Georgiana Slough, while Ryde is on the mainstem below both entrances; thus fish released from Ryde are much less likely to enter the interior Delta. Four pairs were released with the DCC gate closed and nine pairs were released with the DCC gate open. Table 3 shows the numbers released at Courtland and Ryde and the number of recoveries at Chipps Island and the expanded ocean recoveries.

Simple summaries. The combined Chipps Island and ocean fishery recovery fractions for the Courtland ($\hat{r}_{Ct \to CI+Oc}$) and Ryde ($\hat{r}_{Ry \to CI+Oc}$) releases for different gate positions in Figure 3. Given that Courtland is upstream of Ryde, one might expect the Ryde recovery rate to be higher than the Courtland rate no matter what the gate position. However, in 2 of the 4 open gate and 2 of the 9 closed gate situations the point estimate of the Ryde recovery rate is less than the Courtland rate, presumably a reflection of sampling variation. Figure 4, which compares the ratio of recovery fractions, $\hat{r}_{Ct \to CI+Oc}/\hat{r}_{Ry \to CI+Oc}$, for different gate positions, suggests that Courtland releases tend to survive better when the DCC gates are closed. There was one outlier ($\hat{r}_{Ct \to CI+Oc}/\hat{r}_{Ry \to CI+Oc} > 3$) for the open gate release pairs; this is from a 1989 release (Table 3, Group 13), where there were relatively few ocean recoveries from the Ryde release.

Regarding other recoveries, the estimated number of juvenile fish salvaged by the fish export facilities varied widely between releases (Table 3). For only one of the Ryde releases were there ever any salvaged fish at the export facilities. For the Courtland releases there were four releases with a considerable number of salvaged fish, ranging from 182 to 1075; there was no association with gate position, however, in that the gate was closed for two of these four cases. When the gate was closed, some of the salvaged fish likely entered the Delta via Georgiana Slough (since no Ryde fish were recovered for those four cases). Inland recoveries were minimal (fourteen fish total from all 13 pairs), none of which were to their hatchery of origin at Feather River.

Previous USFWS analyses. A USFWS analysis of DCC studies (Brandes and McLain, 2001) was based on survival indices to Chipps Island and expanded ocean recovery rates for both Courtland and Ryde releases. Per release pair, the Chipps Island indices were calculated by dividing the observed number of recoveries at Chipps Island by the estimates of trawl efficiency, f_{Ct} and f_{Ry}, and by the number released, R_{Ct} and R_{Ry}:

$$\hat{I}_{Ct\to CI} = \frac{y_{Ct\to CI}}{f_{Ct}R_{Ct}} = \frac{\hat{r}_{Ct\to CI}}{f_{Ct}} \qquad \hat{I}_{Ry\to CI} = \frac{y_{Ry\to CI}}{f_{Ry}R_{Ry}} = \frac{\hat{r}_{Ry\to CI}}{f_{Ry}}.$$

expanded ocean fishery recovery rates were also calculated, $\hat{r}_{Ct\to Oc}$ and $\hat{r}_{Ry\to Oc}$. Brandes and McLain then carried out four paired t-tests for equality of the indices and ocean recovery rates:

$$H_o : I_{Ct\to CI} = I_{Ry\to CI}| \text{ DCC gate open} \qquad H_o : I_{Ct\to CI} = I_{Ry\to CI}| \text{ DCC gate closed}$$
$$H_o : r_{Ct\to Oc} = r_{Ry\to Oc}| \text{ DCC gate open} \qquad H_o : r_{Ct\to Oc} = r_{Ry\to Oc}| \text{ DCC gate closed}$$

The null hypotheses for the Chipps Island indices were rejected, but were not rejected for the ocean recovery rates.

Manly analyses. The hypotheses tested by Brandes and McLain were hypotheses of no locational differences in survival probabilities between Courtland and Ryde releases *conditional* on a particular DCC gate position.

In contrast, Manly (2002) used the pairing of Courtland and Ryde to advantage by comparing the ratios of Chipps Island indices between the open and closed gate situations using two sample t-tests for the following hypotheses.

$$\begin{aligned} H_o &: \frac{I_{Ct\to CI,t}}{I_{Ry\to CI,t}}|Open = \frac{I_{Ct\to CI,t}}{I_{Ry\to CI,t}}|Closed \\ H_a &: \frac{I_{Ct\to CI,t}}{I_{Ry\to CI,t}}|Open < \frac{I_{Ct\to CI,t}}{I_{Ry\to CI,t}}|Closed \end{aligned}$$

Manly also tested for the equality of differences in indices. In both cases he did *not* find statistically significant differences (using a pooled estimate of variance in each case, the P-values were 0.393 for ratios and 0.250 for differences). These tests are more directly focused on the effect of gate position and are more appropriate than the tests carried out by Brandes and McLain.

2.3. **Interior studies.** In contrast to the DCC studies where the relative survival in the interior Delta was measured indirectly from the Courtland releases which *might* enter the interior Delta (via the DCC or entering Georgiana Slough), the Interior studies focused directly on the relative survival of fish *known to be* in the interior Delta A total of 15 paired releases of *late fall run* fish (reared at Coleman National Fish Hatchery) were made during the months of December and January in Georgiana Slough and at Ryde between 1993/1994 and 2005/2006 to study how the interior Delta releases' survival compared to mainstem releases (and for the related DA 8 study, to study how the relative survival related to exports). The late fall run was chosen with the intent to imitate, to the degree possible, the natural winter run, hoping to to perhaps gain understanding of how export operations impacted the winter run. Releases in Georgiana Slough were made far enough into the slough as to make it unlikely that fish would go upstream to Sacramento River and then travel down the river. Table 4 shows release and recovery data for the Interior studies.

Simple summaries. The overall recovery fractions, recoveries at Chipps Island and in the ocean fisheries divided by release number, are compared for the Georgiana Slough and Ryde release pairs in Figure 5. While there is considerable between-pair variation, the overall recovery fractions for Ryde releases remained higher than those for Georgiana Slough in all cases.

Figure 6 compares the four sets of recovery fractions, at Chipps Island, in the ocean, at the fish facilities, and at inland locations. The straight line drawn on each plot has a slope equal to the mean of the ratio of recovery fractions of Georgiana Slough to Ryde releases, e.g., $(y_{GS\to CI}/R_{GS})/(y_{Ry\to CI}/R_{Ry})$. The means of the ratios were 0.26, 0.43, and 0.39 for at Chipps Island, in the ocean, and inland, respectively, consistent evidence that Georgiana Slough fish were surviving with a lower probability. Conversely, the relative fraction of fish salvaged was proportionately much higher for Georgiana Slough releases compared to Ryde releases, over 16 times greater.

The inland recoveries are perhaps comparable in this study given that the stray rates, calculated as the relative fraction of inland recoveries returning to Coleman National Fish Hatchery (CNFH), e.g., $y_{GS\to CNFH}/y_{GS\to Inland}$, were much the same for Georgiana Slough and Ryde. Excluding one extreme observation, the relationship was quite linear and the correlation coefficient was 0.93.

Previous USFWS analyses. The published analyses (Brandes and McLain, 2001) were made using the data available at the time and it is these results that are discussed below. Since then the analyses have been updated to include the most recent data (Pat Brandes,

personal communication), but the analyses have been similar to what is described here. Brandes and McLain (2001, pp 72-77) calculated survival indices to Chipps Island for the Georgiana Slough and Ryde releases,

$$\hat{I}_{GS\to CI} = \frac{\hat{r}_{GS\to CI}}{f_{GS}} \qquad \hat{I}_{Ry\to CI} = \frac{\hat{r}_{Ry\to CI}}{f_{Ry}},$$

and ocean recovery rates, $\hat{r}_{GS\to Oc}$ and $\hat{r}_{Ry\to Oc}$. Paired t-tests were used to test hypotheses of equality of survival indices or ocean recovery rates for Georgiana Slough and Ryde releases.

$$H_o : I_{GS\to CI} = I_{Ry\to CI} \qquad\qquad H_o : r_{GS\to Oc} = r_{Ry\to Oc}$$

The test results were highly significant in both cases, with Chipps Island survival indices and ocean recovery fractions for Georgiana Slough releases significantly lower than for Ryde releases.

2.4. **Delta Action 8 Experiments.** These experiments overlap with the Interior studies in that the same release-recovery data are used. How the two studies differ is that the Interior studies focus on identifying whether or not differences in survival exist, and, if so, what the magnitude of the differences are, while DA 8 is aimed at *modeling* differences as a function of exports. Thus, on one hand, the DA 8 studies are not so much studies but different analyses of the data provided by the Interior studies. On the other hand, however, export levels have been deliberately manipulated to increase the scope of inference about the possible relationship with survival. Furthermore, in recent years the spatial scope of the DA 8 studies has expanded by additional releases being made at Sacramento, Sherman Island, Vorden, and Port Chicago. These additional releases are, however, not discussed in this report.

Simple summaries. The estimated fractions of juvenile fish salvaged are plotted against exports for both release groups (Figure 7). The loess smooth drawn across the plot suggests a positive association between exports and the fraction of the Georgiana Slough releases that is salvaged. With the exception of the 1995 release, the fraction salvaged for Ryde releases appears to be unrelated to exports.

Previous USFWS analyses. Brandes and McLain (2001, p 75) used an indirect approach to model the ratio of Chipps Island survival indices for Georgiana Slough releases to Ryde releases as a function of exports. Data from some fall run releases (raised at Feather River hatchery) made in the spring months of 1992-1994 were also included in the analysis. The

Chipps Island survival indices were first calculated for the Georgiana Slough and Ryde releases separately and then the ratio of indices was regressed against exports:

$$\frac{I_{GS\rightarrow CI}}{I_{Ry\rightarrow CI}} = \beta_0 + \beta_1 \text{Exports} + \epsilon.$$

The resulting slope estimate, $\hat{\beta}_1$=-0.03, was significantly less than zero, which suggested a negative relationship between exports and the ratio of survival indices.

2.5. **VAMP and earlier studies.** Prior to VAMP which began in 2000, between 1985 and 1999, several release and recovery experiments were carried out in the lower San Joaquin river system and Delta. The objectives of these studies included comparing survival between fish that traveled down Old River, which branches off the San Joaquin River, with the survival of those that continued down the San Joaquin River. Old River passes by the CVP and SWP pumping plants (Figure 1), and water, and fish, from Old River are drawn directly towards the water export pumps. During the first years of experimentation, 1985-1990, paired releases were made directly into Old River and directly into the San Joaquin River near Dos Reis, which is a short distance downstream of the head of Old River. In terms of recovery fractions at Chipps Island, the Old River releases had considerably lower fractions than did Dos Reis releases (the median ratio of fraction for Old River releases to fraction of Dos Reis releases was 0.46 (Table 5)).

Given what was learned about apparent survival in Old River, no further releases were made directly into Old River after 1990, and a removable barrier was installed at the head of Old River (HORB) starting in 1992 to lower the probability that an out-migrating salmon would go down Old River. Partially to study the effectiveness of the HORB, paired releases were made at Mossdale, just upstream of the head of Old River, at Dos Reis, and Jersey Point starting in 1994. The HORB, however, cannot be *placed* in the river when flows are above 5000 cfs and it cannot be *present* in the river at flows above 7000 cfs (San Joaquin River Group Authority 2006), so it has not always been in place every year.

The VAMP studies (year 2000 to the present) have the primary aim of studying the effects of flow and exports on salmon survival given that the HORB is in place. During the VAMP studies exports are not to exceed 3000 cfs. The intended experiment design is to make near-simultaneous releases from three locations: (1) at Durham Ferry on the San Joaquin River, about 12 miles upstream of Old River, (2) Mossdale, and (3) Jersey Point (relatively near the confluence with the Sacramento River); and then to make recoveries downstream at Antioch by a kodiak trawl, further downstream at Chipps Island by a mid-water trawl, and in the ocean fishery (Figure 1). In 2005 and 2006 flows were too high for HORB installation,

however, and releases were made at Dos Reis instead of Mossdale in 2005, and at Mossdale instead of Durham Ferry in 2006.

Table 5 includes the release and recovery data from the pre-VAMP and VAMP studies. Some of the associated covariates used in modeling recoveries are also shown and definitions are provided in Table 6.

The fish used in the pre-VAMP and VAMP studies were all fall run, but the hatchery from which the fish came has varied over time (see the stock column in Table 5). In the earliest years, 1989-1995 most fish came from Feather River Hatchery. For 1996-1999 fish came from both the Feather River Hatchery and the Merced River Fish Facility, but within any given release set all fish came from the same hatchery. Since the VAMP studies began, all fish have come from the Merced River Fish Facility.

A schematic of the release and recovery locations by year is shown in Table 7. A relatively large number of observations (206 in total) have been generated, but imbalance in the release-recovery locations is evident. Lack of balance in the design is also apparent in terms of the covariates of interest, HORB position, flow, and exports (see Figure 8), the export and flow levels are always relatively low when the HORB is in (due to the cfs bound mentioned previously). The imbalance can cloud interpretation of the parameter estimates due to potential confounding. For example, recovery fractions may be higher for Mossdale releases when the barrier is in than when the barrier is out, but exports are (by design), on average, lower when the barrier is in. Fortunately, there are observations with low exports and the barrier being out. Similarly, there are observations with low flows and the barrier out, thus potential confounding may be somewhat alleviated.

A comparison of the combined recovery fractions ($\hat{r}_{x \to Ant+CI+Oc}$) for different release sites is shown in Figure 9. Such a comparison is quite simplistic in that the pairing of releases is not accounted for and sampling variation is ignored. With these limitations in mind, Durham Ferry and Mossdale releases have relatively similar recovery rates, Old River recovery rates are generally lower than Dos Reis recovery rates, and Jersey Point release recovery rates are highest.

Salvage and adult inland recoveries. The estimated numbers of juvenile fish salvaged at the fish facilities have been, on occasion, relatively large (Table 5). For example, a 1986 release from Old River of 100,181 fish had an estimated 62,564 fish salvaged, or about 62% of the number released. The relationship between the HORB (in or out) and the estimated fraction salvaged is plotted in Figure 10 (excluding Old River releases). For Durham Ferry

and Mossdale, both located upstream of the head of Old River, there was a sizeable difference in the fraction salvaged depending on HORB placement with the fraction decreasing with the HORB in; note, however, sampling variation is not being accounted for in this comparison and that for Durham Ferry, in particular, there were only two releases with the barrier out. For Dos Reis and Jersey Point, the HORB had little to no relationship on the fraction salvaged (ignoring the four extreme fractions).

The fraction of observed adult inland recoveries are shown in Figure 11. During the early years (1985-1996) just a few recoveries were made anywhere (it could be due to lower survival or sampling effort); for releases from recent years (2004-2006), adults have yet to return to freshwater (in any numbers). During the intervening years (1997-2003), the observed fraction returning was consistently highest for the Jersey Point releases, while the fraction for Durham Ferry tended to be lower than for Mossdale. When release were made from both Dos Reis and Mossdale, the fraction was slightly higher for Dos Reis releases. Thus the general pattern was higher adult return fractions for releases made further down river. As for the Interior/DA 8 studies, the amount of straying from the natal hatchery was considerable, but an effect of release location on straying was evident in the VAMP releases. For example, for a 2001 release set from Merced River Fish Facility (group 25 in Table 5), fish released from Durham Ferry returned to Feather River Hatchery, Nimbus Hatchery, Stanislaus River, Tuolumne River, as well as the Merced River Fish Facility. Fish released from Jersey Point strayed even more, including above Red Bluff Diversion Dam, Butte Creek, Feather River Hatchery, and Coleman National Fish Hatchery.

Previous USFWS analyses. Previous analyses by the USFWS of the juvenile recoveries (in the trawl samples) and adult recoveries (in the ocean fishery catch samples) from the VAMP and pre-VAMP experiments are described in Chapter 5 of the 2005 Annual Technical Report for the San Joaquin River Agreement (San Joaquin River Group Authority 2006). Discussion herein focuses on some of the analyses on pages 61 through 70 of that report. The VAMP analyses primarily used recovery fractions with no trawl efficiency adjustments. In some cases the observed recovery fraction was calculated with recoveries at a single recovery location, Chipps Island alone or ocean fisheries alone (denoted RR in the Technical Report), i.e., for release x, $\hat{r}_{x\to CI}$ and $\hat{r}_{x\to Oc}$. In other cases the observed recovery rate was based on recoveries at two locations, Antioch and Chipps Island, (denoted CRR for Combined Recovery Rate in the Technical Report), namely, $\hat{r}_{x\to(Ant+CI)}$. In all cases ocean fisheries recoveries were analyzed separately from Antioch and Chipps Island recoveries. The ratio of recovery fractions for upstream releases (Durham Ferry, Mossdale, or Dos Reis) to recovery fractions for downstream releases (Jersey Point) was the response variable used to study

the relationships with flow, export, or HORB effects[2]. Thus releases from Jersey Point were viewed as controls for upstream releases. For example, the response variable used in regression models for Durham Ferry releases relative to Jersey Point releases was $\frac{\hat{r}_{DF\to CI}}{\hat{r}_{JP\to CI}}$. As will be shown later, these ratios can be interpreted as estimates of the ratio of survival probabilities for upstream releases to survival probabilities for downstream releases.

Analysis of the ratios of recovery fractions was carried out in a somewhat piecemeal fashion with freshwater recovery fractions and ocean fishery recovery fractions analyzed separately and analyses primarily examining one covariate at a time, e.g., ratio of ocean fishery recovery fractions regressed on flow, with HORB value fixed (either HORB was in or it was not). Some of the results are summarized in Table 8. In all cases, there were positive associations (although sometimes quite weak) between ratios of recovery rates and flows, but the regression coefficient was statistically significant (at α=0.10 level) with HORB in and non-significant when HORB was not in. Somewhat paradoxically, exports were positively associated with ratios of recovery fractions; an explanation offered for this paradox is that exports and flows were highly positively correlated (the correlation coefficient is 0.88).

2.6. **Comments about previous analyses.**

- *Pairing is advantageous.* A strength of all four designs is the use of paired releases. For the DCC studies, the Ryde releases served as controls to the Courtland releases in that river conditions (temperature, salinity, turbidity, etc) were relatively similar for the two groups. For the Interior and DA 8 studies, the Ryde releases served as controls to the Georgiana Slough releases. For the VAMP studies, the Jersey Point releases were controls for the upstream releases at Dos Reis, Mossdale, and Durham Ferry, although the similarity in river conditions were perhaps weakest in these studies given the greater distances between release locations. This pairing is advantageous in the sense that if these extraneous variables which could (and likely do) affect survival are controlled for, then the statistical efficiency (as measured by standard errors, say) is greater than what unpaired releases could achieve.
- *Trawl efficiency measures and survival indices have questionable accuracy.* Ideally, the trawl efficiency measure would be an estimate of the probability of capturing a fish given that it survived to the trawl location. Then the expected number caught would be the product of number released, survival probability (S) between point of

[2]When the recovery rates in the ratio were based on recoveries at a single location, the ratio was denoted DRR, Differential Recovery Rate. When recovery rates in the ratio were based on recoveries at Antioch and Chipps Island, the ratio was denoted CDRR, Combined Differential Recovery Rate.

release and trawl location, and trawl capture probability p, say , $E[Y] = RSp$. Then an estimate of survival is $y/R\hat{p}$. The survival index calculation implicitly aims to make such an estimate using f as an estimate of p.

However, there are several problems with the calculation of f. Mathematically there is the problem that the observed recovery rate, y/R, can exceed the trawl efficiency measure, f, which then results in survival "indices" exceeding 1. For example, with one of the DCC releases at Courtland (1983), the survival index was 1.22. There is also the potential that prior to the day of first recovery, or after the day of last capture, there were fish passing but none were caught. Assuming, momentarily, that the use of duration of sampling and relative width of river sampled were adequate measures of capture probability, the omission of days prior to first capture and after last capture where fish were still passing would lead to an underestimate of p. Thus the estimate of S, $y/R\hat{p}$, is an overestimate. There is also the practical problem that when there are no captures, the measure of trawl efficiency is zero.

The efficiency calculation should involve a comparison of the volume of water swept by the net with the total volume of water passing Chipps Island during the out-migration period. For example, assuming that the gear has 100% efficiency for fish in the water the mouth of the net passes through, i.e., there is no net avoidance or selectivity for these smolt sized salmon, the probability of capture could be defined to be the fraction of the total water volume passing Chipps Island, say, during the out-migration, that the net passes through.

Due to the likely biases in trawl efficiency estimates, working with the unadjusted recoveries, or raw recovery proportions (numbers caught/number released) seems preferable. Some releases were made downstream of a recovery site, e.g., Chipps Island, and capture probabilities can be estimated directly (Newman 2003 and see Section 6.1).

- *Combined analysis of in-river and ocean recoveries would be more efficient.* Both the Chipps Island and the ocean recoveries provide information about the survival between release points and Chipps Island. Separate analyses of recoveries are not as statistically efficient as analyses that incorporate both sets of recoveries simultaneously, or in the case of VAMP, not as efficient as analyses incorporating Antioch, Chipps Island, and ocean recoveries.
- *Accounting for unequal sampling variability.* None of the analyses for any of the four studies accounts for the fact that the level of sampling variation is not constant. As release numbers change, for one thing, the precision of estimation recovery probabilities will change.

For example, in the 1987 DCC pair, over 100,000 were released from Courtland, in contrast to releases of around 50,000 in 1989; the variances for estimated recovery probabilities will differ even if the underlying true probabilities of recovery were identical.

- *Accounting for between-release pair variability.* The environmental conditions of each paired release vary over time, i.e., between release pairs. The survival and capture probabilities can be viewed as random variables. Ignoring this between-release pair variation may result in overestimates in the precision of the inferences.
- *Indirect analyses may be less accurate than integrated analyses.* Statistical analyses of the data from all four studies proceeded in somewhat of a two-step manner, which will be labeled an indirect analysis. For the DCC studies, the survival indices were calculated first, and then paired t-tests were carried out treating these calculated indices as if they were observations. Similarly, for the Interior studies, the survival indices were calculated for the Georgiana Slough and Ryde releases separately, and then paired t-tests were conducted with these indices. For the DA 8 studies, the ratio of survival indices were first calculated, and then the ratio was regressed against exports. Similarly for the VAMP studies, ratios of recovery fractions were calculated first and then regressed against covariates like flow and exports.

  The criticism leveled at this indirect approach is related to the previously mentioned issues of unequal sampling variability and between-release variability. Ignoring such variability may bias the inferences, or at least provide inaccurate measures of the degree of uncertainty. A more integrated approach for data analysis is to *work directly with the observed recoveries* and to *explicitly allow for unequal sampling variability and environmental variability*, and that is the basis for the hierarchical models described in Section 3.
- *Study-specific comments.* For the DA 8 analyses by Brandes and McLain (2001), the use of fall and late-fall races in the same regression implies a rather strong assumption that the ratio of survival indices, for a fixed export level, is the same for both races. It should be noted that at the time of the previous analysis considerably less data were available (only up through 1998 for Chipps Island recoveries) and fall run results were included to increase sample size. More recent analyses (Pat Brandes, personal communication) have been based on larger sample sizes and only late fall releases.

  For the VAMP analyses, fitting multiple regressions that included flow, exports, and HORB simultaneously would be more statistically efficient and perhaps easier to interpret than doing several simple linear regressions.

3. Hierarchical Probability Models

The objectives of each of the four studies can be restated as aims to estimate unknown parameters of probability models, namely, survival probabilities and parameters for covariates, e.g., water exports, thought to affect survival. Probability models provide a rigorous, statistically defensible basis for both estimating such parameters as well as providing measures of uncertainty about the estimates. Additionally, such models are useful for evaluating study designs and assessing the impact of changes in sample sizes.

Hierarchical, or multi-level, probability models can be used as a common framework for analyzing each of the four studies. Hierarchical models can explicitly account for two levels of variation, temporal and sampling, which exist with the studies. Temporal or environmental variation is the variation over time in survival and capture probabilities. Because each of the studies took place over several years with multiple pairs or sets of releases made, such temporal or between group variation undoubtedly exists. Sampling variation is the between-fish variation within a single release in terms of their fates, e.g., whether or not they are caught at Chipps Island. A third level of variation, reflecting a Bayesian approach, can be included to quantify uncertainty about parameters that characterize the between group variation in survival and capture probabilities.

The hierarchical framework has an additional benefit, which will manifest itself in the VAMP analysis, in that information available in one time period for one spatial location can be used to make inferences for other time periods where such data were not available. For example, releases were only made in Old River during some years of the pre-VAMP period but that data can be used to make inferences about survival in Old River during the other years.

A simplified representation of Bayesian hierarchical models as they relate to the analysis of the release-recovery tag data is shown below.

Level 1, Observations: y's $\sim$ Probability Distribution(R, S_t and p_t)

Level 2, Random effects: S_t, p_t $\sim$ Probability Distribution(η, Covariates)

Level 3, Hyperparameters: $\eta \sim$ Prior Probability Distribution

The first level describes how the number of recoveries varies at random as a function of number released (R) and the survival and capture probabilities, describing sampling variation. The second level describes how survival and capture probabilities vary with time (or release set) and how they depend upon hyperparameters (η) and covariates, e.g., flow. The third level describes prior opinion about the hyperparameters, for example, $\eta = \mathrm{E}[S_t]$, an average or expected survival probability. Scientific interest is largely focused on these hyperparameters. A non-Bayesian hierarchical model would simply remove Level 3 and view the hyperparameters as constants to be estimated along with standard errors and confidence intervals, while Bayesian inference will yield a posterior probability distribution for the hyperparameters.

3.1. **General description of Bayesian hierarchical models (BHMs) for recoveries.** Let $S_{i\to j,t}$ denote the probability of surviving from location i to location j for release pair or set t and let $p_{k,t}$ be the probability of capture at location k for set t. Also let $R_{i,t}$ equal the number of fish released at location i for release set t and let $y_{i\to j,t}$ be the number of fish out of the $R_{i,t}$ that were recovered at location j. Unless deemed necessary, the subscript for set t will often be omitted. The notation r will be used for recovery probabilities which are the product of survival and capture probabilities, e.g., $r = Sp$.

Level 1, within release sampling variation: The first level in the hierarchy is a probability model for the recoveries *given* the release group specific survival and capture probabilities. For example, suppose R_{Ryde} fish are released at Ryde and captures are then made at Chipps Island. The recoveries, $y_{Ryde\to CI}$, follow some distribution that depends on R_{Ryde} and the product $S_{Ryde\to CI}p_{CI}$:

$$y_{Ryde\to CI} \sim \text{Distribution}(R_{Ryde}, S_{Ryde\to CI}p_{CI})$$

Particular distributions will be described later[3].

Level 2, between release temporal variation: The second level in the hierarchy is a probability model for the survival and capture probabilities, S and p. Referring to the previous Ryde to Chipps Island example:

$$\begin{aligned} S_{Ryde\to CI} &\sim \text{Distribution}\left(\mu_{S_{Ryde\to CI}}, \sigma^2_{S_{Ryde\to CI}}\right) \\ p_{CI} &\sim \text{Distribution}\left(\mu_{p_{CI}}, \sigma^2_{p_{CI}}\right) \end{aligned}$$

[3]It should also be noted that the expanded ocean recoveries, $\hat{y}_{i\to Oc}$, will be modeled at this level rather than the observed ocean recoveries. Thus in fairness to previous USFWS analyses, this approach is to some degree an indirect approach and is not fully integrated.

where μ and σ^2 are the mean and variance, respectively. For all four studies the questions to be answered can be re-expressed as questions about how S, or, more basically, how μ_S varies between release locations or under different experimental conditions.

Level 3, parameter value uncertainty. The third level of the hierarchy consists of probability distributions for the unknown parameters of the distributions in the second level. These distributions are called prior probability distributions, or simply priors. In particular, priors are specified for the parameters of the distributions for survival and capture probabilities. For example, again referring to the Ryde to Chipps Island example:

$$\mu_{S_{Ryde\to CI}} \sim \text{Distribution}(\alpha_1, \beta_1) \qquad \sigma^2_{S_{Ryde\to CI}} \sim \text{Distribution}(\alpha_2, \beta_2)$$
$$\mu_{p_{CI}} \sim \text{Distribution}(\alpha_3, \beta_3) \qquad \sigma^2_{p_{CI}} \sim \text{Distribution}(\alpha_4, \beta_4),$$

where α_i, β_i, i=1,2,3,4, are fixed *hyperparameters*.

3.2. **Remarks.** Before describing the specific hierarchical model formulations for the four studies, some general comments about BHMs for release-recovery data are made.

(1) *Bayesian vs Frequentist inference.* With Bayesian methods (Carlin and Louis 1996, Gelman, Carlin, Stern, and Rubin 2004), uncertainty about unknown parameters before analyzing (and sometime before collecting) the data is expressed by means of specifying prior probability distributions for these parameters; e.g., Level 3 above. Bayesian inference proceeds by calculating the *posterior* distribution for the parameters conditional on the data. This procedure is known as updating the prior with the data and proceeds by using Bayes theorem, which can be written generically as follows. Letting θ denote the unknown parameters,

$$\Pr(\theta|Data) \;=\; \frac{\Pr(\theta, Data)}{\Pr(Data)} = \frac{\Pr(Data|\theta)\Pr(\theta)}{\Pr(Data)},$$

where $\Pr(\theta)$ is the prior distribution and $\Pr(\theta|Data)$ is the posterior distribution. Note that $\Pr(Data|\theta)$ is the likelihood, i.e., the probability of the observed data viewed as a function of the parameter θ.

An alternative is classical frequentist inference whereby parameters are viewed simply as unknown constants and no probability distributions are used to characterize uncertainty about them. In the case of a hierarchical model, there are just two levels, the first and second levels. Inference calculations are based solely on the likelihood, $\Pr(Data|\theta)$ and maximum likelihood estimates of the unknown parameters, e.g., $\mu_{S_{i\to j}}$, are calculated. Such estimates are, somewhat confusingly, called empirical Bayes estimates; however, the inference procedure is frequentist, not Bayesian.

A Bayesian approach has been chosen here for pragmatic reasons. With modern computing resources, integration algorithms such as Markov chain Monte Carlo (MCMC, Gilks, Spiegelhalter, and Richards, 1996), and associated software such as WinBUGS (Spiegelhalter, Thomas, and Best, 2003), it is easier to fit a hierarchical model using Bayesian methods than it is using frequentist methods.

However, the most common complaint about Bayesian methods is the influence of prior distributions on the results. If there are sufficient data and if the prior distributions are sufficiently "non-informative", then the resulting posterior distribution is largely a function of the data. In the analyses described later, sensitivity to the choice of prior is assessed.

For the sake of comparison, however, for the DCC and Interior studies it turns out that classical analyses of hierarchical models are relatively easy to carry out and will be presented along with the Bayesian analyses.

(2) *Level 1 models.* Multinomial distributions for recoveries are one possibility for the first level. Such distributions result by assuming that within and between release groups the fates of each fish are independent and that within a particular release group, all fish have the same probabilities of survival and capture. For example, suppose releases are made at Ryde and recoveries are made at Chipps Island and in the ocean fisheries. The conditional distribution for recoveries at Chipps Island and in the ocean fisheries is multinomial (Mn):

$$y_{Ry\to CI}, y_{Ry\to Oc}|\Theta \quad \sim \quad \mathrm{Mn}\left(R_{Ry}, S_{Ry\to CI}p_{CI}, S_{Ry\to CI}(1-p_{CI})r_{CI\to Oc}\right),$$

where $\Theta = (S_{Ry\to CI}, p_{CI}, r_{CI\to Oc})$[4].

On the other hand, if fish within a single release do not behave independently, e.g., they school, then the variability in observed recoveries can be larger than that expected according to multinomial (or binomial) distributions. When the observed variance exceeds that expected for a particular distribution, then it is said that there is overdispersion. For example, suppose R=50,000 fish are released on ten occasions, the expected recovery probability is Sp=0.02, and the number of recoveries is hypothesized to be Binomial(R=50,000, Sp=0.02). The expected number of recoveries is RSp=1000 and the theoretical variance is $RSp(1-Sp)$= 50,000*0.02*0.98 = 980. Suppose the observed number of recoveries from ten groups of 50,000 releases was (951, 1026, 955, 942, 945, 1021, 1059, 955, 1059, 998). The average is 991, close to the expected number, but the variance is 2236, much larger than 980, and evidence for overdispersion. An alternative to the binomial distribution is the negative binomial and details as to its formulation are given later.

[4]The ocean recovery probability $r_{CI\to Oc}$ is a rather coarse summarization. It is a complicated function of survival, movement, maturation, and fishery harvest probabilities.

Overdispersion can also result from the fact that expanded ocean recoveries, $\hat{y}_{1\to 3,t}$, will be used instead of actual recoveries and the negative binomial distribution is again one means to approximately account for this.

(3) *Level 2 models.* The Level 2 models that will be considered are all based on normal distributions for transformations of survival and capture probabilities or their products. The logistic-normal formulation is commonly used to model probabilities (Newman 2003), and often done for convenience. The logit transformation of a probability π is

$$logit(\pi) \;=\; \log\left(\frac{\pi}{1-\pi}\right).$$

While π is restricted to the interval [0,1], $logit(\pi)$ can take on any real number value, thus capable of being modeled by a normal distribution. Logistic-normal probability models for the survival and capture probabilities would be

$$\begin{aligned} logit(S_{i\to j,t}) &\sim \text{Normal}\left(\mu_{S_{i\to j}}, \sigma^2_{S_{i\to j}}\right) \\ logit(p_{k,t}) &\sim \text{Normal}\left(\mu_{p_k}, \sigma^2_{p_k}\right). \end{aligned}$$

The expected values, e.g., $\mu_{S_{i\to j}}$, will in some cases be modeled as functions of covariates.

Even if independence does hold at the observation level (Level 1), the variation in the survival and capture parameters between releases will induce overdispersion in the observations. In other words, the variation in the observed recoveries will be larger than that due to a multinomial distribution with parameters equaling the expected survival and capture probabilities. As a simple example,

$$\begin{aligned} y|S,p &\sim \text{Binomial}(R, Sp) \\ S &\sim \text{Distribution}(\mu_S, \sigma^2_s) \\ p &\sim \text{Distribution}(\mu_p, \sigma^2_p) \end{aligned}$$

While the *conditional* variance of y is RSp, the *unconditional* variance is *not* $R\mu_S\mu_p$, it is larger than that[5].

(4) *Accounting for the pairing of releases.* The grouping or pairing of releases will be reflected in levels 1 and 2 of the hierarchical model. Within a release pair a shared capture probability will be assumed. Thus a single value of p realized at Level 2 will be used for the paired releases in the Level 1 distributions. Furthermore, within a release pair, when one release is made directly upstream of another release, then

[5]Suppose $y|\theta$ is Binomial(R,θ) and E[θ]=μ_θ and Var[θ]=σ^2_θ. The conditional variance of y is $R\theta(1-\theta)$ while the unconditional variance is $R\theta(1-\theta)+\sigma^2_\theta R(R-1)$. Thus $\sigma^2_\theta R(R-1)$ is the amount of overdispersion.

the survival probabilities are assumed the same for the stream sections that both groups travel down. Note that this assumption means that fish released downstream of an upstream release do not experience any additional mortality at time of release, say a release shock effect, as might be due to a temperature difference between water temperature in the truck transporting the fish and the water temperature in the river. Additionally, there is an assumption that the upstream and downstream releases essentially overlap one another spatially and temporally from the downstream location onwards—i.e., the two releases temporally and spatially coincide; the issue of timing is discussed in the next enumerated point.

For example, consider a paired release made at Durham Ferry and Mossdale with kodiak trawl sampling at Antioch. The recovery probability for Durham Ferry releases is the product $S_{DF \to MD} S_{MD \to Ant} p_{Ant}$, while the recovery probability for Mossdale releases is $S_{MD \to Ant} p_{Ant}$.

The efficiency of the paired release design manifests itself by these shared parameter values, e.g., $S_{MD \to Ant}$ and p_{Ant}. Not only are there fewer parameters to estimate, but also variation in capture probabilities and other shared survival probabilities have been *controlled for* within the release pair. There are many environmental conditions, e.g., water temperature, turbidity, or salinity, that can influence survival and capture probabilities in addition to the factors of interest, e.g., DCC gate position, geographic location, exports. With paired releases, however, the environmental conditions are often quite similar meaning that parameters that do differ within a release pair can be estimated more precisely than for unpaired releases.

(5) *Assumption of equal capture probabilities.* Within a release set, parameters for which shared values are assumed include the freshwater capture probabilities (i.e., Chipps Island midwater trawl for all four studies, and Antioch kodiak trawl for VAMP studies). This assumption can be assessed if releases are made downstream of the freshwater trawl sites and if the ocean recovery probabilities are assumed the same, because then estimates of the freshwater capture probabilities can be made (Newman 2003, and see later in this report). In the absence of such data, a less formal comparison can be made by examining the recovery pattern over time along with the trawl fishing schedule and effort. If the trawl effort is more or less consistent throughout the out-migration periods of releases in a release pair, then whether or not the out-migration timing is the same does not matter.

As an informal check, the distributions of recoveries at Chipps Island over time were compared within release pairs for a few cases. Figure 12 shows the percentage of total recoveries by date for three sample sets, one from DCC, one from Interior/DA 8, and one from VAMP. For the DCC example (from 1983),the time intervals of

recovery were very similar (both had first recoveries on 19 May, Courtland's last recovery was 20 June and Ryde's last was 7 June), and the general distribution is relatively similar. For the Interior/DA 8 example (from 1999), the Ryde recoveries tended to arrive earlier than the Georgiana Slough recoveries, but the duration of the recovery period was longer for the Ryde releases. For the VAMP example (from 2000), the recovery distributions by date are consistent with what one would expect, with Jersey Point recoveries tending to precede those from Mossdale which in turn preceding those from Durham Ferry.

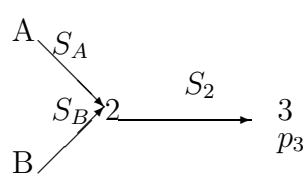
(6) *Estimability of survival and capture probabilities.* The release-recovery design affects the estimability of parameters. Unless a release is made downstream of a recovery location (say j), the capture probability at the recovery location cannot be estimated separately from the survival probability for the next-nearest upstream release (located at i say). What can be estimated is the product of the survival probability and the capture probability, $S_{i\to j}p_j$. In the case of two releases made above a single recovery point, assuming equal recapture probabilities at a downstream location, the ratio of survival probabilities can be estimated. In the case where the furthest upstream releases must travel past the downstream release location, this ratio will be the survival probability between the two upstream locations.

For example, the case where releases are made in the same linear stretch of waterway (locations 1 and 2) with a single downstream recovery site (location 3) is shown schematically as:

$$1 \xrightarrow{S_1} 2 \xrightarrow{S_2} \underset{p_3}{3}$$

In this case the parameter combinations $S_1S_2p_3$ and S_2p_3 are estimable; e.g., $\widehat{S_1S_2p_3} = y_{1\to 3}/R_1$ and $\widehat{S_2p_3} = y_{2\to 3}/R_2$. The upstream survival, S_1, is then estimable, e.g., $\hat{S}_1 = \widehat{S_1S_2p_3}/\widehat{S_2p_3}$, but downstream survival, S_2 is not.

When releases are made at locations upstream of a recovery point where one release group's travel path does not completely coincide with the other group's path is shown schematically as:



where releases are made at locations A and B, but not 2. In this case $S_AS_2p_3$ and $S_BS_2p_3$ are estimable, as is the ratio S_A/S_B. In the case of non-estimable parameters, notation for estimable *combinations* of parameters will be written; e.g., r for Sp.

4. Methods

4.1. **DCC Studies.** The primary objective is to determine how DCC gate position affected the relative survival of Courtland to Ryde releases. This relative survival will be quantified in the hierarchical model(s) by a parameter θ_t that is the ratio of the survival probability between Courtland and Chipps Island to the survival probability between Ryde and Chipps Island, where θ_t is a function of DCC gate position. It was assumed that gate position did not affect Ryde releases.

Several different Bayesian hierarchical models were fit (and one non-Bayesian model) but for all the models the parameterization of the ocean recovery probabilities were the same. The probability that a fish from a Ryde release is recovered in the ocean fishery is denoted $r_{Ry\to Oc}$ and can be viewed as being the following product of survival and capture probabilities:

$$r_{Ry\to Oc} \quad = \quad S_{Ry\to CI}(1-p_{CI})r_{CI\to Oc}.$$

Furthermore, this probability was assumed the same for Ryde and Courtland releases within the same release pair. Within a release pair, it was also assumed that the capture probability at Chipps Island was the same.

Bayesian hierarchical model. The details of one of the BHMs are shown here. Variations on this BHM included changes in all of the three levels of the model (possibilities are discussed in Section 4.6). This BHM was based on the following assumptions (repeating some stated previously):

- individual fish fates are independent;
- within a single release, S and p are identical for all travel paths and recovery locations;
- the survival probability from Courtland to Chipps Island is no greater than the survival probability from Ryde; i.e., $0 \leq \theta_t \leq 1$;
- within a paired release, the capture probability at Chipps Island is the same;
- within a paired release, the probability that a fish alive just below Chipps Island (thus not captured at Chipps Island) is then caught in the ocean fisheries is the same.

Level 1:

$$(1) \qquad y_{Ct\to CI,t}, \hat{y}_{Ct\to Oc,t}|\theta_t, r_{Ry\to CI,t}, r_{Ry\to Oc,t} \quad \sim \quad \mathrm{Mn}\left(R_{Ct,t}, \theta_t r_{Ry\to CI,t}, \theta_t r_{Ry\to Oc,t}\right)$$

$$(2) \qquad y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc,t}|\theta_t, r_{Ry\to CI,t}, r_{Ry\to Oc,t} \quad \sim \quad \mathrm{Mn}\left(R_{Ry,t}, r_{Ry\to CI,t}, r_{Ry\to Oc,t}\right).$$

Level 2:

$$logit(\theta_t) \sim \text{Normal}\left(\beta_0 + \beta_1 I_{DCC_t=closed}, \sigma_\theta^2\right) \tag{3}$$

$$logit(r_{Ry\to CI,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \tag{4}$$

$$logit(r_{Ry\to Oc,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to Oc}}, \sigma^2_{r_{Ry\to Oc}}\right) \tag{5}$$

where $I_{DCC_t=closed}$ equals 1 when the cross-channel gates are closed, and 0 otherwise.

Level 3:

$$\beta_0, \beta_1, \mu_{Ry\to CI,t}, \mu_{Ry\to Oc,t} \sim \text{Normal}(0, 1.0E+6) \tag{6}$$

$$\sigma_\theta^{-2}, \sigma^{-2}_{r_{Ry\to CI}}, \sigma^{-2}_{r_{Ry\to Oc}} \sim \text{Gamma}(0.001, 0.001) \tag{7}$$

Priors for the variances were specified in terms of the inverse of variance, the precision, i.e., inverse gamma prior distributions were used.

The key parameter in this formulation is β_1 in Level 2. Positive values would be consistent with the DCC closure increasing survival.

The Level 2 modeling of the Ryde recovery probabilities, $r_{Ry\to CI,t}$ and $r_{Ry\to Oc,t}$, is simplistic in that variation in the survival and capture probabilities is to some degree a function of nonrandom measurable factors. For example, the capture probabilities at Chipps Island are indeed a function of the amount of trawling that occurs; similarly, capture probabilities in the ocean fishery are a function of fishing seasons and gear regulation. The overall results are thought to be relatively robust to ignoring such structural, i.e., nonrandom, effects, unless there is some systematic trend in such factors, and one consequence of such coarse modeling will likely be relatively large variances in the logit normal model.

Non-Bayesian hierarchical model. In this formulation the Level 1 formulation is identical to the BHM. For Level 2, however, the exact distributions for the survival and capture probabilities were not specified, just the means and variances are denoted.

Level 1:

$$y_{Ct\to CI,t}, \hat{y}_{Ct\to Oc,t}|\Theta \sim \text{Mn}\left(R_{Ct,t}, \theta_t r_{Ry\to CI,t}, \theta_t r_{Ry\to Oc,t}\right)$$

$$y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc,t}|\Theta \sim \text{Mn}\left(R_{Ry,t}, r_{Ry\to CI,t}, r_{Ry\to Oc,t}\right).$$

Level 2:

$$\theta_t \sim \text{Distribution}\left(\mu_{\theta(DCC_t)}, \sigma^2_{\theta(DCC_t)}\right) \tag{8}$$

$$r_{Ry\to CI,t} \sim \text{Distribution}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \tag{9}$$

$$r_{Ry\to Oc,t} \sim \text{Distribution}\left(\mu_{r_{Ry\to Oc}}, \sigma^2_{r_{Ry\to Oc}}\right) \tag{10}$$

where DCC_t= Open or Closed and μ and σ^2 denote the mean and variance of the (unspecified) distribution.

Under this formulation, the key parameter is $\mu_{\theta(Closed)}/\mu_{\theta(Open)}$. To estimate this ratio, the individual release specific θ's are estimated as follows.

$$\hat{\theta} = \frac{\hat{r}_{Ct\to CI+Oc}}{\hat{r}_{Ry\to CI+Oc}} \tag{11}$$

The parameters $\mu_{\theta(Open)}$ and $\mu_{\theta(Closed)}$ can be estimated by weighted averages of the $\hat{\theta}$'s:

$$\hat{\mu}_{\theta(Open)} = \sum_{t=1}^{n_{Open}} w_{t|Open}\hat{\theta}_{t|Open} \tag{12}$$

$$\hat{\mu}_{\theta(Closed)} = \sum_{t=1}^{n_{Closed}} w_{t|Closed}\hat{\theta}_{t|Closed}, \tag{13}$$

where the weights are inversely proportional to the estimated variances:

$$w_t = \frac{1/var(\hat{\theta}_t)}{\sum_{i=1}^{n} 1/var(\hat{\theta}_i)}. \tag{14}$$

The variances are estimated using the delta method. Details of the delta method are given Appendix A (in particular a sample based estimate of $V(\hat{\theta}_t)$, shown in the lines following Equation (59), is used).

The ratio of $\mu_{\theta(Open)}$ and $\mu_{\theta(Closed)}$ can be estimated using (12) and (13):

$$\widehat{\left(\frac{\mu_{\theta(Open)}}{\mu_{\theta(Closed)}}\right)} = \frac{\hat{\mu}_{\theta(Open)}}{\hat{\mu}_{\theta(Closed)}} \tag{15}$$

The standard error for (15) can be calculated by using a hierarchical bootstrapping procedure (described in Appendix B) to produce resampled estimates of $\hat{\mu}_{\theta(Closed)}$ and $\hat{\mu}_{\theta(Open)}$.

4.2. **Interior studies.** For the Interior studies, interest is solely in the ratio of survival probabilities of interior Delta releases (Georgiana Slough) and mainstem releases (Ryde), which will be denoted θ and defined equal to $S_{GS\to CI}/S_{Ry\to CI}$.

Several BHMs and one non-Bayesian hierarchical model were fit to the Interior data. Just one of the BHMs is shown in detail here, and the assumptions for this model are essentially identical to the one shown for DCC and are not repeated here.

Bayesian hierarchical model.

Level 1:

$$y_{GS\to CI,t}, \hat{y}_{GS\to Oc,t}|\theta_t, r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{GS,t}, \theta_t r_{Ry\to CI,t}, \theta_t r_{Ry\to Oc,t}\right) \tag{16}$$

$$y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc,t}|r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{Ry,t}, r_{Ry\to CI,t}, r_{Ry\to Oc,t}\right). \tag{17}$$

Level 2:

$$log(\theta_t) \sim \text{Normal}\left(\mu_\theta, \sigma_\theta^2\right) \tag{18}$$

$$logit(r_{Ry\to CI,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \tag{19}$$

$$logit(r_{Ry\to Oc,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to Oc}}, \sigma^2_{r_{Ry\to Oc}}\right) \tag{20}$$

Level 3:

$$\mu_\theta, \mu_{Ry\to CI,t}, \mu_{Ry\to Oc,t} \sim \text{Normal}(0, 1.0E+6) \tag{21}$$

$$\sigma_\theta^{-2}, \sigma^{-2}_{r_{Ry\to CI}}, \sigma^{-2}_{r_{Ry\to Oc}} \sim \text{Gamma}(0.001, 0.001) \tag{22}$$

The key parameter in this model is the parameter μ_θ, where negative values would indicate lower survival for Georgiana Slough releases relative to Ryde releases.

Non-Bayesian hierarchical model. The level 1 model is identical to the BHM.

Level 1:

$$y_{GS\to CI,t}, \hat{y}_{GS\to Oc,t}|\theta_t, r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{GS,t}, \theta_t r_{Ry\to CI,t}, \theta_t r_{Ry\to Oc,t}\right)$$

$$y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc,t}|r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{Ry,t}, r_{Ry\to CI,t}, r_{Ry\to Oc,t}\right).$$

Level 2:

$$\theta_t \sim \text{Distribution}\left(\mu_\theta, \sigma_\theta^2\right) \tag{23}$$

$$r_{Ry\to CI,t} \sim \text{Distribution}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \tag{24}$$

$$r_{Ry\to Oc,t} \sim \text{Distribution}\left(\mu_{r_{Ry\to Oc}}, \sigma^2_{r_{Ry\to Oc}}\right) \tag{25}$$

The parameter of primary interest in this formulation is μ_θ which can be estimated by

$$\hat{\mu}_\theta = \sum_{t=1}^{n} w_t \frac{\hat{r}_{GS\to CI+Oc,t}}{\hat{r}_{Ry\to Ci+Oc,t}}, \tag{26}$$

where the weight, w_t, is equation (14). For the 2005 and 2006 release pairs, only the Chipps Island recoveries are available (Table 4), and $\hat{r}_{GS\to CI}/\hat{r}_{Ry\to CI}$ was used instead. Bootstrapping was used to estimate standard errors and calculate confidence intervals.

4.3. **Delta Action 8 Experiments.** The Bayesian hierarchical models tried were nearly identical to those for the Interior study except that the ratio $\theta = S_{GS\to CI}/S_{Ry\to CI}$ was modeled as a function of exports.

The assumptions are the same as for the Interior model with an additional assumption about export effects.

- releases from Ryde are unaffected by export levels.

One of the Bayesian hierarchical models fit (similar to the Interior model shown in Equations 16 - 22) is the following.

Level 1:

$$y_{GS\to CI,t}, \hat{y}_{GS\to Oc,t} | \theta_t, r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{GS}, \theta_t r_{Ry\to CI,t}, \theta_t r_{Ry\to Oc,t}\right) \tag{27}$$

$$y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc,t} | r_{Ry\to CI,t}, r_{Ry\to Oc,t} \sim \text{Mn}\left(R_{Ry}, r_{Ry\to CI,t}, r_{Ry\to Oc,t}\right) \tag{28}$$

Level 2:

$$logit(\theta_t) \sim \text{Normal}\left(\beta_0 + \beta_1 Exp_t^*, \sigma_\theta^2\right) \tag{29}$$

$$logit(r_{Ry\to CI,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \tag{30}$$

$$logit(r_{Ry\to Oc,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to Oc}}, \sigma^2_{r_{Ry\to Oc}}\right) \tag{31}$$

Exp_t^* were scaled exports, $\frac{(Exports_t - \overline{Exp})}{s_{Exp}}$.

Level 3:

$$\beta_0, \beta_1, \mu_{Ry\to CI}, \mu_{Ry\to Oc} \sim \text{Normal}\,(0, 1.0E+6) \tag{32}$$

$$\sigma_\theta^{-2}, \sigma^{-2}_{r_{Ry\to CI}}, \sigma^{-2}_{r_{Ry\to Oc}} \sim \text{Gamma}\,(0.001, 0.001) \tag{33}$$

The key parameter in terms of an export effect is β_1; if β_1 equals 0 there is no export effect, while $\beta_1 < 0$ indicates a negative export effect.

4.4. **VAMP studies.** The hierarchical models considered for the VAMP studies were much more complicated than for the other three studies due to the greater number of release and recovery locations, more complex stream geometry, and additional covariates of interest (flow, exports, HORB). The models defined below aim to estimate, and model as a function of covariates, the survival through different "reaches" of the out-migration path. For example, suppose a release is made at Durham Ferry, and assume that with the HORB in place, there is 100% probability that a fish passing the entrance to Old River will stay in the San Joaquin River. Then the probability of surviving to Antioch, say, could be viewed as the product of four reach-specific survival probabilities:

$$S_{DF\to Ant} = S_{DF\to MD} S_{MD\to DR} S_{DR\to JP} S_{JP\to Ant}$$

The hierarchical models aim to model *some* of these reach-specific survival probabilities when they are estimable. Before describing the hierarchical model details, the geometry of the out-migration routes and the issue of estimability of survival probabilities are discussed.

4.4.1. *Geometry of out-migration routes.* A simplistic network of the relative positioning of the five release locations and the three recovery locations for the VAMP and pre-VAMP studies is shown below, with approximate distances (miles) between locations in parentheses.

```
                                  (40*)                (15)
                             OR----------------------\---------------
     (15)      (2) (1/4)/                             \              \
DF---------> MD--->HOR---->DR-------------------->JP---->Ant----->CI----->Ocean
                        (3)     (38*)                (7)     (8)
```

HOR denotes the head of Old River.

The actual geometry is considerably more complex. The distances marked with an asterisk, Dos Reis to Jersey Point and Old River to Jersey Point, denote situations where the actual distances traveled by salmon between locations can vary considerably. Between Dos Reis and Jersey Point there are multiple routes that salmon could take, e.g., after passing Stockton on the San Joaquin River they could turn toward the CVP and SWP facilities at several other locations (Turner Cut, Middle River, and at Franks Tract where Old River reconnects with the San Joaquin River).

Similarly, distances traveled between "an" Old River release site and Jersey Point can vary for several reasons: (a) there are multiple alternate channels a fish can take to reach Jersey Point, (b) some of the Old River releases are "salvaged" at the CVP and SWP fish facilities and then transported by truck to one of four possible locations on the Sacramento or San Joaquin rivers (see Section 2), thus some of the surviving Old River releases would have less chance of passing Jersey Point than others; (c) in 1985 the Old River release site was approximately 6 miles further downstream than the location used for 1986-1990 releases.

While the term reach-specific survival probability will be used, it admittedly may be a misnomer due to this complex stream geometry. One may want to mentally substitute the phrase, "probability of reaching point B from point A", for the notation $S_{A \to B}$.

4.4.2. *Estimability of survival probabilities using paired releases.* Survival probabilities are a component of the second level of the hierarchical models and these survival probabilities can, in principle, be modeled as functions of covariates. One might reasonably question whether or not such functional models can be fit given the complex geometry and variation in the grouping of release locations, i.e., "are the parameters of such models estimable?". Explanations for the estimability, or not, of some of the survival probabilities in the context of paired releases are given first and followed by explanations for the use of underlying models for survival to facilitate reach-specific survival probability estimation at time t when releases were not made at both endpoints of the release.

To begin, survival probabilities immediately above recovery locations *cannot* be estimated separately from capture probabilities. The lack of releases below the recovery locations (Table 7), e.g., between Antioch and Chipps Island, means that the survival and capture probabilities are confounded. However, the recovery probabilities, combinations of survival and capture probabilities, between Jersey Point and the three recovery locations are estimable; e.g., the recovery probability from Jersey Point to Antioch, $r_{JP\to Ant}$, is estimable, but the components of $r_{JP\to Ant}$, namely the survival probability for that reach, $S_{JP\to Ant}$, and the capture probability at Antioch, p_{Ant}, are not individually estimable. The following notation is used for these recovery probabilities.

$$\begin{aligned} r_{JP\to Ant} &\equiv S_{JP\to Ant}p_{Ant} \\ r_{JP\to CI} &\equiv S_{JP\to Ant}(1-p_{Ant})S_{Ant\to CI}p_{CI} \\ r_{JP\to Oc} &\equiv S_{JP\to Ant}(1-p_{Ant})S_{Ant\to CI}(1-p_{CI})S_{CI\to Oc}p_{Oc} \end{aligned}$$

The survival probability between Durham Ferry and Mossdale can be estimated quite simply, given paired releases at both locations and assuming that survival and capture probabilities are identical from Mossdale onwards, namely the assumption that pairing of releases is intended to ensure. For example, given recoveries at Antioch, Chipps Island, and in the ocean,

$$\hat{S}_{DF\to MD} = \frac{(y_{DF\to Ant}+y_{DF\to CI}+y_{DF\to Oc})/R_{DF}}{(y_{MD\to Ant}+y_{MD\to CI}+y_{MD\to Oc})/R_{MD}}. \tag{34}$$

Such an estimate is a method of moments estimate. This can be made clear by substituting the expected number of recoveries for the observed recoveries.

$$\hat{S}_{DF\to MD} \approx \frac{(R_{DF}\ S_{DF\to MD}\ (r_{MD\to Ant}+r_{MD\to CI}+r_{MD\to Oc}))/R_{DF}}{(R_{MD}\ (r_{MD\to Ant}+r_{MD\to CI}+r_{MD\to Oc}))/R_{MD}} = S_{DF\to MD}$$

Similarly, the survival between Dos Reis and Jersey Point can be estimated for paired releases, assuming identical survival and capture probabilities from Jersey Point onwards:

$$\hat{S}_{DR\to JP} = \frac{(y_{DR\to Ant}+y_{DR\to CI}+y_{DR\to Oc})/R_{DR}}{(y_{JP\to Ant}+y_{JP\to CI}+y_{JP\to Oc})/R_{JP}} \tag{35}$$

To estimate survival for a reach including the head of Old River, however, is not so straightforward. For example, for a release at Mossdale, located just above the head of Old River, the expected number of recoveries at Antioch (or Chipps Island or in the ocean) is a weighted sum of survival probabilities. Assuming that all surviving fish will go by Jersey

Point, the expected number of recoveries at Antioch is:

$$E[y_{MD\to Ant}] \;=\; R_{MD}(p_{OR}S_{OR\to JP}r_{JP\to Ant} + (1-p_{OR})S_{MD\to DR}S_{DR\to JP}r_{JP\to Ant}),$$

where p_{OR} is the probability of going down Old River, $S_{OR\to JP}$ is the survival probability between the head of Old River and Jersey Point, and survival between Mossdale and Old River is assumed to be 100%. The ratio of recovery fractions at Antioch between a Mossdale release and a Dos Reis release is approximately

$$\frac{y_{MD\to Ant}/R_{MD}}{y_{DR\to Ant}/R_{DR}} \;\approx\; \frac{p_{OR}S_{OR\to JP} + (1-p_{OR})S_{MD\to DR}S_{DR\to JP}}{S_{DR\to JP}}. \tag{36}$$

If one assumes that the probability of going down Old River is zero when the HORB is in place, then the right hand side of the above equation reduces to $S_{MD\to DR}$. However, if that assumption is not made, or if the HORB is not in place, then to estimate $S_{MD\to DR}$, one needs estimates of p_{OR}, $S_{OR\to JP}$, and $r_{JP\to Ant}$. If releases are made in Old River and at Jersey Point, then $S_{OR\to JP}$ and $r_{JP\to Ant}$ can be estimated. Estimation of p_{OR} is problematic, however, due to a lack of data.

4.4.3. *Modeling of survival probabilities.* The previous examples of estimating reach-specific survival were based on the use of paired releases that were made at both endpoints of the reach. Implicit to the calculations was the notion that the survival estimates were release-time specific. Unfortunately, as was discussed previously and as Table 7 makes clear, the release location "pairings" have varied considerably. For example, direct estimation of $S_{DR\to JP}$ between 2000 and 2004 using equation (35) is not possible due to the absence of Dos Reis releases[6].

However, if an underlying structure is assumed for reach-specific survival, one which is not over-parameterized given the number of observations, survival for reaches which lack releases at both endpoints can be estimated (or predicted) so long as such paired releases at those endpoints have occurred at *some time* during the study. The following heuristic example is given to provide some intuition as to why this is possible, but the actual estimation details are omitted.

Suppose that at time t releases were made at Mossdale and Jersey Point but not Dos Reis and the objective is to separately estimate $S_{MD\to DR,t}$ and $S_{DR\to JP,t}$. To keep the example simple, assume the HORB was in place and prevented all fish from entering Old River, thus

[6]As an aside, the HORB was in place during this period, 2000-2004, and if one assumes 100% survival between Mossdale and Dos Reis when the barrier is in place, then $S_{DR\to JP}$ can be directly estimated since $S_{MD\to JP}$ can be estimated and $S_{MD\to JP} = S_{MD\to DR}S_{DR\to JP} = 1^{*}S_{DR\to JP}$.

all the Mossdale fish reaching Old River stayed in the San Joaquin River, and $S_{MD\rightarrow JP,t}$ can be defined as the product $S_{MD\rightarrow DR,t}S_{DR\rightarrow JP,t}$. Also assume that $S_{MD\rightarrow DR}$ is a function of flow at Mossdale and $S_{DR\rightarrow JP}$ is a function of flow at Dos Reis. Note first that $S_{MD\rightarrow JP,t}$ can be directly estimated using the method of moments procedure (e.g., equation 35). $S_{MD\rightarrow DR,t}$ and $S_{DR\rightarrow JP,t}$ can be individually estimated given (a) recovery data from *other* sets of paired releases made at Mossdale and Dos Reis and at Dos Reis and Jersey Point; (b) underlying models for $S_{MD\rightarrow DR}$ and $S_{DR\rightarrow JP}$; (c) relevant covariates at time t. Given a sufficient number of these *other* paired releases and corresponding flow data, the following models can be fit:

$$\begin{aligned} logit(S_{MD\rightarrow DR}) &= \beta_0 + \beta_1 Flow_{MD} \\ logit(S_{DR\rightarrow JP}) &= \gamma_0 + \gamma_1 Flow_{DR}. \end{aligned}$$

Given estimates of β_0, β_1, γ_1, and γ_2 and the flow measurements at time t, $S_{MD\rightarrow DR,t}$ and $S_{DR\rightarrow JP,t}$ can be predicted. Thus, if $S_{MD\rightarrow JP,t}$ can be directly estimated and $S_{MD\rightarrow DR,t}$ and $S_{DR\rightarrow JP,t}$ can be predicted, then one can imagine (in a hand-waving way) that an integrated procedure could be carried out to use all the release-recovery data simultaneously to both estimate the parameters β_0, β_1, γ_0, and γ_1 and the time t-specific probabilities $S_{MD\rightarrow DR,t}$ and $S_{DR\rightarrow JP,t}$.

4.4.4. *Hierarchical models.* Several different formulations for the modeling of reach-specific survival were considered, but a common underlying out-migration framework was assumed. Durham Ferry releases go downstream to Mossdale. Fish at Mossdale go to the head of Old River and proceed on to Dos Reis if they stay in the San Joaquin or they enter Old River. Fish entering Old River then pass the Old River release site(s) and proceed to Jersey Point (even fish that are salvaged at the fish facilities are assumed to have a positive probability of going by Jersey Point). Fish passing Dos Reis proceed to Jersey Point, too. From Jersey Point, fish pass Antioch, then Chipps Island, and then enter the ocean.

The following additional assumptions were made:

- When the HORB is in place, Durham Ferry and Mossdale releases do not enter Old River.
- When the HORB is not in place, Durham Ferry and Mossdale releases enter Old River with probability p_{OR}, which is either a constant or a function of relative flow.
- Survival between the head of Old River and Dos Reis (about 3 miles) is 100%, and survival between the head of Old River and the Old River release point(s) (about 0.25 miles) is 100%.

The last assumption is made for reasons of parameter estimability for releases at Durham Ferry or Mossdale. The survival probability from Mossdale to Jersey Point can be written as follows.

$$S_{MD\to JP} \;=\; S_{MD\to HOR}\,[p_{OR}S_{HOR\to OR}S_{OR\to JP} + (1-p_{OR})S_{HOR\to DR}S_{DR\to JP}]$$

Given paired releases from Old River and Jersey Point, and Dos Reis and Jersey Point and recoveries at Chipps Island, say, it is clear that $S_{OR\to JP}$ and $S_{DR\to JP}$ can be estimated; e.g., $\hat{S}_{OR\to JP} = [y_{OR\to CI}/R_{OR}]/[y_{JP\to CI}/R_{JP}] \approx [S_{OR\to JP}r_{JP\to CI}]/r_{JP\to CI} = S_{OR\to JP}$. That leaves four unknown parameters, $S_{MD\to HOR}$, p_{OR}, $S_{HOR\to OR}$, and $S_{HOR\to DR}$, and only one can be estimated using Mossdale or Durham Ferry recoveries at Chipps Island, say. Assuming that $S_{HOR\to OR}$=1 and $S_{HOR\to DR}$=1, leaves $S_{MD\to HOR}$ and p_{OR} unknown. The probability of traveling down Old River, p_{OR}, was, for some models, set equal to the relative flow-based values shown in Table 5, and then $S_{MD\to HOR}$ was estimable. The basis for the calculated values of p_{OR} are described in Table 6. In other models, p_{OR} was a fixed but unknown parameter to be estimated and $S_{MD\to HOR}$ was set equal to 1.0.

The three levels of the hierarchical models are as follows; release set subscripts (t) have been omitted.

Level 1: the distributions for the recoveries of fish released at Durham Ferry, Mossdale, Dos Reis, Old River, and Jersey Point (Θ denotes survival and recovery probabilities)

$$\begin{aligned}
(37)\qquad y_{DF\to Ant}, y_{DF\to CI}, \hat{y}_{DF\to Oc}|\Theta \;&\sim\; \mathrm{Mn}(R_{DF}, S_{DF\to MD}S_{MD\to JP}r_{JP\to Ant},\\
&\qquad S_{DF\to MD}S_{MD\to JP}r_{JP\to CI},\\
&\qquad S_{DF\to MD}S_{MD\to JP}r_{JP\to Oc})\\
(38)\qquad y_{MD\to Ant}, y_{MD\to CI}, \hat{y}_{MD\to Oc}|\Theta \;&\sim\; \mathrm{Mn}(R_{MD}, S_{MD\to JP}r_{JP\to Ant},\\
&\qquad S_{MD\to JP}r_{JP\to CI}, S_{MD\to JP}r_{JP\to Oc})\\
(39)\qquad y_{DR\to Ant}, y_{DR\to CI}, \hat{y}_{DR\to Oc}|\Theta \;&\sim\; \mathrm{Mn}(R_{DR}, S_{DR\to JP}r_{JP\to Ant},\\
&\qquad S_{DR\to JP}r_{JP\to CI}, S_{DR\to JP}r_{JP\to Oc})\\
(40)\qquad y_{OR\to CI}, \hat{y}_{OR\to Oc}|\Theta \;&\sim\; \mathrm{Mn}(R_{OR}, S_{OR\to JP}r_{JP\to CI}, S_{OR\to JP}r_{JP\to Oc})\\
(41)\qquad y_{JP\to Ant}, y_{JP\to CI}, \hat{y}_{JP\to Oc}|\Theta \;&\sim\; \mathrm{Mn}(R_{JP}, r_{JP\to Ant}, r_{JP\to CI}, r_{JP\to Oc})
\end{aligned}$$

where by assumption

$$(42)\qquad S_{MD\to JP} \;=\; S_{MD\to HOR}\,[p_{OR}S_{OR\to JP} + (1-p_{OR})S_{DR\to JP}]$$

and when HORB is in place, $S_{MD\to JP} = S_{MD\to HOR}S_{DR\to JP}$.

Level 2: Random effects models for survival and recovery probabilities; (X = covariates)

$$logit(S_{DF\to MD}) \sim \text{Normal}\left(X_1'\beta, \sigma^2_{DF\to MD}\right) \tag{43}$$
$$logit(S_{MD\to HOR}) \sim \text{Normal}\left(X_2'\gamma, \sigma^2_{MD\to DR}\right) \tag{44}$$
$$logit(S_{DR\to JP}) \sim \text{Normal}\left(X_3'\xi, \sigma^2_{DR\to JP}\right) \tag{45}$$
$$logit(S_{OR\to JP}) \sim \text{Normal}\left(X_4'\zeta, \sigma^2_{OR\to JP}\right) \tag{46}$$
$$logit(r_{JP\to Ant}) \sim \text{Normal}\left(\mu_{JP\to Ant}, \sigma^2_{JP\to Ant}\right) \tag{47}$$
$$logit(r_{JP\to CI}) \sim \text{Normal}\left(\mu_{JP\to CI}, \sigma^2_{JP\to CI}\right) \tag{48}$$
$$logit(r_{JP\to Oc}) \sim \text{Normal}\left(\mu_{JP\to Oc}, \sigma^2_{JP\to Oc}\right) \tag{49}$$

Level 3:

$$\beta, \gamma, \xi, \kappa, \zeta, \mu_{JP\to Ant}, \mu_{JP\to CI}, \mu_{JP\to Oc} \sim \text{Normal}\left(0, 1.0E+6\right) \tag{50}$$
$$\sigma^{-2}_{i\to j}, \sim \text{Gamma}\left(0.001, 0.001\right). \tag{51}$$

The Level 1 models for the years 1985-1999 excluded Antioch recoveries (since the trawl was not in place) and for the years 2005-2006 excluded ocean recoveries (because none were available at the time of analysis). Also the first release set used spray-dying to mark individuals and ocean recoveries were not available (Table 5). When flow and export levels were used as covariates in the Level 2 models they were standardized (mean was subtracted and the difference divided by standard deviation); how flow and exports were calculated is described in Table 6.

Given the multiple reaches and branching, the number of potential models is very large, far more than for the other three data sets. A relatively small set was fit, however, due to time constraints. As a demonstration of the general utility, or not, of random effects, some models were fit without any random effects (thus resulting in Bayesian logistic regressions) and some were fit with random effects only in the recovery probabilities, the $r_{JP\to Ant}$, $r_{JP\to CI}$, and $r_{JP\to Oc}$ terms, with the intent of allowance for temporal variation in capture probabilities but not survival probabilities.

4.5. **BHM fitting and assessment.** For the Bayesian analysis of the hierarchical models, the program `WinBUGS` (Spiegelhalter, Thomas, and Best 2003) was used to generate samples

from the posterior distributions for the parameters, random effects, and expected numbers of recoveries. `WinBUGS` is based on a technique known as Markov chain Monte Carlo, MCMC (Gilks, Richardson, and Spiegelhalter 1996). MCMC is a computer simulation method where samples are generated from a Markov chain which has a limiting distribution equal to the distribution of interest, in this case the posterior distribution.

By a limiting distribution it is meant that the samples do not initially come from the desired distribution, but once "enough" samples are generated, the so-called burn-in period, all additional samples do come from the desired distribution. WinBUGS includes measures (e.g., the Brooks-Gelman-Rubin statistic) for determining an adequate burn-in period which are based upon the results of simulating from multiple Markov chains. Informally stated, the point at which the chains begin to overlap is the necessary burn-in period. For all four studies, three different chains were run in parallel and the summary statistics are based on the pooled output.

Quality of fit was assessed in two general ways, by making between model comparisons of DIC, deviance information criterion (Gelman, et al. 2004), and, within a given model, by examining the quality of fit to individual observations. The deviance for a particular observation y and a particular parameter value θ is defined as follows:

$$D(y, \theta) \quad = \quad -2\log(p(y|\theta)),$$

where $p(y|\theta)$ is the probability (or density) of y given θ. The total deviance for a set of observations is the sum of individual deviances. When comparing two models, say two different values of θ, the model with the smaller deviance is preferred. In the case of normal linear models, the total deviance is proportional to the sum of squared deviations of the observed values from the fitted values; e.g., with a simple linear model, $D(y, \beta_0, \beta_1) = \frac{1}{2\sigma^2}(y - \beta_0 - \beta_1 x)^2$. MCMC yields a sample from the posterior distribution of θ and the mean deviance, based on an MCMC sample of size L, is calculated by

$$\hat{D}_{avg}(\mathbf{y}) \quad = \quad \frac{1}{L}\sum_{l=1}^{L} -2\log(p(\mathbf{y}|\theta^l)),$$

where $\mathbf{y}$ is the entire vector of observed values.

Increasing the number of parameters typically decreases deviance and to compare models with differing numbers of parameters, a measure that includes deviance but exacts an increasing penalty for an increasing number of parameters is DIC, the deviance information criterion, defined as follows.

$$DIC \quad = \quad 2\hat{D}_{avg}(y) - D(\mathbf{y}, \hat{\theta}),$$

where $\hat{\theta}$ is the posterior mean for θ.

Assessment of quality in terms of fit to individual observations was examined by calculating Bayesian P-values and scaled residuals. Bayesian P-values are defined as the proportion of time a predicted value exceeds the observed value:

$$\text{Bayesian P-value} \quad = \quad \frac{1}{L}\sum_{l=1}^{L} I(y_l^{pred} \geq y),$$

where $I()$ is an indicator function equaling 1 when the condition inside () is met. The predicted value, y_l^{pred} is found by simulating y from its probability distribution evaluated at the parameter value θ^l (taken from the MCMC sample). Bayesian P-values near 0 or 1 are indicative of a poor fit. Scaled residuals are defined by

$$\text{Scaled residual} \quad = \quad \frac{y - \overline{y}^{pred}}{s_{y^{pred}}},$$

where $\overline{y}^{pred}$ and $s_{y^{pred}}$ are the mean and standard deviation of the predicted values.

4.6. **Sensitivity analysis.** The sensitivity of the results to the particular Bayesian hierarchical formulations was evaluated by making changes in each of the three levels of the hierarchy. In Bayesian methods sensitivity analysis is often focused on the choice of prior distributions (Level 3), however, it can also include comparisons with alternative likelihood models (Level 1) and random effects models (Level 2). The latter comparisons sometimes are viewed as problems of model selection, but they can also be viewed as a form of sensitivity analysis. Several of the alternatives discussed below were either directly suggested or indirectly stimulated by comments from reviewers.

Negative Binomial likelihood (Level 1): A distribution sometimes used for overdispersed count data is the negative binomial. Overdispersed in this case is with reference to a Poisson distribution where the variance equals the mean. The Poisson distribution itself is often used as an approximation to the binomial distribution when the probability of success is relatively small, the number of trials is large, and the expected number of successes is relatively small; and in that case, if $X \sim \text{Binomial}(n, p)$, then $X \approx \text{Poisson}(np)$. Thus the negative binomial can be used to approximate "overdispersed" binomial data in such a setting (large n, small p, etc).

An example formulation for one of the outcomes, recoveries at Chipps Island of releases from Ryde, is the following.

$$y_{Ry\to CI} \sim \text{NegBinom}\left(k_{CI}, \frac{k_{CI}}{R_{Ry}r_{Ry\to CI} + k_{CI}}\right),$$

where k is a non-negative constant that affects the degree of overdispersion (relative to a Poisson, or indirectly a Binomial, random variable). The larger k is, the less the overdispersion. Let $p = \frac{k_{CI}}{R_{Ry}r_{Ry\to CI}+k_{CI}}$

$$E[y_{Ry\to CI}] = \frac{k_{CI}(1-p)}{p} \equiv R_{Ry}r_{Ry\to CI}$$

and

$$V[y_{Ry\to CI}] = \frac{k_{CI}(1-p)}{p^2} \equiv R_{Ry}r_{Ry\to CI}\frac{R_{Ry}r_{Ry\to CI} + k_{CI}}{k_{CI}}$$

Negative binomial formulations were applied independently to recoveries at two (Chipps Island and the ocean) or three (Antioch, Chipps Island, and the ocean) locations from the same release. This univariate treatment ignores the Level 1 probabilistic dependence between y_{CI} and y_{Oc}, say, that the multinomial likelihood models recognize. While multivariate negative binomial distributions do exist (Winkelmann 2000), the use of independent marginal negative binomial distributions for each of the outcomes is probably adequate given how extremely small the covariances are between the outcomes (due to the very small capture probabilities).

Alternative random effects models (Level 2): Reviewers of an earlier draft had several useful suggestions regarding Level 2 models. They are described below for completeness, but all suggestions were not tried for all four studies.

(1) *Log link function for θ.* A ratio between survival probabilities, denoted by θ, was of interest in all four studies. The logit link function bounds the ratio between 0 and 1, thus the survival in the numerator of the ratio was implicitly assumed to be less than the value in the denominator. An alternative link function is the natural log which would allow the survival in the numerator to exceed that in the denominator; e.g., in the case of the Interior and DA 8 studies, the Georgiana Slough releases could potentially have higher survival rates than the Ryde releases. In contrast to the logit link function, there is the potential that fitted probabilities could mathematically exceed 1 (which will cause the fitting algorithm in the multinomial case to fail).

(2) *Correlated random effects.* Survival rates in different parts of the river, particularly for the VAMP studies, might be positively correlated in the sense that when conditions are good in one part of the river, it could well be that conditions are good in other parts of the river (Bryan Manly, personal communication). One way to allow for this possibility to specify a multivariate distribution for the Level 2 random effects. For example, with the Interior study, a multivariate normal distribution could be specified for the (logit transformed) vector of (θ, $r_{Ry\to CI}$, $r_{Ry\to Oc}$):

$$\begin{bmatrix} logit(\theta) \\ logit(r_{Ry\to CI}) \\ logit(r_{Ry\to Oc}) \end{bmatrix} \sim \text{Multivariate Normal}\left(\begin{bmatrix} \mu_\theta \\ \mu_{r_{Ry\to CI}} \\ \mu_{r_{Ry\to Oc}} \end{bmatrix}, \begin{bmatrix} \sigma^2_\theta & \sigma_{\theta,r_{Ry\to CI}} & \sigma_{\theta,r_{Ry\to Oc}} \\ \sigma_{\theta,r_{Ry\to CI}} & \sigma^2_{r_{Ry\to CI}} & \sigma_{r_{Ry\to CI},r_{Ry\to Oc}} \\ \sigma_{\theta,r_{Ry\to Oc}} & \sigma_{r_{Ry\to CI},r_{Ry\to Oc}} & \sigma^2_{r_{Ry\to Oc}} \end{bmatrix} \right)$$

(3) *Extended logit-type link functions for $r_{i\to j}$ and $r_{i\to k}$.* For both the non-Bayesian and Bayesian formulations the sum $r_{Ry\to CI,t} + r_{Ry\to Oc,t}$ must be less than 1 by definition, but such constraints are not built in. However, recovery probabilities are so small in practice that the chance of estimating $r_{Ry\to CI,t} + r_{Ry\to Oc,t}$ to be > 1 is negligible. An alternative logit-like formulation (Russell Millar, personal communication) that does satisfy this constraint is the following:

$$\log\left(\frac{r_{Ry\to CI,t}}{1 - r_{Ry\to CI,t} - r_{Ry\to Oc,t}}\right) \tag{52}$$

$$\log\left(\frac{r_{Ry\to Oc,t}}{1 - r_{Ry\to CI,t} - r_{Ry\to Oc,t}}\right). \tag{53}$$

Then in the case of the Bayesian model,

$$E[r_{Ry\to CI,t}] \approx \frac{\exp(\mu_{r_{Ry\to CI}})}{1 + \exp(\mu_{r_{Ry\to CI}}) + \exp(\mu_{r_{Ry\to Oc}})}.$$

(4) *Secondary release-specific covariates.* The random effects components at Level 2 will to some degree account for factors influencing survival over and above the *primary* covariates that are being structurally modeled, namely DCC gate position (DCC), location (Interior), location and exports (DA 8), and flow, exports, and HORB (VAMP). For example with the Interior study, $\theta_t \sim \text{Normal}(\mu_\theta, \sigma^2_\theta)$. Deviations from μ_θ are in a sense a function of *secondary* covariates that are not modeled, such as temperature (Baker, Speed, and Ligon, 1995). If the values of such covariates vary widely and have a large effect on survival, then the variation in the random effects parameter will be large, e.g., σ^2_θ is large, and predictions of release-specific parameters, such as θ_t, will have considerable uncertainty. Including such covariates into the Level 2 model can however increase precision. After-the-fact assessment of secondary covariate influence can be done by comparing fitted values, e.g., $\hat{\theta}_t$, or random effect "residuals",

with covariate values, and/or by including such covariates in the Level 2 model and comparing the quality of fit.

Alternative priors (Level 3): Gelman (2006) has discussed potential problems with inverse gamma priors for the variance components of a hierarchical model. While he describes sophisticated alternatives, a relatively simple choice is the use of a uniform distribution for the standard deviation. For example,

$$\sigma_\theta, \sigma_{r_{Ry \to CI}}, \sigma_{r_{Ry \to Oc}} \quad \sim \quad \text{Uniform}(0, 20)$$

was tried for some of the models.

Sensitivity to the above changes were assessed in terms of changes in the posterior means for observations and parameters and by examining DIC, Bayesian p-values, and scaled residuals.

5. Results

The `R` package `R2WinBUGS` was used as an interface to `WinBUGS` to fit the BHMs and the code for both are given in the appendices. For all models fit, three Markov chains were run using different starting values. The Brooks-Gelman-Rubin statistic (see documentation in `WinBUGS` and Brooks and Gelman (1998)) was calculated to assess convergence; values near 1 are consistent with convergence, i.e., the variance within a chain is more or less the same as the variance between chains.

5.1. **DCC studies.**

5.1.1. *Non-Bayesian results.* Recall $\hat{\theta} = \hat{r}_{Ct\to CI+Oc}/\hat{r}_{Ry\to CI+Oc}$, $\theta = S_{Ct\to CI}/S_{Ry\to CI}$, and μ_θ=E[θ]. The weighted estimates of μ_θ were 0.40 when the DCC gate was open and 0.64 when the gate was closed. The estimate of $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$ was $0.40/0.64 = 0.63$ with a standard error of 0.20. The bootstrapped 95% confidence interval (using the percentile method, Efron and Tibshirani (1993, p 170)) was (0.28, 1.10). Thus there is evidence suggesting that when the gate is open, the survival of Courtland releases decreases, but there is considerable uncertainty about this conclusion (see the bootstrap histogram of ratio estimates in Figure 13).

The weighting of the $\hat{\theta}$'s had considerable effect on the results. Assigning equal weights to each release pair yielded $\hat{\mu}_{\theta(Open)} = 0.92$ and $\hat{\mu}_{\theta(Closed)} = 1.02$ and the estimate of $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$ was 0.89. If the 1989 observation was removed (an apparent outlier), however, the equally weighted estimate of $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$ was 0.60, quite similar to the weighted results.

5.1.2. *Bayesian results.* A combination of model formulations were fit, with multinomial or negative binomial likelihoods at Level 1, logit or log transformations of θ at Level 2, and inverse gamma or uniform priors for the variances or standard deviations of the random effects at Level 3. One combination that did not work was the multinomial with a log transformation of θ which sometimes led to the recovery "probabilities", θr_c and θr_o, exceeding one. Table 9 shows the DIC values for some of the models tried. The model selected for inference was the negative binomial with log transformed θ and uniform priors for the standard deviations. The `R` and `WinBUGS` program code are shown in Appendix E.1. For the negative binomial binomials, a burn-in of 10,000 samples was used for each chain and an additional 40,000 samples were generated. Based on the Brooks-Gelman-Rubin statistic for

convergence, all values lying between 1.00 and 1.04, the chains had converged to the posterior distribution.

Parameters of interest. Summaries of the posterior distributions of the selected model are shown in Table 9. Of most relevance to the objectives of the DCC studies is the slope coefficient β_1, which when positive, suggests that closing the DCC gate increases survival for Courtland releases. The mean value of β_1 was 0.33, but the posterior distribution is quite wide. A more direct measure of the DCC gate effect is the ratio of the closed gate ratio (Courtland/Ryde) to the open gate ratio, $\theta_{Open}/\theta_{Closed}$, which when less than 1.0 indicates that survival for Courtland releases relative to Ryde releases is less with the DCC gates open than with the gates closed. The posterior median for $\theta_{Open}/\theta_{Closed}$[7] is 0.72, but the probability that $\theta_{Open}/\theta_{Closed}$ is less than 1.0 is only 64%.

While not of direct relevance to the DCC studies, some of the other parameters are of interest. The median recovery probability for Ryde releases at Chipps Island was 0.0008, and for ocean recoveries it was 0.0080, an order of magnitude larger. The negative binomial parameter k_{CI} for Chipps Island recoveries is very large (mean value = 493), which indicates little evidence for overdispersion, in contrast to k_{Oc} for ocean recoveries which was considerably smaller (mean value = 17). The group 13 pair is perhaps to some degree responsible for k_{Oc}'s value since the estimated ocean recoveries for Ryde were so much less than those for Courtland.

Quality of fit. Forty-seven of the 52 observations (90%) had Bayesian P-values within the middle 90% of the posterior predictive distributions. The five "outlying" observations were the group 13 Ryde recoveries at Chipps Island (P-value=0.98) and in the ocean fisheries (P-value=0.99) (see Figures 14 and 15), and Courtland recoveries at Chipps Island for groups 3, 9, and 10 (Figure 16). The scaled residuals are plotted against mean posterior predictions in Figure 17 The largest scaled residuals are for the Chipps Island recoveries from Courtland releases in groups 3 and 9, but, in contrast to the P-values, the group 13 Ryde residuals are not outliers.

The influence of group 13 was assessed by removing those observations and re-fitting the negative binomial model. The median value for $\theta_{Open}/\theta_{Closed}$ changed only slightly (from 0.72 to 0.65) and the probability that $\theta_{Open}/\theta_{Closed}$ was less than 1.0 only went from 64% to 70%. Thus the effect of this group on the most relevant parameters was minor.

[7]The mean is 1.32, reflecting strong right skewing in the posterior distribution. Note that an approximate estimate of $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$ is $\text{logit}(\beta_0)^(-1)/\text{logit}(\beta_0+\beta_1)^(-1)$, or $(1+\exp(\beta_0+\beta_1))/(\exp(\beta_1)+\exp(\beta_0+\beta_1))$. Substituting the posterior means for β_0 and β_1 yields 0.82.

Random effects. Sensitivity to the Level 2 formulation was also examined by fitting a multivariate normal random effects model for θ, $r_{Ry\to CI}$, and $r_{Ry\to Oc}$. The extended logit transformation was used for $r_{Ry\to CI}$ and $r_{Ry\to Oc}$. An inverted Wishart distribution was used for the joint prior distribution of random effects. `WinBUGS` model code is shown in Appendix E.2. The DIC value (Table 9) was slightly higher than for uncorrelated multinomial models, and considerably higher than for the negative binomial models. The posterior median for the ratio of ratios was 0.96. Negative correlations (on the logit and extended logit scales) were found between θ and $r_{Ry\to CI}$ (correlation coefficient = -0.58), between θ and $r_{Ry\to Oc}$ (correlation coefficient = -0.53), while the correlation between $r_{Ry\to CI}$ and $r_{Ry\to Oc}$ was positive (correlation coefficient = 0.62).

The value of random effects in the model was examined by fitting a negative binomial model without any random effects for θ_t, $r_{Ry\to CI}$, and $r_{Ry\to Oc}$, i.e., purely deterministic Level 2 models. The apparent benefit to survival of having the DCC gates closed increased sizeably, the probability that $\theta_{Open}/\theta_{Closed}$ was less than 1.0 went from 64% to 95%. However, the model fit and predictive power worsened notably: the DIC increasing from 567.3 to 656.7, the Bayesian P-values tended to become more extreme (particularly for ocean recoveries), and the magnitude of scaled residuals in some cases nearly doubled (Figure 18).

5.2. **Interior studies.**

5.2.1. *Non-Bayesian results.* The estimate of the expected ratio of Georgiana Slough survival to Ryde survival, μ_θ, based on a weighted average of $\hat{\theta}$ ($\hat{r}_{GS\to CI+Oc}/\hat{r}_{Ry\to CI+Oc}$) was 0.33 with a bootstrap standard error of 0.038 and a 95% confidence interval of (0.26,0.41). The unweighted average of the $\hat{\theta}$'s was 0.40 (median=0.33) with a standard error 0.055 and a 95% confidence interval of (0.30,0.51). In either case the evidence that the survival for Georgiana Slough releases was low relative to Ryde releases was strong.

5.2.2. *Bayesian results.* Several combinations of models were fit to the Interior data. Based on the DIC values, the multinomial models were all quite similar in terms of fit and preferable to the negative binomial models (Table 10). However, the parameter estimates under the negative binomial were very similar to those for the multinomial distribution. There was little evidence for overdispersion based on the negative binomial model; e.g., for the log transformed θ and uniform priors on the σ's of the random effects, the median values for k_{CI} and k_{Oc} equaled 15 and 208. The results presented below are based on the multinomial model with log transformed θ and uniform priors for the σ's. The WinBUGS program code

for the multinomial model is shown is shown in Appendix E.3. For each of the three chains a burn-in of 50,000 samples was used and an additional 150,000 samples were generated. The Brooks-Gelman-Rubin statistics were between 1.00 and 1.04 for all parameters.

Parameters of interest. Summary statistics for the posterior distributions are shown in Table 10. The key parameter is θ, the ratio of Georgiana Slough to Ryde recoveries, and the posterior mean predicted value was around 0.44, strong evidence, consistent with the non-Bayesian analysis, that the Georgiana Slough recovery rates are considerably less than the recovery rates for Ryde releases. However, the upper 4.9% of the distribution for θ was above 1.0, meaning that there was a 4.9% chance that Georgiana Slough recovery probabilities could be higher than the Ryde recovery probabilities. The posterior mean predicted value of θ was quite similar for all models, ranging from 0.41 to 0.44. The median recovery probability at Chipps Island, $r_{Ry \to CI}$, was 0.0004 and, as for DCC studies, the ocean fisheries recovery probability was an order of magnitude higher, 0.0036.

Quality of fit. Of the 60 observations, 55 (or 92%) fell within the middle 90% of the posterior predictive distributions. The five observations with extreme Bayesian P-values were groups 1 and 6 Ryde recoveries at Chipps Island, the group 5 Georgiana Slough recoveries at both Chipps Island and in the ocean, and the group 12 Georgiana Slough recoveries at Chipps Island. In each case, the observed value was either exceptionally small or large relative to the predicted values; e.g., for the group 1 Ryde releases, the observed 37 recoveries at Chipps Island were larger than 98% of the predicted values (Figure 19). The scaled residuals are plotted against mean posterior predictions in Figure 20, and the largest residuals are for those Chipps Island recoveries of Ryde releases with extreme P-values.

Random effects. A multivariate normal random effects model was also fit (using the same approach as for the DCC implementation). Based on the DIC value, this model was of nearly equivalent quality to the uncorrelated multinomial models (Table 10). The correlations between the random effects were relatively low; correlation between θ and $r_{Ry \to CI}$ (on the logit scales) was 0.11, between θ and $r_{Ry \to Oc}$ it was 0.23, and between $r_{Ry \to CI}$ and $r_{Ry \to Oc}$ it was 0.31.

To determine the impact on results of including random effects, the multinomial model with log transformed θ was fit without any random effects, i.e., deterministic Level 2 models. The posterior mean for the expected value of θ, μ_θ, was -0.86, in contrast to -1.02 for the value for the model that included random effects. However, $\exp(\mu_\theta) = 0.42$, which is quite similar to the posterior mean for the simulated value θ in the model including random effects (E[θ] $\approx$ 0.44). The key difference was in the considerably greater variability in the distribution

for θ, with the coefficient of variation for the random effects model equal to 82% compared to 3% for the model without random effects. The expected recovery probability for Ryde releases at Chipps Island was 0.00045 and in the ocean was 0.0044, about 20% less than for the random effects model. The prediction ability and quality of fit was considerably worse when random effects were removed: the DIC value increased from 428 to 2184, the frequency of relatively extreme Bayesian P-values increased considerably, and the magnitude of scaled residuals increased four- to five-fold (Figure 21). The variation in the observed recovery fractions was simply far larger than could be explained by a model without random effects.

Secondary covariates. The effect of secondary covariates was examined by plotting the median fitted θ's per release set against release temperature at Georgiana Slough and average length of fish at release (Figure 22). No pattern was apparent. The release temperatures at Ryde were very similar to those at Georgiana Slough with one exception, the tenth set, in year 2000 with tags 05-51-31 and 05-51-33, where Ryde temperature was 50 degrees Fahrenheit in contrast to 63 degrees at Georgiana Slough. However, this release pair was not unusual in terms of Bayesian P-values or scaled residuals, and it may be that the 63 degrees was a data recording error (Pat Brandes, personal communication).

It is worth noting that the use of temperature at time of release is only a very limited measure of the temperatures possibly experienced by a fish as it out-migrates. Potentially, during the period of out-migration the variation in water temperatures could be extreme and temperature at time of release would not necessarily be very reflective of the temperatures encountered enroute.

Analyses with inland recoveries. Given the relatively similar stray rates for inland recoveries between Georgiana Slough and Ryde releases, additional model runs were made using the inland recoveries in combination with the expanded ocean recoveries. The results for the selected multinomial model (log transformed θ and uniform priors for the σ's) were very similar, e.g., the posterior mean for μ_θ was -1.03 compared to -1.02 for the results without inland recoveries, but the posterior standard deviations for some of the fitted θ's were slightly smaller with inland recoveries included.

5.3. **Delta Action 8 Experiments.**

5.3.1. *Exploratory data analysis.* Non-BHM estimates of the ratio $\theta = S_{GS\to CI}/S_{Ry\to CI}$, namely $\hat{\theta} = \hat{r}_{GS\to CI+Oc}/\hat{r}_{Ry\to CI+Oc}$, are plotted against exports in Figure 23. The vertical lines in the plot mark $\pm$ 1 standard error, which was calculated using delta method (i.e.,

the sample based estimates of $\sqrt{V(\hat{\theta}_t)}$ shown in Appendix A). Thus these standard errors reflect within release pair variability only. The two especially large standard errors (middle and right side of the plot) are for 2005 and 2006 and their magnitude is due to the lack of ocean recovery information to date.

Also plotted in Figure 23 is a weighted,nonparametric regression curve. The curve was fit using a supersmoother function in `R` and weights based on the delta method standard errors. While this graph is a non-Bayesian, non-hierarchical, and indirect analysis, the gist of the results is, as will be shown next, consistent with the Bayesian, hierarchical, and integrated analysis, i.e., suggesting a slight negative association between exports and θ.

5.3.2. *Bayesian analysis.* As for the Interior analysis multinomial and negative binomial distributions, logit and log transformations of θ (with θ now defined as a function of exports), and uniform and gamma distributions for σ's were all tried. The WinBUGS code for the multinomial distribution is shown in Appendix E.4. Burn-in time was set at 50,000 iterations and then at least 100,000 iterations were used for the posterior samples. The Brooks-Gelman-Rubin statistics were between 1.0 and 1.03 for all parameters and trace plots of the parameters were consistent with good mixing.

The preferred model based on DIC is the multinomial with log transformed θ and uniform priors for the σ's (Table 11), but all the multinomial models yielded quite similar results. The DIC for this model, 427.0, however, was only slightly less than the DIC for the models without exports (the "Interior" models where minimum DIC was 427.7). Summary statistics from the posterior distributions are shown in Table 11. The negative binomial's overdispersion parameters were quite large (median values of 192 for k_{CI} and 311 for k_{Oc}) indicating very little overdispersion relative to a multinomial distribution.

Parameters of interest. The key parameter is β_1 (the coefficient for exports in the logistic regression of θ; see equation 29). It had a 98% probability of being negative, indicative of a negative association between the relative survival of Georgiana Slough and Ryde releases (θ) and exports. A posterior sample of predicted θ for different levels of exports was generated and the results are plotted in Figure 24. The plot shows the decline in mean θ as exports increases (when exports are at 2000 cfs, mean θ is 0.62, and when exports are at 10,000 cfs, mean θ is 0.31). The plot also shows the considerable range of variability in θ for any given level of exports. The noise in this relationship is indirectly apparent given that the DIC value for a model *without* exports (an Interior model) was not much higher than the corresponding model with exports. Note that upper bounds on θ for lower levels exceed 1.0,

allowing for the possibility that Georgiana Slough releases could have better survival than Ryde releases (consistent with results for the Interior model).

Figure 25 compares the BHM *predicted* values of θ at different export levels with predictions from indirect, non-Bayesian analyses. Model M1 mimics Brandes and McLain (2001) in that a linear regression of the ratio of Chipps Island recovery fractions ($\hat{r}_{GS\rightarrow CI}/\hat{r}_{Ry\rightarrow CI}$) was regressed against (standardized) exports. Another model, M2, is a regression of the natural logarithm of $\hat{r}_{GS\rightarrow CI+Oc}/\hat{r}_{Ry\rightarrow CI+Oc}$ against (standardized) exports; the predicted values are $\exp(\hat{\beta}_0 + \hat{\beta}_1 Exp^* + \sigma^2/2)$. All three models had a negative association with exports but the BHM results (M3) had a higher relative survival for Georgiana Slough releases than the two non-Bayesian models.

Table 12 compares the BHM *fitted* values of θ compared to non-BHM estimates. The BHM fitted values are the posterior means for the particular releases in contrast to posterior predicted values for any release at a specified export level (as shown in Figure 25). The non-BHM estimates are simply the release-specific ratios, $r_{GS\rightarrow CI+Oc}/r_{Ry\rightarrow CI+Oc}$, i.e., not modeled as a function of exports. Despite the underlying differences in estimation procedures, the posterior means of fitted values and non-BHM estimates are quite similar. The posterior standard deviations and standard errors are also similar with the exception of the two most recent years without ocean data, where the posterior standard deviations are considerably smaller than the standard errors, indicative of the information from other releases that BHMs utilize. The last column of Table 12 shows the estimates of the survival ratios using the method of Brandes and McLain (2001) with the Chipps Island recoveries. While there are several release pairings with values similar to θ (a 1995 pairing, a 1999 pairing, 2000, 2004, and 2005), there are several, sometimes large differences as well (e.g., 1994 and a 1995 pairing).

The posterior distributions of recovery probabilities for Ryde releases at Chipps Island and in the ocean fisheries were nearly identical to the Interior study (Table 11).

Quality of fit. The Bayesian P-values and scaled residuals were essentially the same as for the fitted Interior model. The relationship between temperature and length and fitted θ's would be similar to that for the fitted Interior model, too.

Additional analyses. The multivariate random effects model was also fit. The DIC value was only slightly higher for the uncorrelated random effects models with log transformed θ. The correlation between random effects, as compared to the Interior study, was slightly

higher: between θ and $r_{Ry \to CI}$ (on the logit scales) it was 0.33, between θ and $r_{Ry \to Oc}$ it was 0.47, and between $r_{Ry \to CI}$ and $r_{Ry \to Oc}$ it was 0.33.

As for the *Interior* model, the inland recoveries were added to the ocean recoveries and the preferred multinomial model was fit. The results were quite similar to those excluding the inland recoveries. The DIC value was 427.6 (versus 427.0). The probability that $\beta_1 < 0$ was again 98%, although the posterior mean fitted values for $\theta|Exports$ differed by as much as 10% from the model without inland recoveries (e.g., for group 10, the posterior fitted value of θ was 0.55 versus 0.65, Table 12).

Based on suggestions from anonymous reviewers, the ratio of exports to flow was substituted for absolute exports as a covariate. The DIC value was very similar (426.9 versus 427.0) and the probability that $\beta_1 < 0$ was 0.98 still. Bayesian P-values and scaled residuals were nearly identical.

5.4. **VAMP studies.** Initial analyses compared multinomial and negative binomial formulations at Level 1. For the negative binomial model, three dispersion parameters were included, for Antioch, Chipps Island, and the ocean recoveries. For further analyses and the results presented here, the multinomial formulation was selected over the negative binomial based on the facts that the dispersion parameters were all very large (at least 500 in all three cases), indicating little overdispersion, and that the Bayesian P-values and and scaled residuals were considerably better for the multinomial model.

The particular multinomial model used for inference used logit transformations of survival probabilities for Level 2 and uniform priors for the σ's for Level 3. The use of log transformations for Level 2 was not tried to lessen problems with probabilities exceeding one during the fitting process. Inverse gamma priors for σ^2 at Level 3 led to similar results. The `R` and `WinBUGS` code used to fit a multinomial model is shown in Appendix E.5.

Including random effects had a considerable impact on DIC values. Table 13 compares the DIC values for three models with only a single covariate (an indicator for HORB was used to model $S_{DR \to JP}$). When no random effects were included, the DIC was about six times larger than for a model with random effects for the recovery probabilities, and inclusion of random effects for survival and recovery probabilities further reduced DIC by about 2/3's. Thus including random effects considerably improved the DIC values.

Models where p_{OR} was assumed known and a function of the relative flow into Old River (see Table 6) were compared to models where p_{OR} was fixed but unknown were compared. To otherwise make the two situations equal, in both cases $S_{MD\rightarrow HOR}$ was fixed equal to 1.0, even though it was estimable with p_{OR} known. For a model with no covariates, the DIC values were nearly equal (DIC=1499 with p_{OR} known and DIC=1496 with p_{OR} estimated). Somewhat arbitrarily, believing that p_{OR} does in fact vary as a function of flow, and not wanting to necessarily assume $S_{MD\rightarrow HOR}$=1.0, results for varying p_{OR} are presented and discussed below. The quality of fit and the relative magnitude of coefficients were much the same for known and varying p_{OR} and unknown and fixed p_{OR}, however.

Table 14 summarizes results for some of the models (with varying p_{OR}). The model with the smallest DIC value models $S_{DR\rightarrow JP}$ and $S_{OR\rightarrow JP}$ both as functions of flow and export levels (labeled Null.FE.FE); i.e.,

$$\begin{aligned} logit(S_{DR\rightarrow JP}) &\sim \text{Normal}\left(\xi_0 + \xi_1 Flow_{DR} + \xi_2 Exports_{DR}, \sigma^2_{DR\rightarrow JP}\right) \\ logit(S_{OR\rightarrow JP}) &\sim \text{Normal}\left(\zeta_0 + \zeta_1 Flow_{UOR} + \xi_2 Exports_{MD}, \sigma^2_{OR\rightarrow JP}\right). \end{aligned}$$

Figure 26 contains histograms of a sample from the posterior distribution for the flow and export coefficients (ξ_1, ξ_2, ζ_1, ζ_2) for this model. While the DIC value was lower than for models without export coefficients and upper Old River flow, the posterior probabilities suggested only weak effects of exports and the upper Old River flow on survival. Also based on this model, Figure 27 plots, for each of the 35 release sets, the posterior mean survival probabilities for travel down Old River exclusively, travel down the San Joaquin River exclusively, and the expected values down the combination of rivers (given HORB and p_{OR}). The expected survival probability down Old River was always less than the survival down the San Joaquin River. Different models yielded somewhat different expected values, but the survival down Old River was generally, if not always, lower than those for the San Joaquin.

The PI for the VAMP study asked how different the results would be if the release sets from 2003 through 2006 were removed, since these were years with particularly low recovery numbers for Durham Ferry and Mossdale releases. Only a couple of models were tried, but the results were quite similar to those for the full data set. The most practically significant results were that the positive effect of flow on $S_{DR\rightarrow JP}$ and $S_{OR\rightarrow JP}$ was considerably stronger: the probability that the coefficients was positive was 100% for $S_{DR\rightarrow JP}$ and 97% for $S_{OR\rightarrow JP}$.

Quality of fit. The posterior mean predicted values for the Null.FE.FE model are plotted against the observed values for some of the data in Figure 27 (excluding Old River just to avoid clutter). Note that these are predicted, not fitted values which include case-specific

random effects. The observed values are in many cases far from the mean predicted values; for cases of relatively large numbers of ocean recoveries in particular, the posterior mean values are underestimates. The Bayesian P-values are perhaps more informative in that they indicate just how extreme, or not, the observations are relative to the entire predictive distribution. Of the 206 outcomes, 197 (96%) of the observations fell within the middle 90% of the posterior predictive distributions. The "minimum" P-values, and posterior predictive samples, for the worst fitting subset, recoveries at Antioch from Mossdale releases, are shown in Figure 28, where there were three releases with one or zero recoveries at Antioch. The scaled residuals, grouped by release-recovery category (again excluding Old River releases), are plotted against posterior predictive means in Figure 29. For a few observations, e.g., Chipps Island recoveries from a Jersey Point release, the residuals exceeded 2 in absolute value.

Secondary covariates. At a presentation of preliminary results to the VAMP science group, the question of the effects of water temperature on survival was raised. The observed, or in some cases estimated, water temperatures at release points were compared to the Level 2 random effects residuals, i.e., deviations from the mean value (on the logit scale), using the Null.FE.FE model. For example, the survival, on the logit scale, between Durham Ferry and Mossdale for release set t can be written as follows.

$$logit(S_{DF \to MD,t}) \quad = \quad \beta_0 + \epsilon_{DF \to MD,t},$$

where

$$\epsilon_{DF \to MD,t} \quad \sim \quad \text{Normal}(0, \sigma^2_{S_{DF \to MD}}).$$

`WinBUGS` output included samples from the posterior distribution for these ϵ's and the means from these samples are what are plotted against the stream section temperatures in Figure 30. The Jersey Point plot is based on the residuals for relative survival to Chipps Island, where $\epsilon_{JP \to Ant \to CI,t}$ and $\epsilon_{JP \to CI,t}$ have been combined. The scatterplot smooths over the plots suggests at most a slightly negative association between temperature and the random effects for Durham Ferry releases, i.e., as release temperature increases the estimated survival (on a logit scale) tends to decrease, but otherwise there was no evidence for an association.

As an aside, there was a single very large negative random effect for one of the Durham Ferry releases (this was from a year 2000 release, group 24), as can be seen in Figure 30. This was undoubtedly the cause of the very large variance term, $\sigma^2_{DF \to MD}$. The reason for the large "residual" may be due to the low percentage of ocean recoveries, 0.2%, relative to Jersey Point release which had 1.5%, in comparison to other Durham Ferry releases. It is worth noting that the scaled residuals did not reveal this outlier because the large random

effects variance scaled down the residual considerably. Thus scaled residuals alone are not an adequate diagnostic of model fit in some cases.

Another concern raised by the VAMP science group and one of the reviewers was the use of two different hatchery stocks, from Feather River Hatchery and Merced River Fish Facility. There is some degree of temporal confounding in that Feather River Hatchery fish were used only during the early years (1985-1998), while Merced River Fish Facility fish were (mostly) used in the later years (1996-2006). If environmental conditions during the early years were particularly poor for survival, for any stock, then it would be incorrect to attribute the cause to stock. It should also be noted that another possible confounding factor is that beginning in 1998, the sampling effort at Chipps Island essentially doubled, relative to previous years. With these caveats in mind, the random effects residuals (Null.FE.FE model) for two river sections, $DR \rightarrow JP$ and $JP \rightarrow CI$ for the two stocks were compared and side-by-side boxplots are shown in Figure 31. The Durham Ferry to Mossdale section was not included since all releases from Durham Ferry came from Merced River Fish Facility; and the Mossdale to Dos Reis section was treated as having constant survival. Evidence for a higher survival probability for the MRFF stock is apparent, particularly for the Jersey Point releases. To allow for a stock effect, an expanded model for the recovery probabilities was fit, i.e.,

$$logit(r_{JP \rightarrow x}) \quad \sim \quad \text{Normal}\left(\mu_{JP \rightarrow x} + \chi I_{MRFF}, \sigma^2_{JP \rightarrow x}\right)$$

where x=Ant, CI, or Oc and I_{MRFF} is an indicator variable for Merced River Fish Facility stock. Some results for a model including this stock effect and $S_{DR \rightarrow JP}$ modeled as a function of flow are shown in Table 14. The DIC was higher than for a model without the stock effect but the posterior means for parameters were much the same, suggesting that general conclusions are robust to a possible stock effect.

Lastly, another concern expressed by reviewers was how recoveries of fish at the fish facilities at CVP and SWP might affect results. Random effects residuals (Null.FE.FE model) for different reaches were plotted against the estimated salvage (Figure 32). The residuals for the logit of $S_{OR \rightarrow JP}$ did not necessarily always apply to the Durham Ferry and Mossdale releases because the HORB was sometimes in position and by assumption those fish would only travel down the San Joaquin River. For the Old River releases, the residuals for the logit of $S_{OR \rightarrow JP}$ did tend to increase as fish salvaged increased, i.e., the fitted survival probabilities were elevated somewhat as number of fish salvaged increased. For the Durham Ferry, Mossdale, Dos Reis, and Jersey Point releases there is no apparent relationship between number salvaged and the survival random effects.

6. Study design and sample size issues

The objectives for all four multi-year studies have been translated into parameter estimation problems, namely

- *DCC*: for comparing open gate to closed gate effects on survival, estimate $\mu_{\theta(Close)}/\mu_{\theta(Open)}$ (equation 8);
- *Interior*: for comparing survival from Georgiana Slough to survival from Ryde, estimate μ_θ (equation 23);
- *DA 8*: for evaluating the effect of exports on the survival of Georgiana Slough releases (relative to the survival of Ryde releases), estimate β_1 (equation 29);
- *VAMP*: for evaluating the effect of flow on survival from Dos Reis to Jersey Point, for example, estimate a parameter ξ_1, say (equation 45).

Sample size and design issues translate into statements about bias and precision of these parameter estimates.

6.1. **Bias.** Bias in parameter estimates depends primarily on model correctness, i.e., whether or not the model assumptions hold. For example, at Level 1 were multinomial models appropriate? Were the fish fates independent? Were the capture probabilities the same for all fish within a paired release, e.g., the same probability of capture at Chipps Island or in the ocean fisheries? At Level 2 were normal distributions appropriate for the random effects?

The question of independence was addressed indirectly by using the negative binomial model as an alternative to the multinomial, and in the case of the DCC studies, the negative binomial was preferable[8]. The question of equal capture probabilities within a release pair was addressed non-rigorously (Section 3.2) by comparing the distribution of recovery times at Chipps Island within a release pair for a few cases (Figure 12). To better answer these two questions, two additions to the general release-recovery design are recommended.

(1) *Use embedded replicates for some release groups.* Embedded replicate tags provide a means of detecting whether or not the assumption of independence has been violated. With embedded replicate tags, the tag numbers vary from tag to tag within the same "spool" of tagging wire that is used to tag a given release group. Schnute (1992)

[8]Although the better fit of the negative binomial in this case could be due to the estimation error in the ocean recoveries more so than dependence between fish.

pointed out that embedded replicate tags provide no additional information regarding sampling variation *if* fish are independent and identically distributed. However, if fish are not independent and identically distributed, then embedded replicates can provide evidence for lack of independence, e.g., clustering. If variation between embedded replicates is higher than expected according to the underlying multinomial models, then dependence, such as clustering, could be the explanation. The negative binomial distribution is one possible remedy in that case, but the development of other alternative probability models would be worth exploring.

While embedded replicate data are not currently available, there were some "near" replicate tag codes used for some of the releases in the VAMP studies. Table 15 contains information from five sets of Durham Ferry releases. The fish within each set were reared in the same pond but differed by tag code. This is not exactly the same as embedded replicate groups in that the lots tagged with different tag numbers were tagged at different times. For each set a χ^2 test was carried out to test that the proportions recovered by location were the same within a set. The P-values shown in Table 15 suggest departures from homogeneous multinomial distributions for four of the five sets. The underlying probability distribution for the χ^2 test is multinomial. However, because ocean recoveries are estimated, not observed directly, this assumption is not true and some extra-multinomial variation undoubtedly exists. The ocean recoveries were then aggregated into the "non-caught" group and the χ^2 tests were repeated, and this time no departures from homogeneity were observed. Note that these results indicate that using multinomial distributions for Level 1 of the hierarchical model is likely inaccurate, but they do not necessarily indicate a lack of independence between fish.

(2) *Make releases below the recovery locations.* By making releases immediately downstream of capture locations, i.e. Chipps Island and Antioch, *assuming* that subsequent ocean recovery probabilities are the same for releases within a pair or grouping, the capture probabilities at Chipps Island or Antioch can be estimated separately of the survival probability of the immediately upstream section (Newman 2003). Furthermore, estimates of capture probabilities provide a means of evaluating the assumption of constant capture probabilities for paired releases.

For some of the releases in the DCC and the Interior/DA8 studies, downstream releases were made below Chipps Island at Port Chicago or Benicia (see Tables 3 and 4). Method of moments estimates of the capture probabilities for the Courtland or Georgiana Slough releases and the Ryde releases were calculated as follows

$$\hat{p}_{CI} = \frac{y_{Up \to CI}}{y_{Up \to CI} + \frac{\hat{y}_{Up \to Oc} * R_{PC}}{\hat{y}_{PC \to Oc}}},$$

where the subscript Up is for any release location above Chipps Island. The resulting estimates of p_{CI} for the paired upstream releases are shown in Table 16. On average the capture probabilities were higher for Ryde releases than for the Courtland or Georgiana Slough releases. For the DCC studies, a simple paired t-test of equal capture probabilities yielded a P-value of 0.21, suggesting that the differences could be due to sampling variation alone (a more refined test would account for different estimation errors). For the Interior/DA8 studies, however, the same test resulted in a P-value of 0.017 suggesting that Ryde releases were indeed captured with a higher probability than Georgiana Slough releases.

If in fact, the Ryde releases were recovered at a higher rate, then estimates of the relative survival rates of Georgiana Slough to Ryde releases are likely biased low, i.e., Georgiana Slough releases are surviving at a higher rate. Excluding the three release pairs without associated Port Chicago releases, the non-Bayesian estimate of μ_θ (equation 26) assuming equal capture probabilities is 0.46, while if different capture probabilities are allowed the estimate is 0.57.

The hierarchical model can be modified to accommodate both recoveries of Port Chicago releases, and separable upstream survival and capture probabilities, e.g., for the Interior studies,

Level 1:

$$\begin{aligned}
y_{GS\to CI}, y_{GS\to Oc} &\sim \text{Mn}\left(R_{GS}, \theta S_{Ry} p_{GS,CI}, \theta S_{Ry}(1-p_{GS,CI}) r_{PC\to Oc}\right) \\
y_{Ry\to CI}, y_{Ry\to Oc} &\sim \text{Mn}\left(R_{Ry}, S_{Ry} p_{Ry,CI}, S_{Ry}(1-p_{Ry,CI}) r_{PC\to Oc}\right) \\
y_{PC\to Oc} &\sim \text{Binomial}\left(R_{PC}, r_{PC\to Oc}\right)
\end{aligned}$$

Level 2:

$$\begin{aligned}
logit(\theta) &\sim \text{Normal}\left(\mu_\theta, \sigma^2_\theta\right) \\
logit(S_{Ry}) &\sim \text{Normal}\left(\mu_{S_{Ry}}, \sigma^2_{S_{Ry}}\right) \\
logit(p_{GS,CI}) &\sim \text{Normal}\left(\mu_{p_{GS,CI}}, \sigma^2_{GS,CI}\right) \\
logit(p_{Ry,CI}) &\sim \text{Normal}\left(\mu_{p_{Ry,CI}}, \sigma^2_{Ry,CI}\right) \\
logit(r_{PC\to Oc}) &\sim \text{Normal}\left(\mu_{r_{PC\to Oc}}, \sigma^2_{PC\to Oc}\right)
\end{aligned}$$

The assumption of equal ocean recovery probabilities has not been addressed. Earlier unpublished work by the author used cluster analyses to analyze the ocean recovery patterns for some Sacramento River and Delta releases. The estimated proportions caught by age-port-time strata were used as the variable to cluster on and

the results indicated greater similarities between releases made in the same year than between years. More work is needed in this area.

6.2. **Precision.** Precision is the magnitude of the sampling error as measured by the size of the standard error of parameter estimates (classical analysis) or the size of the standard deviation of posterior distributions (Bayesian analysis). Sampling error of estimated survival probabilities and related parameters is a function of the parameter values, capture probabilities, inherent between year variation, sample size, and the degree of blocking or controlling for variation. With regard to blocking, the pairing (or tripling, etc) of releases is a positive feature of all the studies because it controls for at least some confounding factors and thereby increases precision.

As sample sizes increase and capture probabilities increase, the standard error or standard deviation of posterior distributions for the survival probabilities will generally decrease. For these multi-year studies there are two kinds of sample sizes: the number of fish released (R) and the number of years (or replications) of study (n). Increasing R or n will increase precision.

With paired releases there are at least two R's and how fish numbers are allocated to each R will affect precision. For example, in a VAMP release group with 100,000 total fish available, one could allocate 25,000 fish each to Durham Ferry, Mossdale, Dos Reis, and Jersey Point, or one could put 40,000 at Durham Ferry and 20,000 each at the other three sites. Determining "optimal" allocation is thus another problem.

Covariate values affect precision, too. For the DA 8 studies, increasing the number of observations at the "extremes" of export levels will increase the precision in the estimate of the slope parameter (β_1 in Equation 29). Similarly, for the VAMP studies, increasing the number of observations at the "extremes" of flow and exports will increase the precision of the related (partial) slope parameters (Equations 43-46).

Thus there are an infinite number of ways to achieve a desired precision by varying the number of years of study, varying the total number of fish released, varying the allocation of fish to release sites within a pairing, and by manipulating the covariate values to the degree possible. Ideally an analytic formula is derived which takes as input n, the total release numbers, e.g., R_1+R_2, and the allocation to release sites (R_1, R_2), covariate values when appropriate, guesses as to parameter values, and inherent between year variation (e.g., σ_θ^2), and then outputs the standard error or standard deviation of the posterior distribution for

the parameter of interest. Or, more directly, an analytic formula takes as input the desired standard error or posterior standard deviation, and whatever non-manipulable factors there are (e.g., σ_θ^2), and outputs the combinations of n, R_1, R_2, and covariate values that will achieve the target precision.

The complexity of the hierarchical models for the DCC, DA 8, and VAMP studies is such that analytic solutions are difficult, at best, to derive. In these cases, simulation studies are an alternative: for different sample sizes and input values, simulate the data generation and estimation processes and then look at the resulting standard deviation of estimates (or posterior means). The following sections discuss sample size determination for each of the studies.

6.2.1. *DCC: Sample size for estimating* $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$. Simulations of the data generation and data analysis processes were used to study the effect of changing n, the number of replications of paired releases, on the standard error of the estimate of $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$. Results from the Bayesian analysis were used for the simulation of observations, but the estimation procedure was non-Bayesian and bootstrapping was used to calculate standard errors. Carrying out a full Bayesian analysis using `WinBUGS` to produce posterior standard deviations would have taken considerably longer.

The simulations used recovery probabilities estimated from a BHM fit to the DCC data. The BHM used the multinomial distribution at Level 1 and the 1989 outlier had been removed from the data set. The median posterior values for β_0 and β_1 were used to generate the relative survival probability for Courtland releases compared to Ryde releases (θ); the true value of θ was around 0.73. Similarly recovery probabilities at Chipps Island and in the ocean were generated. Recoveries at Chipps Island and in the ocean were simulated using the multinomial distributions, and $\mu_{\theta(Open)}/\mu_{\theta(Closed)}$ was estimated using equation (15). Bootstrapping was then used to estimate the standard error. The `R` code for this exercise is given in Appendix D.4.

The above procedure was carried out 100 times for n=10, 14, 20, and 24, where gates were open in exactly half the replications, i.e., 5, 7, 10 and 12 replications of open gates. The release numbers were fixed at 100,000 each for Courtland and for Ryde releases. The bootstrap standard errors for the estimates are plotted in Figure 33. The median standard errors for 10, 14, 20, and 24 replications were 0.72, 0.46, 0.42, and 0.36, which are large relative to ratio value of 0.73.

The effect of doubling the release numbers to 200,000 was examined. The reduction in standard errors was negligible, indicating that the between replication variation, as reflected in σ_θ, $\sigma_{Ry\to CI}$, and $\sigma_{Ry\to Oc}$, overshadows the sampling variation (given that R is at least 100,000).

The DCC studies consisted of only 13 replications, 4 with gates closed and 9 with gates open, and the average release numbers were 90,000 for Courtland releases and 64,000 for Ryde releases. Thus even if the true value of the ratio were 0.73, the chance of an estimated value being found to be "statistically significant" is likely relatively low for this amount of data.

6.2.2. *Interior: Sample size for estimating μ_θ.* An analytic formula for the variance of $\hat{\mu}_\theta$ was calculated in a classical, non-Bayesian framework (Appendix A). The resulting formula can be used to determine the effect of release numbers and the number of replicate pairs on the variance. Assuming that the same number are released in each group every year, i.e., $R_{1t} = R_{2t} = R$, simplifies the weights to w_t=1/n. The formula, in this case, for $\hat{\mu}_\theta$ (equation (26)) is:

$$\hat{\mu}_\theta = \frac{1}{n}\sum_{t=1}^{n}\hat{\theta}_t = \frac{1}{n}\sum_{t=1}^{n}\frac{y_{13,t}+y_{14,t}}{y_{23,t}+y_{24,t}}.$$

Calculation of the variance of $\hat{\mu}_\theta$ is quite lengthy and the details are provided in Appendix A. After some algebra the theoretical variance of $\hat{\mu}_\theta$ can be rewritten as follows:

$$V(\hat{\mu}_\theta) \approx \frac{1}{n}\left[\frac{X}{R}+\sigma_\theta^2\right], \tag{54}$$

where X is a long tedious calculation (see Appendix C, where X=$A + 0.5B$ and equation (62)).

For a given release number R and specified variance, the necessary number of years can be calculated:

$$n = \frac{\frac{X}{R}+\sigma_\theta^2}{V}. \tag{55}$$

Similarly for a fixed number of years n and specified variance, the necessary release numbers can be calculated:

$$R = \frac{X}{Vn-\sigma_\theta^2}. \tag{56}$$

One crucial factor in sample size determination is σ_θ^2. The output from a BHM fit (logit transformed θ with inverse gamma priors for the σ^2's) was used to estimate σ_θ^2. A median value for σ_ϵ^2 of 1.05 and the median value for μ_θ of -0.40 were used to generate a sample of 1000 $logit(\theta)$'s. The inverse logit transformation was applied to calculate θ and the sample variance of θ, an estimate of σ_θ^2, was calculated to be 0.044. Also needed (in the "X" term) are values for the means and variances of the recovery probabilities at the two recovery locations. For the demonstration below values were chosen arbitrarily, but similar to estimated values from BHM fits to the real data.

Figure 34 is a plot of the number of replications, n, to achieve a range of desired standard errors for $\hat{\mu}_\theta$ based on $\sigma_\theta^2 = 0.044$ and R = 50,000, 75,000, or 150,000. The effect of numbers released (over this range of values) is minor in comparison to the number of years of experimentation. If σ_θ^2 were smaller, then the relative importance of R would increase.

As a check on the theoretical calculations, the plotted values were compared to the bootstrap standard error for $\hat{\theta}$ in the Interior studies. There were 14 "years" of release pairings and the bootstrap standard error for $\hat{\theta}$ was 0.055. The mean number released at Georgiana Slough was 58,000 and at Ryde it was 45,000, so assume roughly 50,000 for both groups. If one plots the point (0.055, 14) on Figure 34, the point is very close to the line for R=50,000.

6.2.3. *DA 8: estimating* β_1. To study the effect of sample size (both n and R) on the precision of estimates of β_1, the slope coefficient in a linear model of the relative survival of Georgiana Slough releases regressed against exports (equation 29)), simulation of the data generation and data estimation was processes was used. To be consistent with a fully Bayesian analysis, `WinBUGS` would be used to generate samples from the posterior distribution for β_1 and calculate the standard deviations. This would be very computer intensive and take a considerable amount of time.

An approximate, but easier alternative was chosen. Recoveries were simulated according to the hierarchical model but the approximate indirect estimation procedure (which ignores unequal sampling and between pair variation) was used to estimate β_1. To simulate the recoveries the medians of the posterior distributions for the parameters (σ_θ^2, $\sigma^2_{r_{Ry\to CI}}$, $\sigma^2_{r_{Ry\to Oc}}$, β_0, and β_1) from one of the fitted BHMs were used. The export levels were randomly selected from a Uniform(1500, 11000) distribution, and then standardized using the mean (6376) and standard deviation (3284) of the observed data. The logit transform of θ was simulated using Equation 29. The fitted regression was of the logit transform of $\hat{\theta}$ on standardized exports.

The standard errors of $\hat{\beta}_1$ based on 10,000 simulations per combination of R and n are shown in Table 17. The `R` code is given in Appendix D.6. Again the standard errors are more sensitive to n than R, at least for $R \geq 50{,}000$ per release. In relative terms the standard errors were large given that the true value of β_1 was 0.57; even with 25 release pairs with R=150,000, the coefficient of variation was 40% (0.228/0.57). Thus the between pair variation is the factor most affecting how easily a "significant" export effect can be detected. The coefficient of variation could be reduced to around 20% if $n = 100$ paired releases were made.

6.2.4. *VAMP: estimating regression coefficients for flow, exports, and HORB.* As for the DA 8 studies, linear regression coefficients are of primary interest. The analysis of sample size effects on estimates of coefficients discussed here is based on a version of a VAMP model that precedes those presented in this report (subsequently modified based on suggestions from reviewers). With the earlier version there were no branching probabilities at the head of Old River and survival between Mossdale and Dos Reis was modeled without explicit allowance for travel down Old River when the HORB was not in place. Due to time limitations, the sample size analysis was not repeated with the newer models. However, the analysis was based on data simulated from the earlier model and the general conclusions are expected to be consistent with what would be observed if the analysis were carried out using simulated data from the final VAMP models.

Data were simulated according to the following reach-specific survival probability models:

$$\begin{aligned}
logit(S_{DF\rightarrow MD}) &\sim \text{Normal}\left(\beta_0 + \beta_1 Flow, \sigma^2_{DF\rightarrow MD}\right) \\
logit(S_{MD\rightarrow DR}) &\sim \text{Normal}\left(\gamma_0 + \gamma_1 Flow + \gamma_2 I_{HORB} + \gamma_3 Exports \times (1 - I_{HORB}, \sigma^2_{MD\rightarrow DR}\right) \\
logit(S_{DR\rightarrow JP}) &\sim \text{Normal}\left(\xi_0 + \xi_1 Flow + \xi_2 I_{HORB} + \xi_3 Exports, \sigma^2_{DR\rightarrow JP}\right)
\end{aligned}$$

Again, for convenience, simulations from the hierarchical model were used to generate observations, then non-Bayesian estimates of the section-specific survival probabilities (or θs) were regressed, on a per river segment basis, against the relevant covariates.

The simulated model structure and parameter values are shown in Appendix D.7. A positive flow effect was assumed between Durham Ferry and Mossdale. To reduce the probability of maximum likelihood estimates being truncated at 1, the intercepts for the logit transforms were made relatively negative. For reporting the effect of sample sizes, the interquartile range was calculated instead of the standard deviation to lessen the impact of potentially skewed sampling distributions.

The results are shown in Table 18. Again number of replications of the release sets has a larger effect on the variability of point estimates than number released. The relative error, IQR/true value, tends to decrease the further downstream the releases are made. This is presumably due to the fact that more fish are providing information about survival for the lower reaches; e.g., from Dos Reis to Jersey Point there are the Dos Reis releases as well as surviving fish from the Durham Ferry and the Mossdale releases. This suggests that a more refined sample size determination could lead to fewer releases for further downstream releases relative to upstream releases.

6.3. **Acoustic tagging studies as an alternative.** Acoustic tagging experiments have been, and are currently being, conducted in the Sacramento-San Joaquin system. It would be worthwhile to make a cost and precision comparison between acoustic tagging and CWTs in terms of estimating survival probabilities and related parameters. Acoustic tags and receivers are quite expensive compared to CWTs; e.g., the cost for a single acoustic tag in early 2008 was around $300 while an individual CWT costs a fraction of a cent. On the other hand, detection probabilities using hydrophonic receivers are orders of magnitude greater than capture probabilities at Chipps Island, for example, and the precision of estimated survival probabilities, per number of fish, are considerably greater with acoustic tags compared to CWTs. Furthermore, acoustic tags combined with strategically placed receivers can more readily provide information about the out-migration route taken by the juvenile salmon. Statistical analysis procedures are not yet entirely worked out for such studies but Skalski, et al. (2002) and Muthukumarana, Schwarz and Swartz (2008) have developed methodologies for radio-tagged salmon that could be applicable to the Sacramento-San Joaquin system. The general features of BHMs would still be appropriate for multi-year studies using acoustic tags.

7. Conclusions and Recommendations

7.1. **Comparison with previous analyses.** The reanalysis of the four studies within a Bayesian hierarchical framework led to conclusions that were more often consistent with previous analyses than not and a comparison of the alternative analyses is summarized below. Major differences between previous analyses and the BHM analyses for all studies were that previous analyses did not account for unequal sampling variation and between release pair variation while the BHMs did.

(1) *DCC:* The analysis of Manly (2002) is more directly comparable to the hierarchical model than the previous USFWS analyses (Brandes and McLain, 2001). Manly used only Chipps Island recoveries and calculated survival indices (recovery rates adjusted by Chipps Island sampling effort). The ratio of the Courtland to Ryde survival indices when the gates were open was estimated to be 0.650, and 0.705 when the gates were closed. Using t-tests, Manly found no significant difference in these ratios.

The Bayesian hierarchical model analysis used Chipps Island and ocean recoveries simultaneously and, with the negative binomial formulation, allowed for overdispersion relative to binomial models. The *conclusions were similar to those of Manly*: survival for Courtland releases relative to Ryde releases appears to be lower with the gates open (median=0.54) than with the gates closed (median=0.75), with the median ratio of ratios equal to 0.72. The BHM median ratio of ratios was lower than Manly's implied value of 0.92 (0.650/0.705), but the BHM posterior 97.5 percentile value was over 5.

(2) *Interior:* Brandes and McLain (2001) had a shorter time series available when they did their analyses so results are not directly comparable with the BHM results. They analyzed the available recoveries from Georgiana Slough and Ryde releases of Chipps Island (using survival indices) and ocean recoveries separately. Based on paired t-tests of the null hypothesis of equal survival indices for Georgiana Slough and Ryde, they found statistically significant differences between the two release locations.

The Bayesian hierarchical model (while using Chipps Island and ocean recoveries simultaneously) led to *conclusions similar to Brandes and McLain*: Georgiana Slough releases have a lower survival probability than Ryde releases with the median value of the posterior distribution for the ratio of the survival probabilities equal to 0.36.

(3) *DA 8:* Again, using the shorter time series available at the time Brandes and McLain (2001) used an indirect approach (applied separately to Chipps Island and ocean recoveries, and using a combination of fall run and late fall run releases) to analyze

the effect of exports on the relative survival of Georgiana Slough releases. They found a statistically significant negative association between exports and survival.

The Bayesian hierarchical model (fitted only to the late fall run) used Chipps Island and ocean recoveries simultaneously, and modeled the relationship between exports and survival directly. The hierarchical model results again led to *conclusions similar to Brandes and McLain*: there is over a 98% probability that as exports increase the survival decreases for Georgiana Slough releases. The posterior median value for the slope coefficient was -0.31. This is just slightly less negative than a non-Bayesian indirect estimate of -0.39, where $logit(\hat{\theta})$ was regressed on exports. However, the intercept in the linear model regression survival against exports was considerably higher for the BHM than for the non-Bayesian models; thus the BHM was suggesting an overall higher relative survival for Georgiana Slough releases.

(4) *VAMP:* Previous analyses of VAMP and pre-VAMP data (2005 Annual Technical Report by San Joaquin River Group Authority) were carried out in a piecemeal fashion using several simple linear regressions of release-specific recovery rates against flow, exports, and flow/exports when HORB was either in or out (see Table 8. Also the recovery fractions for the freshwater recoveries (Antioch and Chipps Island combined) and ocean recoveries were analyzed separately, and releases at Durham Ferry and Mossdale were treated as a single release. The results were that with the HORB out, survival of releases above the head of Old River was *not* significantly related to flow, exports, or flow/exports (at α=0.05). However, with HORB in, survival of releases made above the head of Old River was significantly related to flow, but the relationship with exports and flow/exports was inconsistent and sometimes paradoxical (e.g., exports were positively associated with survival, weakly statistically significant using Antioch and Chipps Island recoveries and insignificant using ocean recoveries). The fact that the presence of the HORB affected the relationships with flow suggests an interaction between flow and HORB.

The Bayesian hierarchical model analyzed the multiple release and recovery data, including Antioch, Chipps Island, and ocean recoveries, simultaneously. Reach-specific survival probabilities were linked together, along with recovery probabilities at the three recovery sites. Logit transformations of survival and recovery probabilities were modeled with random effects and various covariates, particularly flow and exports, were tried. For the various models fitted, there were two in-common conclusions: (1) flow is positively associated with the probability of surviving from Dos Reis to Jersey Point and (2) the survival probability for that reach is generally greater than the survival probability for fish traveling down Old River. Assuming that the HORB effectively keeps out-migrating salmon from entering Old River, the

second conclusion implies that the HORB can increase salmon survival. For fish that do enter Old River, there was some evidence that flow in Old River was positively associated with survival between Old River and Jersey Point, but the evidence was not as consistently strong as for the Dos Reis to Jersey Point reach. There was little evidence for any association between exports and survival, and what evidence there was pointed towards a somewhat surprising positive association with exports.

7.2. **Criticisms of and concerns about the BHMs.** The BHMs as formulated for the CWT release-recovery data do not provide the ultimate definitive explanations of what affects the survival of out-migrating juvenile Chinook salmon through the Delta, nor of the magnitude of effect of the factors of interest. Some of the limitations are inherent to CWT release-recovery data: the fish can only be captured once, the capture probabilities are relatively low, and information about out-migration paths through the Delta is difficult to acquire unless recoveries can be made at multiple locations.

Other limitations are a function of the accuracy of assumptions made, in particular, that capture probabilities are the same for temporally paired releases, relatedly that ocean survival, spatial-distribution, and maturation probabilities are the same for such paired releases, and, in the case of the VAMP model, that the survival in downstream sections is the same for all fish within a paired release that pass through the section. A potential violation of this last assumption could occur if downstream releases experienced some additional mortality at the time of release, such as might be caused by extreme differences in truck water temperatures and river water temperatures, a shock effect (Newman 2003), that is not experienced by fish released upstream that are passing by. Regarding the assumption of equal ocean capture probabilities, a relatively simple cluster analysis of catch recoveries (unpublished work) had been done prior to earlier analyses of Sacramento River releases (Newman and Rice 2002). The results suggested greater between release year variation than within release year variation, but a more rigorous examination may be fruitful.

The BHMs for the DCC, Interior, and Delta Action 8 studies are relatively simple and the number of models considered was relatively few. However, for the VAMP data, the number of models and complexity of models considered was much greater. The use of DIC to select amongst the different VAMP models is not entirely satisfying and the use of posterior model probabilities may be a better alternative (see comments by Giminez, et al. (in review)). A Reversible Jump MCMC add-on procedure for `WinBUGS`, which allows one to search through model space, is now available (`http://www.winbugs-development.org.uk/rjmcmc.html`)

and might be usable for some of the BHMS considered. In short, a more thorough model selection procedure needs to be carried out, particularly for the VAMP models.

While acoustic tags and receivers are not necessarily a complete solution, due to occasional difficulty in successfully placing receivers in the Sacramento-San Joaquin system (Pat Brandes, personal communication), they potentially offer considerable advantages over CWT release-recovery data. First, multiple recaptures are possible, which thereby increases precision. Second, capture probabilities with acoustic receivers are sometimes two orders of magnitude greater than capture probabilities by a mid-water trawl. Third, judicious placement of receivers at junctions can provide information about out-migration paths that are much more difficult to determine using CWT data, which require trawling at the same junctions, and preferably the release of additional fish at those same points.

7.3. **Recommendations.** Recommendations on alternative data generation procedures were made earlier (Section 6.1). These recommendations are summarized briefly here along with additional recommendations.

(1) Use embedded replicate tags to check for violations of the assumption of independence between fish.
(2) Make releases below freshwater recovery locations, e.g., below Chipps Island, so as to allow separate estimation of capture probabilities at the recovery location.
(3) Carry out a more detailed analysis of the ocean catch recovery patterns by age-port-month of recovery to better determine how similar the recovery patterns are within paired releases.
(4) Carry out a benefit-cost comparison of CWTs and acoustic tags, including a comparison of the precision of estimates of survival probabilities per number of fish released.
(5) Specify an underlying probability model for any analyses of release-recovery data, and in the case of multi-year survival studies, in particular, formulate hierarchical probability models.
(6) Use such probability models *prior* to carrying out release-recovery experiments to evaluate design and sample size options.
(7) Estimate the sampling errors for estimated ocean recoveries and incorporate the errors into the probability model for observed and estimated recoveries; hierarchical models can be extended to another level to include such variation.
(8) Carry out a more rigorous model-selection procedure for the various VAMP models using Reversible Jump MCMC.

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9. References

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TABLES

Table 1. Overview of the release and recovery locations, and duration, of the four studies.

Study	Duration	Primary Release Locations	Recovery Locations
DCC	1983-1989	Courtland and Ryde	Chipps Island, Ocean
Interior and DA 8	1994-present	Georgiana Slough and Ryde	Chipps Island, Ocean
VAMP (and pre-VAMP)	1985-present	Durham Ferry, Mossdale, Dos Reis, Jersey Point	Antioch, Chipps Island, Ocean

TABLE 2. Summary of notation for releases, recoveries, and model parameters.

Symbol	Definition
Ct, Ry, GS	release locations: Courtland, Ryde, Georgiana Slough
DF, MD, DR, JP	release locations (VAMP): Durham Ferry, Mossdale, Dos Reis, and Jersey Point
CI, Oc, A	recovery locations: Chipps Island, Ocean, and Antioch
R_a	number of fish released at location a
$y_{a\to b}$	number of recoveries at location b of CWT fish that were released at location a
$\hat{y}_{a\to Oc}$	estimated number of ocean recoveries of CWT fish that were released at location a
$\hat{r}_{a\to b}$	observed recovery fraction, $y_{a\to b}/R_a$
$S_{a\to b}$	probability of surviving between location a and location b
p_b	probability of capture at location b (given alive at that location)
$logit(\pi)$	logistic transform of a probability, π, $\log\left(\frac{\pi}{1-\pi}\right)$
μ_θ	expected (average) value of a random variable θ
σ^2_θ	standard deviation of a random variable θ
	Notation used in DCC BHM
$\theta(DCC)$	$S_{Ct\to CI}/S_{Ry\to CI}$, which varies as a function of DCC gate position
$I_{DCC=closed}$	indicator variable that equals 1 when DCC gate is closed, else equals 0
β_0, β_1	intercept and slope in logit model for $\theta(DCC)$, $\mathrm{E}[logit(\theta(DCC))]=\beta_0+\beta_1 I_{DCC=closed}$
$r_{Ry\to CI}$	Pr(fish released from Ryde survives to and is captured at Chipps Island)
$r_{Ry\to Oc}$	Pr(fish released from Ryde survives to and is captured in the ocean)
	Notation used in Interior BHM
θ	$S_{GS\to CI}/S_{Ry\to CI}$
$r_{Ry\to CI}$	Pr(fish released from Ryde survives to and is captured at Chipps Island)
$r_{Ry\to Oc}$	Pr(fish released from Ryde survives to and is captured in the ocean)
	Notation used in Delta Action 8 BHM
β_0, β_1	intercept and slope in logit model for θ (as a function of standardized exports), $\mathrm{E}[logit(\theta)]=\beta_0+\beta_1\left(\frac{(Exports-\overline{Exp})}{s_{Exp}}\right)$
	Notation used in VAMP BHM
$r_{JP\to A}$	Pr(fish released from JP survives to and is captured at Antioch)
$r_{JP\to CI}$	Pr(fish released from JP survives to and is captured at Chipps Island)
$r_{JP\to Oc}$	Pr(fish released from JP survives to and is captured in Ocean)
β	parameter(s) for $\mathrm{E}[\mathrm{logit}(S_{DF\to MD})]$
γ	parameter(s) for $\mathrm{E}[\mathrm{logit}(S_{MD\to DR})]$
ξ	parameter(s) for $\mathrm{E}[\mathrm{logit}(S_{DR\to JP})]$
ζ	parameter(s) for $\mathrm{E}[\mathrm{logit}(S_{OR\to JP})]$

Table 3. DCC: Release and recovery data. Recoveries at Chipps Island, in the ocean fisheries, and at the SWP and CVP fish salvage facilities are in the columns headed CI, Oc, and FF, respectively. Ryde releases were occasionally made at Isleton and some of the Port Chicago releases were actually at Benicia.

		Tag Codes			DCC	Courtland				Ryde				Pt.Chicago	
Year	Grp	Courtland	Ryde	Pt Chicago	Gate	R_{Ct}	CI	Oc	FF	R_{Ry}	CI	Oc	FF	R_{PC}	Oc
1983	1	06-62-24	06-62-23	06-62-30	closed	96,706	89	428	0	92,693	96	368	0	43,374	129
1987	2	06-62-53:54	06-62-55	NA	closed	100,302	73	1981	182	51,103	47	1607	0	NA	NA
1988	3	B6-14-02:03	06-31-01	B6-14-08	closed	107,249	151	1188	1075	52,741	104	1076	0	55,265	1115
1988	4	06-62-59:60	06-62-63	06-31-04	closed	106,901	37	1037	0	53,961	44	252	0	54,151	1022
1984	5	06-62-27	06-62-29,06-42-09	06-62-31,06-62-37	open	62,604	37	399	0	59,998	38	268	0	42,000	316
1985	6	06-62-38,06-62-41	06-62-35	06-62-45	open	100,626	38	313	0	107,161	89	926	0	48,143	465
1986	7	06-62-43	06-62-48	06-62-51	open	98,866	39	1692	8	101,320	75	1979	0	47,995	1377
1987	8	06-62-56:57	06-62-58	NA	open	100,919	43	1434	187	51,008	47	1039	0	NA	NA
1988	9	B6-14-04:05	06-31-02	B6-14-08	open	102,480	145	936	450	53,238	145	1324	0	55,265	1115
1988	10	06-62-50	06-31-03	06-31-04	open	99,827	5	70	0	53,942	38	285	0	54,151	1022
1989	11	06-31-11	06-31-12	NA	open	51,211	46	240	26	51,046	58	417	18	NA	NA
1989	12	06-31-08	06-31-07	06-31-09	open	50,659	19	41	0	50,601	26	82	0	45,446	181
1989	13	06-01-14-01-03,06-58-05	06-01-14-01-02	06-01-14-01-04	open	90,720	21	84	0	51,134	8	10	0	48,329	352

Table 4. Interior and DA 8: Release and recovery data. Recoveries at Chipps Island, in the ocean fisheries, at the SWP and CVP fish salvage facilities, and at Inland locations (expanded numbers) are in the columns headed CI, Oc, FF, and IL, respectively. Ryde releases were occasionally made at Isleton (denoted by asterisk by tag code) and some of the Port Chicago releases were actually at Benicia (denoted by asterisk by tag code). Exports are a three day average volume of water exported from SWP and CVP.

Release			Tag Codes		Georgiana Slough					Ryde						Pt.Chicago	
Date	Grp	Georg.Sl.	Ryde	Pt Chicago	R_{GS}	CI	Oc	FF	IL	R_{Ry}	CI	Oc	FF	IL	Exports	R_{PC}	Oc
12/02/93	1	06-45-21	06-45-22	NA	33,668	5	80	248	12	34,650	37	292	10	36	10,434	NA	NA
12/05/94	2	05-34-25	05-34-26*	NA	31,532	4	11	87	8	30,220	15	29	6	13	5,988	NA	NA
01/04-05/95	3	06-25-25	06-25-24*	NA	31,328	2	101	837	53	31,557	13	266	231	138	10,403	NA	NA
01/10-11/96	4	05-41-13	05-41-14	05-41-11	33,670	5	146	768	9	30,281	21	240	12	23	9,523	34,596	265
12/04-05/97	5	05-50-50	05-50-60	05-50-61	61,276	2	7	153	4	46,756	22	41	18	11	10,570	48,080	141
01/13-14/97	6	05-50-49	05-50-62	”	66,893	18	240	24	51	49,059	48	167	0	70	3,887	”	”
12/01-02/98	7	05-23-08	05-23-20	05-23-22	69,180	12	173	28	44	48,207	30	182	0	102	1,868	45,195	140
12/29-30/98	8	05-23-12	05-23-21	”	68,843	12	150	48	54	48,804	17	156	0	88	1,984	”	”
12/10-11/99	9	05-51-30	05-51-32*	05-51-34	65,517	3	43	24	9	53,426	16	128	0	20	3,237	49,208	274
12/20-21/99	10	05-51-31	05-51-33*	”	64,515	21	151	82	32	49,341	19	161	4	66	4,010	”	”
01/03-05/02	11	05-07-76	05-07-67	05-07-68	77,053	18	248	390	110	52,327	34	520	18	366	7,789	47,876	314
12/05-06/02	12	05-10-98,05-11-68	05-11-67	05-11-66	90,219	1	68	700	10	49,629	18	147	42	15	5,007	47,048	458
12/09-10/03	13	05-17-71:72	05-17-81:82	05-17-80*	68,703	5	50	306	2	45,981	13	128	24	12	4,016	24,785	156
12/08-09/04	14	05-22-92:93	05-22-80:81	05-22-82	72,082	10	NA	0	NA	50,397	28	NA	0	NA	6,092	25,132	NA
12/08-09/05	15	05-27-84:87	05-27-88:91	05-27-94,95	70,414	6	NA	165	NA	51,017	23	NA	12	NA	10,837	NA	NA

Table 5. VAMP: Release and recovery data from pre-VAMP (1985-1991, 1994-1999) and VAMP (2000-2006) studies. Recovery locations are Antioch (Ant), Chipps Island (CI), ocean fisheries (Oc), and the SWP and CVP fish salvage facilities (FF). Stock designations FRH and MRFF denote Feather River Hatchery and Merced River Fish Facility (excepting group 4, all releases in same group have same stock). Flow and Exports (Exp) column headings DF, MD, DR, and UOR are for Durham Ferry, Mossdale, Dos Reis, and Upper Old River. Flows, exports, p_{OR}, and temperature are defined in Table 6.

Group No.	Stock	Release Location	Release Date	Tag Codes	Release Number	Recovery Location Ant	CI	Oc	FF	HORB	DF Flow	MD Flow	DR Flow	UOR Flow	MD Exp	DR Exp	p_{OR}	Temp
1	MRFF	Dos Reis	4/30/85	Yellow	149968	—	94	—	4450	Out	—	—	384	—	—	5794	81	21.1
		Old River	4/29/85	Red	150048	—	99	—	37299		—	2475	—	1928	5257	5709		21.1
2	MRFF	Dos Reis	5/29/86	064658,B61101	95595	—	36	2068	2960	Out	—	—	2442	—	—	5626	73	20.0
		Old River	5/30/86	064659,B61102	100181	—	21	1139	62564		—	7140	—	4842	4096	5626		21.1
3	MRFF	Dos Reis	4/27/87	06450:3,4,5	92612	—	79	1219	5469	Out	—	—	391	—	—	5856	90	21.1
		Old River	4/27/87	06450:6,7,8	90952	—	17	500	24019		—	2480	—	2057	7370	5856		22.2
4	MRFF	Dos Reis	5/02/89	06011101:07,08,13	76073	—	12	78	428	Out	—	—	577	—	—	1798	66	21.7
		Old River	5/03/89	060111010:4-6	74341	—	4	16	1439		—	2500	—	1522	1797	1798		21.7
	FRH	Jersey Pt	5/05/89	06011101:09,10	56233	—	56	283	824		—	—	—	—	—	—		20.0
5	FRH	Dos Reis	4/20/89	063114	52962	—	11	34	2714	Out	—	—	-17	—	—	10212	104	20.6
		Old River	4/21/89	063113	51972	—	5	38	2916		—	1945	—	2049	10295	10212		19.5
		Jersey Pt	4/24/89	060111011:1-2	56816	—	53	180	144		—	—	—	—	—	—		17.8
6	FRH	Dos Reis	4/16/90	060114010:7-8	105742	—	4	23	1766	Out	—	—	48	—	—	9597	119	20.0
		Old River	4/17/90	060114010:5-6	106267	—	2	14	2613		—	1400	—	1060	9400	9597		21.1
		Jersey Pt	4/18/90	0601140109	52962	—	32	224	156		—	—	—	—	—	—		17.2
7	FRH	Dos Reis	5/02/90	060114011:0-1	103533	—	4	34	150	Out	—	—	431	—	—	2353	84	20.0
		Old River	5/03/90	060111011:2-3	103595	—	1	11	1346		—	1400	—	934	3276	2242		22.2
		Jersey Pt	5/04/90	063119	50143	—	56	204	62		—	—	—	—	—	—		20.0
8	FRH	Dos Reis	4/15/91	060114011:4-5	102999	—	17	86	7130	Out	—	—	-49	796	—	5990	126	15.6
		Jersey Pt	4/19/91	0601140206	52139	—	94	358	331		—	—	—	—	—	—		17.2
9	FRH	Mossdale	4/11/94	0601140315	51804	—	0	62	705	Out	—	1580	466	1018	2087	1725	67	17.2
		Jersey Pt	4/13/94	0601140403	50689	—	10	420	14		—	—	—	—	—	—		17.8
10	FRH	Mossdale	4/26/94	0601140404	50726	—	2	89	0	In	—	3115	2891	0	1120	1598	11	15.6

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Group No.	Stock	Release Location	Release Date	Tag Codes	Release Number	Recovery Location Ant	CI	Oc	FF	HORB	DF Flow	MD Flow	DR Flow	UOR Flow	MD Exp	DR Exp	p_{OR}	Temp
		Jersey Pt	4/27/94	0601140408	53810	—	16	756	0		—	—	—	—	—	—		17.2
11	FRH	Mossdale	4/17/95	0601140:414,501	100969	—	20	461	2682	Out	—	18700	8267	9192	3707	3684	55	13.9
		Dos Reis	4/17/95	0601140412	50848	—	8	234	0		—	—	8267	—	—	3684		13.9
		Jersey Pt	4/19/95	0601140413	50779	—	26	280	0		—	—	—	—	—	—		15.6
12	FRH	Mossdale	5/05/95	06315:0-1	102562	—	13	392	1883	Out	—	21250	9316	9801	3770	3958	58	16.7
		Dos Reis	5/05/95	063147	52097	—	21	393	0		—	—	9316	—	—	3958		17.2
13	FRH	Mossdale	5/17/95	0601140504, 63148	1041245	—	8	353	1628	Out	—	23100	9545	10066	3507	4209	59	17.2
		Dos Reis	5/17/95	063149	51665	—	9	245	12		—	—	9545	—	—	4209		18.3
14	FRH	Mossdale	4/15/96	060106011:4-5	100742	—	2	100	1084	Out	—	6665	3296	3499	2040	1614	53	15.6
		Jersey Pt	4/18/96	0601060113	50041	—	25	332	0		—	—	—	—	—	—		16.7
15	FRH	Mossdale	4/30/96	060106020:1,5	99656	—	1	26	1432	Out	—	6565	3113	3378	1660	1629	52	17.8
		Dos Reis	5/01/96	0601060:110,203	98638	—	3	67	0		—	—	3113	—	—	1629		17.2
		Jersey Pt	5/03/96	0601060109	50820	—	24	311	12		—	—	—	—	—	—		17.8
16	MRFF	Dos Reis	5/01/96	0601110:412-415	107961	—	10	58	0	Out	—	—	3113	3378	—	1629	52	17.2
		Jersey Pt	5/03/96	0601110501	51737	—	39	186	0		—	—	—	—	—	—		18.9
17	FRH	Mossdale	4/28/97	060106030:2-3	48730	—	10	329	226	In	—	6135	4709	284	2330	2329	16	16.1
		Dos Reis	4/29/97	060106030:4-5	49784	—	10	259	125		—	—	4709	—	—	2329		15.6
		Jersey Pt	5/02/97	060106020:7-8	49815	—	55	697	12		—	—	—	—	—	—		17.2
18	MRFF	Dos Reis	4/29/97	06254:5,6	102431	—	16	348	394	In	—	—	4709	284	—	2329	16	15.6
		Jersey Pt	5/02/97	062547	51540	—	27	355	24		—	—	—	—	—	—		17.8
19	MRFF	Dos Reis	5/08/97	062548	46682	—	5	90	78	In	—	—	4740	268	—	2410	21	17.2
		Jersey Pt	5/12/97	062549	47208	—	18	192	14		—	—	—	—	—	—		19.4
20	MRFF	Mossdale	4/16/98	06011108:09-11	77430	—	88	157	48	Out	—	24950	9645	10356	805	1722	60	13.9
		Dos Reis	4/17/98	06011108:06-08	77180	—	93	145	0		—	—	9645	—	—	1722		15.0
		Jersey Pt	4/20/98	06011108:12-13	50050	—	187	201	0		—	—	—	—	—	—		17.2

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Group No.	Stock	Release Location	Release Date	Tag Codes	Release Number	Recovery Location Ant	CI	Oc	FF	HORB	DF Flow	MD Flow	DR Flow	UOR Flow	MD Exp	DR Exp	p_{OR}	Temp
21	FRH	Mossdale	4/23/98	060106050:5-6	33800	—	7	13	192	Out	—	20250	8447	9404	1932	1926	57	18.9
		Dos Reis	4/24/98	060114060:6-7	47874	—	17	56	0		—	—	8447	—	—	1926		18.9
		Jersey Pt	4/28/98	060106050:3-4	31091	—	40	47	0		—	—	—	—	—	—		18.9
22	MRFF	Mossdale	4/19/99	06264:2-4	74646	—	36	395	2940	Out	—	6905	3180	3429	2683	3105	55	16.7
		Dos Reis	4/19/99	06264:5-6	49636	—	39	376	185		—	—	3180	—	—	3105		17.2
		Jersey Pt	4/21/99	062647, 0601110815	48907	—	59	715	60		—	—	—	—	—	—		17.2
23	MRFF	Durham F.	4/17/00	06040:1-2,64563	72094	27	28	693	521	In	6690	6995	5918	296	2265	2366	18	13.9
		Mossdale	4/18/00	06440:1-2	46111	30	18	381	457		—	6995	5918	—	2265	2366		13.3
		Jersey Pt	4/20/00	06440:3-4	51098	97	65	1353	0		—	—	—	—	—	—		17.8
24	MRFF	Durham F.	4/28/00	060106091:4-5, 601110814	74001	31	22	162	279	In	5665	5969	5062	560	2238	2196	11	17.2
		Jersey Pt	5/01/00	060106100:1-2	49871	152	78	589	6		—	—	—	—	—	—		17.2
25	MRFF	Durham F.	4/30/01	0644:29-31	68192	76	53	366	84	In	4125	4170	3630	687	1475	1482	12	21.7
		Mossdale	5/01/01	06443:2-3	44923	33	31	232	48		—	4170	3630	—	1475	1482		19.4
		Jersey Pt	5/04/01	06443:4-5	49161	329	111	1031	0		—	—	—	—	—	—		20.0
26	MRFF	Durham F.	5/07/01	06443:6-8	71744	29	9	92	39	In	4135	4145	3610	654	1566	1495	12	18.9
		Mossdale	5/08/01	0644:39-40	48888	19	8	52	36		—	4145	3610	—	1566	1495		21.1
		Jersey Pt	5/11/01	06444:1,2	51107	96	44	581	0		—	—	—	—	—	—		22.8
27	MRFF	Durham F.	4/18/02	06447:1-4	97318	63	21	270	207	In	3165	3255	2671	549	1536	1532	19	15.0
		Mossdale	4/19/02	06445:7-8	50411	42	13	145	234		—	3255	2671	—	1536	1532		13.9
		Jersey Pt	4/22/02	0644:59-60	48496	190	83	951	48		—	—	—	—	—	—		18.0
28	MRFF	Durham F.	4/25/02	0644:70,75-77	98082	18	15	58	175	In	3356	3356	2814	570	1523	1507	20	17.0
		Mossdale	4/26/02	06447:8-9	48924	7	5	40	129		—	3356	2814	—	1523	1507		17.5
		Jersey Pt	4/30/02	06448:0-1	46469	75	46	597	0		—	—	—	—	—	—		17.5
29		Durham F.	4/21/03	06028:2-3,62742	74377	6	3	19	51	In	3430	3345	2904	297	1494	1497	7	15.0
		Mossdale	4/22/03	06274:3,8	49827	4	5	8	0		—	3345	2904	—	1494	1497		15.2
		Jersey Pt	4/25/03	062744	24441	71	57	263	0		—	—	—	—	—	—		16.5
30	MRFF	Durham F.	4/28/03	06274:5-7	74491	0	0	10	24	In	3370	3370	3017	299	1481	1479	11	16.5
		Mossdale	4/29/03	0627:49-50	48317	0	1	5	12		—	3370	3017	—	1481	1479		15.7
		Jersey Pt	5/02/03	062751	25732	35	39	415	0		—	—	—	—	—	—		15.0
31	MRFF	Durham F.	4/22/04	06275:2-5	91867	2	3	3	96	In	3170	3160	2831	297	1483	1483	11	15.5

Continued on next page

Group No.	Stock	Release Location	Release Date	Tag Codes	Release Number	Recovery Location Ant	CI	Oc	FF	HORB	DF Flow	MD Flow	DR Flow	UOR Flow	MD Exp	DR Exp	p_{OR}	Temp
		Mossdale	4/23/04	064670,06458:2-3	73258	1	3	2	30		—	3160	2831	—	1483	1483		17.0
		Jersey Pt	4/26/04	064580	22708	22	25	117	12		—	—	—	—	—	—		21.5
32	MRFF	Durham F.	5/02/05	06467:2-5	93833	6	12	—	1527	Out	8250	8195	3743	3934	1961	2293	56	16.0
		Dos Reis	5/03/05	064591,06469:7,8	69125	7	3	—	7		—	—	3743	—	—	2293		17.0
		Jersey Pt	5/06/05	064588	22767	31	32	—	0		—	—	—	—	—	—		18.0
33	MRFF	Durham F.	5/09/05	06458:4-6	91563	7	6	—	844	Out	8940	9085	4147	4529	2303	2300	55	14.9
		Dos Reis	5/10/05	0645:89-90, 064699	68646	7	6	—	6		—	—	4147	—	—	2300		15.0
		Jersey Pt	5/12/05	064700	23231	27	38	—	0		—	—	—	—	—	—		19.0
34	MRFF	Mossdale	5/04/06	06471:3-4	48828	9	9	—	18	Out	—	29350	10756	11130	1538	1544	61	18.0
		Dos Reis	5/05/06	064716	25463	3	7	—	0		—	—	10756	—	—	1544		17.5
		Jersey Pt	5/06/06	064715	26119	26	58	—	0		—	—	—	—	—	—		19.0
35	MRFF	Mossdale	5/19/06	0647:2-3	73764	0	8	—	48	Out	—	24650	10018	10423	6283	6046	59	19.5
		Jersey Pt	5/22/06	064724	24757	14	44	—	0		—	—	—	—	—	—		19.5

TABLE 6. VAMP: Definitions of covariates used in modeling (and listed in Table 5). DAYFLOW is a California Department of Water Resources (CDWR) database and DSM2 is a CDWR model; Yiguo Liang and Min Yu (personal communication) supplied the DSM2 model-based values. Vernalis is 6 miles upstream of Durham Ferry.

Covariate	Definition	Source
DF Flow	Mean flow at Vernalis for day of and day after release at Durham Ferry.	DAYFLOW
MD Flow	Mean flow at Vernalis for day of and day after release at Mossdale.	DAYFLOW
DR Flow	Median flow at Stockton for 8 days starting on day of release at Dos Reis. In absence of Dos Reis release, day of release = day of a Mossdale release or day after a Durham Ferry release.	
UOR Flow	Median (Vernalis Flow- Stockton Flow) starting on day of release at Upper Old River, Dos Reis, or Mossdale, in that order of priority. For group 24, started day after release at Durham Ferry	1985-1989: Vernalis Flow (DAYFLOW) Stockton Flow (DWR equ'ns) 1990-2006: Flows (DSM2)
MD Exp	Mean of combined CVP and SWP exports for the day of and day after release at Mossdale.	
DR Exp	Median of combined CVP and SWP exports for 8 days starting on day of release at Dos Reis.	
p_{OR}	Proportion of San Joaquin River flow diverted into Old River = 1-(Dos Reis or Stockton flow)/Vernalis flow calculated for day of Mossdale or upper Old River release, or day before a Dos Reis release, or day after a Durham Ferry release.	1985-1989: Dos Reis, Stockton Flows (DWR equ'ns Vernalis Flow (DAYFLOW) 1990-2006: Dos Reis, Stockton Flows (DSM2)
Temp	Temperature (in Celcius) in the river at the release site	

TABLE 7. VAMP: Year specific schematic of the release and recovery locations in the VAMP and related San Joaquin studies since 1985. Release locations (marked by R) are Durham Ferry (DF), Mossdale (MD), Old River (OR), Dos Reis (DR), and Jersey Point (JP). Recovery locations (marked by X) are Antioch (Ant), Chipps Island (CI), and ocean fisheries (Oc). X* denotes recoveries that are not yet available.

		Release Locations					Recovery Locations			
Group	Year	DF	MD	OR	DR	JP	Ant	CI	Oc	#Obs'ns
1	1985			R	R			X		2
2	1986			R	R			X	X	4
3	1987			R	R			X	X	4
4	1989			R	R	R		X	X	6
5	1989			R	R	R		X	X	6
6	1990			R	R	R		X	X	6
7	1990			R	R	R		X	X	6
8	1991				R	R		X	X	4
9	1994		R			R		X	X	4
10	1994		R			R		X	X	4
11	1994		R		R	R		X	X	6
12	1995		R		R			X	X	4
13	1995		R		R			X	X	4
14	1996		R			R		X	X	4
15	1996		R		R	R		X	X	6
16	1996				R	R		X	X	4
17	1997		R		R	R		X	X	6
18	1997				R	R		X	X	4
19	1997				R	R		X	X	4
20	1998		R		R	R		X	X	6
21	1998		R		R	R		X	X	6
22	1999		R		R	R		X	X	6
23	2000	R	R			R	X	X	X	9
24	2000	R				R	X	X	X	6
25	2001	R	R			R	X	X	X	9
26	2001	R	R			R	X	X	X	9
27	2002	R	R			R	X	X	X	9
28	2002	R	R			R	X	X	X	9
29	2003	R	R			R	X	X	X	9
30	2003	R	R			R	X	X	X	9
31	2004	R	R			R	X	X	X	9
32	2005	R			R	R	X	X	X*	6
33	2005	R			R	R	X	X	X*	6
34	2006		R		R	R	X	X	X*	6
35	2006		R			R	X	X	X*	4

TABLE 8. VAMP: Summary of analyses in 2005 Annual Technical Report for San Joaquin River Agreement. Response variable, $RR_{a/b \to c}$, denotes ratio of recovery fractions at location c from releases at location a and location b. Abbreviations are DF (Durham Ferry), MD (Mossdale), DR (Dos Reis), JP (Jersey Point), Ant (Antioch), CI (Chipps Island), and Oc (ocean fisheries). Sign refers to the slope coefficient. The P-value refers to a test that the slope coefficient equals 0.

Response variable	Covariate(s)	Sign	P-value	R^2	n
$RR_{(DF+MD)/JP \to Ant+CI}$	Vernalis Flow (HORB in)	+	< 0.01	0.50	15
$RR_{(DF+MD)/JP \to Ant+CI}$	Vernalis Flow (HORB out)	+	> 0.10	0.29	8
$RR_{(DF+MD)/JP \to Ant+CI}$	Vernalis Flow/Exports (HORB in)	+	< 0.02	0.30	18
$RR_{(DF+MD)/JP \to Ant+CI}$	CVP+SWP Exports (HORB out)	+	< 0.10	0.38	9
$RR_{(DF+MD)/JP \to Oc}$	Vernalis Flow (HORB in)	+	< 0.01	0.58	15
$RR_{(DF+MD)/JP \to Oc}$	Vernalis Flow (HORB out)	+	> 0.10	0.36	7
$RR_{(DF+MD)/JP \to Oc}$	Vernalis Flow/Exports (HORB in)	+	< 0.10	0.20	17
$RR_{(DF+MD)/JP \to Oc}$	CVP+SWP Exports (HORB out)	+	> 0.10	0.40	7
$RR_{MD/JP \to Ant+CI}$	Vernalis Flow/Exports (HORB out)	+	> 0.10	0.10	9
$RR_{MD/JP \to Oc}$	Vernalis Flow/Exports (HORB out)	+	> 0.10	0.08	6
$RR_{DR/JP \to Ant+CI}$	Modeled SJ Flow	+	> 0.10	0.19	12
$RR_{DR/JP \to Oc}$	Modeled SJ Flow	+	< 0.01	0.64	12

TABLE 9. DCC: Summary of BHMs fit and model selected for inference. Top table compares DIC values for several BHMs. Column headed $f(\theta)$ refers to the transformation used and column headed σ's refers to the priors used for standard deviations of random effects. The column headed by $\frac{\theta_{Open}}{\theta_{Closed}}$ gives the posterior median of the ratios. Bottom table contains summaries for the model selected for inference. The σ^2 values are the posterior medians for σ^2_θ, $\sigma^2_{\mu_{Ry\to CI}}$, and $\sigma^2_{\mu_{Ry\to Oc}}$.

Level 1 Dist'n	$f(\theta)$	σ's	DIC	$\frac{\theta_{Open}}{\theta_{Closed}}$
Negative Binomial	log	Uniform	567.3	0.73
Multinomial	logit	Uniform	649.8	0.94
Multinomial (correlated))	logit	Inv. Wishart	655.1	0.96

Negative Binomial, log θ, Uniform priors for σ

		Percentiles			
Parameter	Mean	0.025	0.50	0.975	σ^2
β_0	-0.62	-1.06	-0.62	-0.13	
β_1	0.32	-0.56	0.32	1.18	
θ (open)	0.69	0.13	0.54	2.20	0.62^2
θ (closed)	1.00	0.17	0.75	3.33	0.62^2
θ(open)/θ(closed)	1.32	0.09	0.73	5.67	
k_{CI}	492.9	17.1	492.1	974.7	
k_{Oc}	16.9	2.68	7.12	25.1	
$\mu_{Ry\to CI}$	-7.09	-7.49	-7.09	-6.71	0.67^2
$\mu_{Ry\to Oc}$	-4.82	-5.57	-4.82	-4.06	1.24^2
$r_{Ry\to CI}$	0.0011	0.0002	0.0008	0.0037	
$r_{Ry\to Oc}$	0.0195	0.0005	0.0081	0.1108	

TABLE 10. Interior: Summary of BHMs fit and model selected for inference. Top table compares DIC values for several BHMs and the mean posterior predicted survival of Georgiana Slough relative to Ryde survival ($\overline{\theta}$). Column headed $f(\theta)$ refers to the transformation of θ used and column headed σ's refers to the priors used for standard deviations of random effects (the inverse gamma is actually the gamma on the precision, inverse of σ^2). Bottom table contains summaries for the model selected for inference. The σ^2 values are the posterior medians for σ^2_θ, $\sigma^2_{\mu_{Ry\to CI}}$, and $\sigma^2_{\mu_{Ry\to Oc}}$.

Level 1 Dist'n	$f(\theta)$	σ's	DIC	$\overline{\theta}$
Multinomial	log	Uniform	427.6	0.44
Multinomial	log	Inv. Gamma	427.6	0.43
Multinomial	logit	Inv. Gamma	428.2	0.42
Multinomial	logit	Uniform	428.3	0.42
Multinomial (correlated)	logit	Inv. Wishart	428.8	0.41
Negative Binomial	log	Uniform	441.7	0.42

Multinomial, log θ, Uniform priors for σ

		Percentiles			
Parameter	Mean	0.025	0.50	0.975	σ^2
μ_θ	-1.02	-1.35	-1.02	-0.70	0.50^2
$\mu_{Ry\to CI}$	-7.72	-7.94	-7.72	-7.51	0.36^2
$\mu_{Ry\to Oc}$	-5.61	-6.11	-5.61	-5.12	0.88^2
θ	0.44	0.10	0.36	1.26	
$r_{Ry\to CI}$	0.0005	0.0002	0.0004	0.0009	
$r_{Ry\to Oc}$	0.0057	0.0006	0.0036	0.0226	

TABLE 11. DA 8: Posterior distribution summaries for the multinomial model (with log transformed θ and uniform priors on the σ's). The σ^2 values are the posterior medians of σ^2_θ, $\sigma^2_{r_{Ry\to CI}}$, and $\sigma^2_{r_{Ry\to Oc}}$.

		Percentiles			
Parameter	Mean	0.025	0.50	0.975	σ^2
β_0	-1.05	-1.38	-1.04	-0.75	
β_1	-0.29	-0.61	-0.28	0.02	0.54^2
$\mu_{Ry\to CI}$	-7.72	-7.94	-7.72	-7.65	0.36^2
$\mu_{Ry\to Oc}$	-5.61	-6.08	-5.61	-5.07	0.86^2
$r_{Ry\to CI}$	0.0005	0.0002	0.0004	0.0010	
$r_{Ry\to Oc}$	0.0057	0.0006	0.0036	0.0227	

TABLE 12. DA 8: Comparison of BHM and non-Bayesian estimates of release pair-specific θ, ratio of the Georgiana Slough survival probability to the Ryde survival probability. BHM values are mean and standard deviation of posterior distribution. Non-Bayesian values are the MLEs (maximum likelihood estimates) and standard errors (using the delta method). Ratio of survival indices is based upon the Chipps Island recoveries alone (Pat Brandes, personal communication).

	BHM		Non-Bayesian		Ratio of
Group	Mean	Std Dev	MLE	Std Error	Survival Indices
1	0.27	0.032	0.27	0.032	0.14
2	0.33	0.085	0.33	0.098	0.27
3	0.37	0.041	0.37	0.043	0.16
4	0.51	0.052	0.52	0.053	0.26
5	0.14	0.041	0.11	0.039	0.05
6	0.87	0.080	0.88	0.081	0.28
7	0.61	0.060	0.61	0.061	0.24
8	0.65	0.069	0.66	0.072	0.72
9	0.27	0.044	0.26	0.044	0.16
10	0.72	0.075	0.73	0.078	0.67
11	0.33	0.024	0.33	0.024	0.31
12	0.24	0.033	0.23	0.033	0.04
13	0.27	0.041	0.26	0.041	0.28
14	0.30	0.089	0.25	0.226	0.32
15	0.22	0.076	0.19	0.298	0.16

TABLE 13. VAMP: Comparison of DIC values for simple models with and without random effects. Only covariate is an indicator variable for HORB in a logit transformation of $S_{DR \to JP}$.

Model Class	DIC
No Random Effects	25,000
Recovery random effects	4,300
Survival and recovery random effects	1,500

TABLE 14. VAMP: Comparison of model results for p_{OR} known, multinomial distributions, logit θ's, and Uniform priors for σ's. When entries under S are decimals, the value shown is the posterior median probability of survival. When entries contain covariate names, the reported percentage is the posterior probability that the flow coefficient is positive or that the exports coefficient is negative.

Label	$S_{DF \to MD}$	$S_{DR \to JP}$	$S_{OR \to JP}$	DIC
Null.Null.Null	0.62	0.21	0.09	1499.1
Null.FE.FE	0.63	Flow: 89%+ Exports: 21%-	Flow: 65%+ Exports: 33%-	1474.8
Null.F.Null	0.63	Flow: 86%+	0.10	1491.4
Null.F.Null.Stk (Stock, 100%+)	0.63 Flow: 90%+	0.10	1494.5	

TABLE 15. Recoveries from replicate releases made at Durham Ferry and χ^2 tests of homogeneity. χ^2 values are based on Antioch, Chipps Island, and Ocean recoveries. P-values were calculated by Monte Carlo simulations; P-values were calculated with Antioch, Chipps Island, and Ocean categories (w/ ocean) and with Antioch and Chipps Island categories (w/o ocean). Number in parentheses next to year is the release set number.

						P-Values	
Set	R	y_{Ant}	y_{CI}	y_{Oc}	χ^2	w/ ocean	w/o Oc
2000 (19)							
60401	23529	6	7	217			
60402	24177	10	10	232			
64563	24457	11	11	247	3.1	0.80	0.70
2001 (21)							
64429	23351	28	14	96			
64430	22720	30	22	159			
64431	22376	18	17	112	24.0	<0.01	0.27
2001 (22)							
64436	24029	8	2	17			
64437	23907	11	5	47			
64438	24054	10	2	28	17.8	<0.01	0.64
2002 (23)							
64471	23920	11	4	33			
64472	23920	20	9	96			
64473	23872	12	4	73			
64474	24747	20	4	68	34.6	<0.01	0.32
2002 (24)							
64470	24680	6	3	23			
64475	24659	2	5	22			
64476	24783	4	3	8			
64477	24381	6	4	6	19.6	0.02	0.78

TABLE 16. Estimated capture probabilities at Chipps Island for the DCC and Interior/DA 8 studies (based on ocean recoveries of Port Chicago releases).

DCC

Year	Tag Code	Ct	Ryde
83	6-62-24,6-62-23	0.00062	0.00078
87	6-62-53,6-62-54-6-62-55	NA	NA
88	B6-14-2,B6-14-3,6-31-1	0.00256	0.00195
88	6-62-59,6-62-60,6-62-63	0.00067	0.00328
84	6-62-27,6-62-29,6-42-09	0.00070	0.00107
85	6-62-38:6-62-41,6-62-35	0.00095	0.00093
86	6-62-43,6-62-48	0.00095	0.00093
87	6-62-56,6-62-57,6-62-58	NA	NA
88	B6-14-4,B6-14-5,6-31-2	0.00312	0.00222
88	6-62-50,6-31-3	0.00135	0.00251
89	6-31-11,6-31-12	NA	NA
89	6-31-8,6-31-7	0.00184	0.00126
89	6-1-14-1-3,6-58-5,6-1-14-1-2	0.00182	0.00579

Interior/DA 8

Year	Tag Code	GS	Ryde
1996	5-41-13,5-41-14	0.00026	0.00067
1998	5-50-50,5-50-60	0.00084	0.00157
1998	5-50-49,5-50-62	0.00022	0.00084
1999	5-23-08,5-23-20	0.00021	0.00051
1999	5-23-12,5-23-21	0.00025	0.00034
2000	5-51-30,5-51-32	0.00039	0.00070
2000	5-51-31,5-51-33	0.00077	0.00066
2002	5-07-76,5-07-67	0.00048	0.00043
2003	5-11-68,5-11-67	0.00020	0.00119
2004	5-17-71/72,5-17-81/82	0.00060	0.00065

TABLE 17. DA 8: Standard errors for $\hat{\beta}_1$, estimated slope coefficient, as a function of R (number released, $R_{GS} = R_{Ryde}$) and n (number of release pairs). Calculations are based upon simulations and regression of $logit(\hat{\theta})$ against standardized exports where the true value of β_1 was 0.57.

R	n		
	15	20	25
50,000	0.333	0.275	0.236
100,000	0.299	0.261	0.230
150,000	0.300	0.267	0.228

TABLE 18. VAMP: Interquartile range for parameter estimates for different stream sections as a function of number released ($R = R_{DF} = R_{MD} = R_{DR} = R_{JP}$) and number of release sets (n). Calculations are based upon 10,000 simulations and regressions of point estimates of survival probabilities (logit transformed) against the covariates. The true values are shown for each parameter. HORB is an indicator equal to 1 when the barrier is in.

Durham Ferry to Mossdale

	$\beta_1 = 1.0$ flow		
	n		
R	15	20	25
50,000	1.476	1.279	1.123
100,000	1.418	1.200	1.063
150,000	1.388	1.179	1.018

Mossdale to Dos Reis

	$\gamma_1 = 0.32$ flow			$\gamma_2 = 5$ HORB			$\gamma_3 = -1.4$ exports×(1-HORB)		
	n			n			n		
R	15	20	25	15	20	25	15	20	25
50,000	1.347	1.097	0.965	3.048	2.529	2.244	1.264	1.077	0.896
100,000	1.270	1.060	0.898	2.868	2.429	2.135	1.230	1.029	0.877
150,000	1.209	1.030	0.873	2.778	2.415	2.087	1.184	0.997	0.854

Dos Reis to Jersey Point

	$\xi_1 = 0.71$ flow			$\xi_2 = 5$ HORB			$\xi_3 = -0.5$ exports		
	n			n			n		
R	15	20	25	15	20	25	15	20	25
50,000	0.527	0.447	0.396	1.839	1.533	1.336	0.529	0.432	0.375
100,000	0.520	0.427	0.375	1.654	1.419	1.265	0.484	0.415	0.360
150,000	0.517	0.433	0.367	1.579	1.365	1.215	0.487	0.408	0.352

FIGURES

FIGURE 1. Map of release and recovery locations used by the USFWS for the multi-year studies.

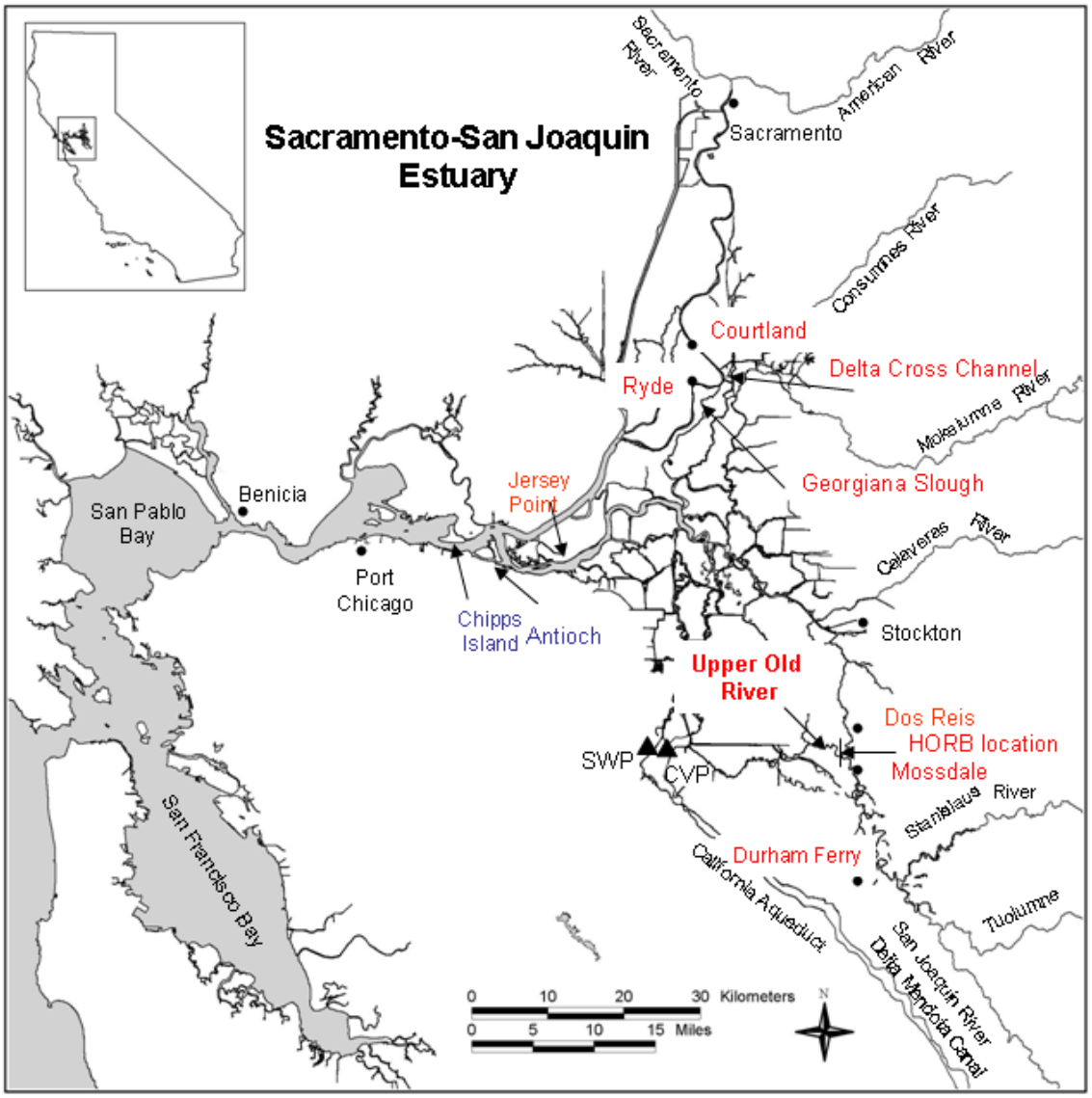
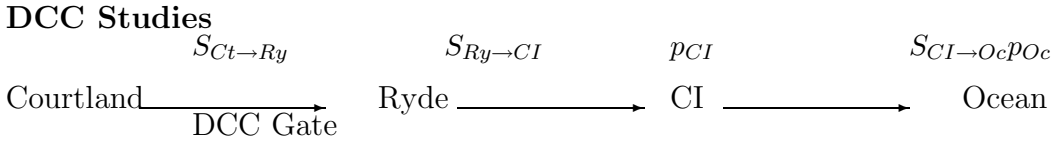
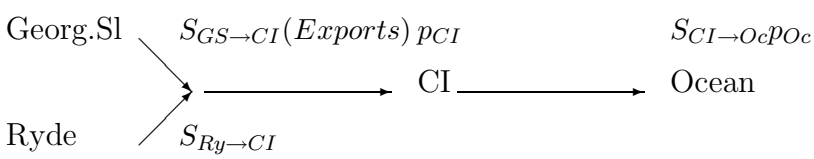


FIGURE 2. Schematics of release and recovery locations for the four multi-year studies. $S_{A\to B}$ is the survival probability between point A and point B, and p_C is the capture probability at location C.

DCC Studies



Interior/DA 8 Studies



VAMP Studies

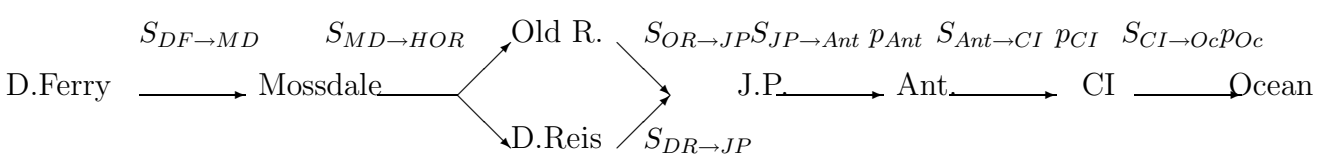


FIGURE 3. DCC: Recovery fractions for Courtland ($\hat{r}_{Ct \to CI+Oc}$) and Ryde ($\hat{r}_{Ry \to CI+Oc}$) releases by release pair. First four pairs are from releases that occurred when the gates were closed (with plotting character C), and the last nine are when the gates were open (plotting character O).

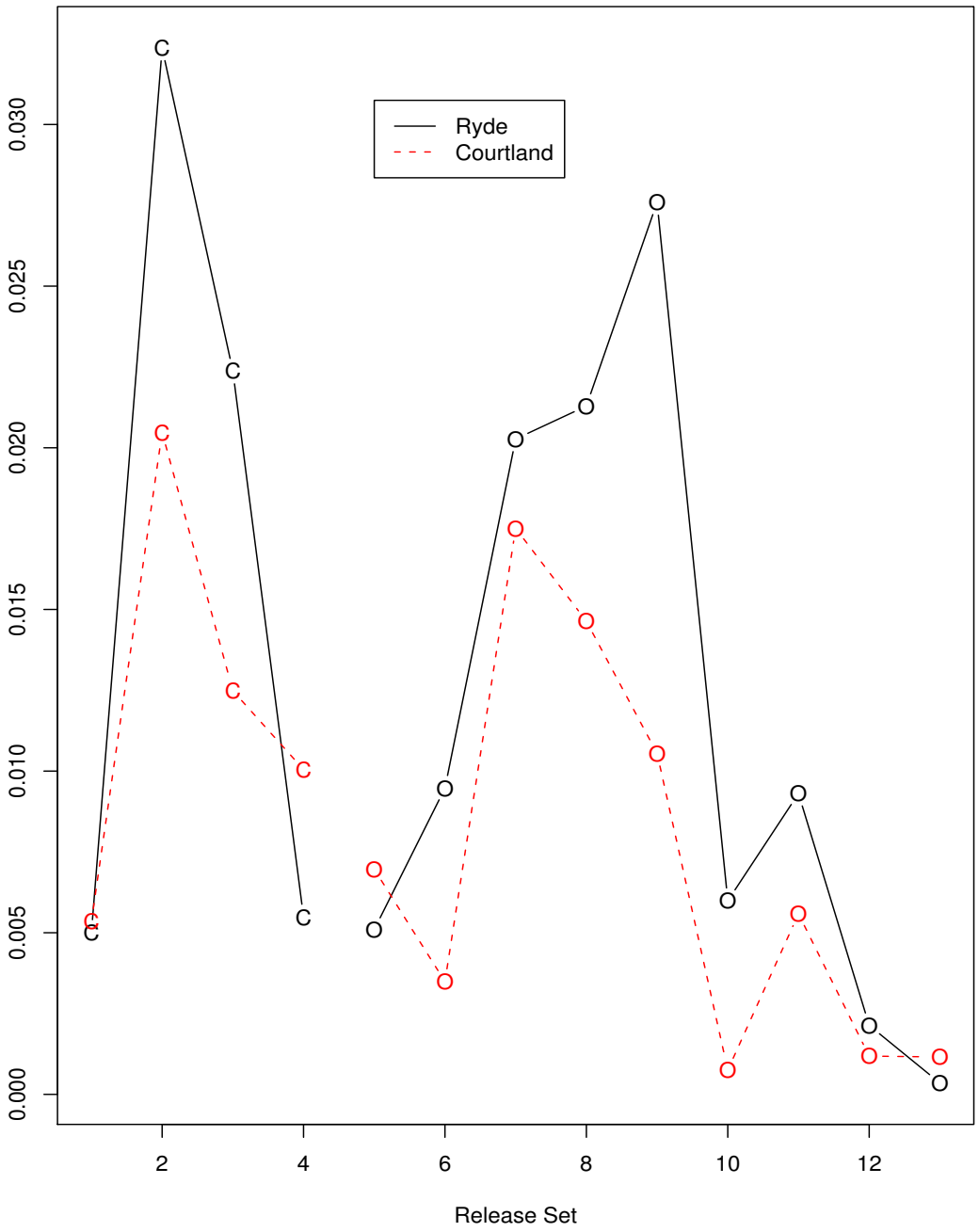


FIGURE 4. DCC: Boxplots of the ratio of recovery fractions for Courtland to Ryde releases, $\hat{r}_{Ct \to CI+Oc}/\hat{r}_{Ry \to CI+Oc}$, when the DCC gates were open and closed.

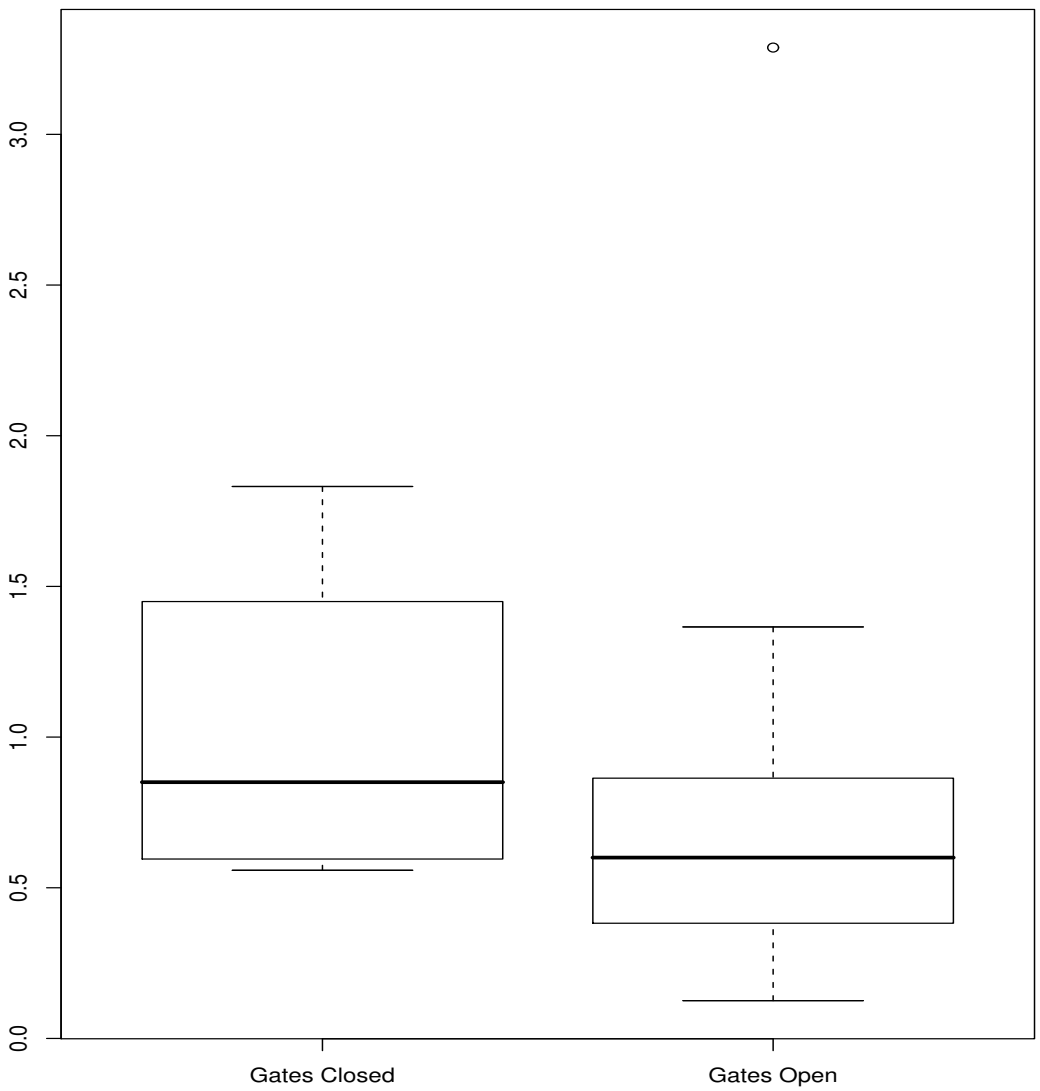


FIGURE 5. Interior/DA 8: Recovery fractions for Georgiana Slough ($\hat{r}_{GS \to CI+Oc}$) and Ryde ($\hat{r}_{Ry \to CI+Oc}$) releases by release pair.

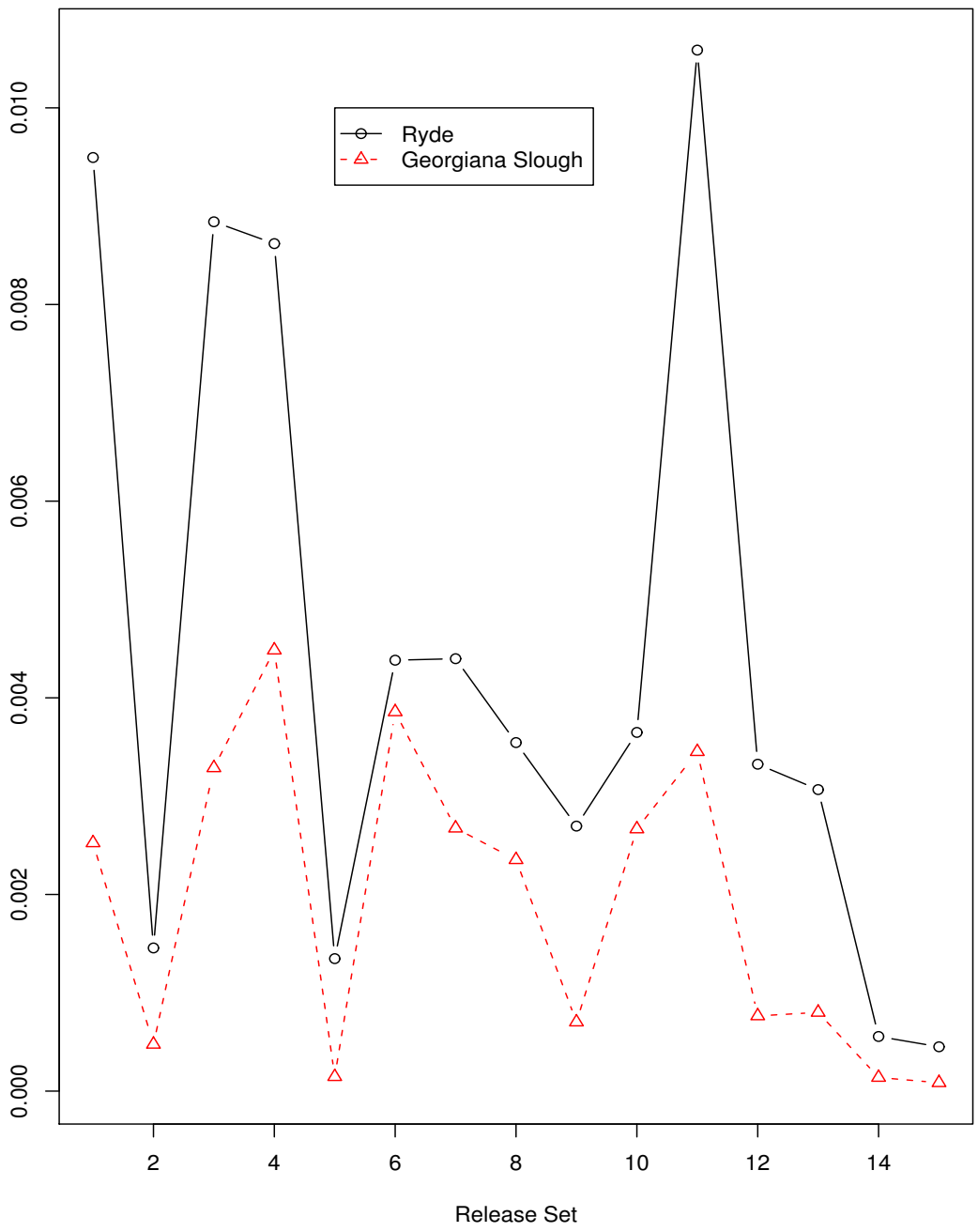


FIGURE 6. Interior/DA 8: Comparison of recovery fractions at Chipps Island, in the ocean fisheries, in fish facility salvage, and from inland recoveries for Georgiana Slough and Ryde releases by release pair. Straight lines on plots have slope equal to mean of the ratios of recovery fractions, with slope written below x-axis label.

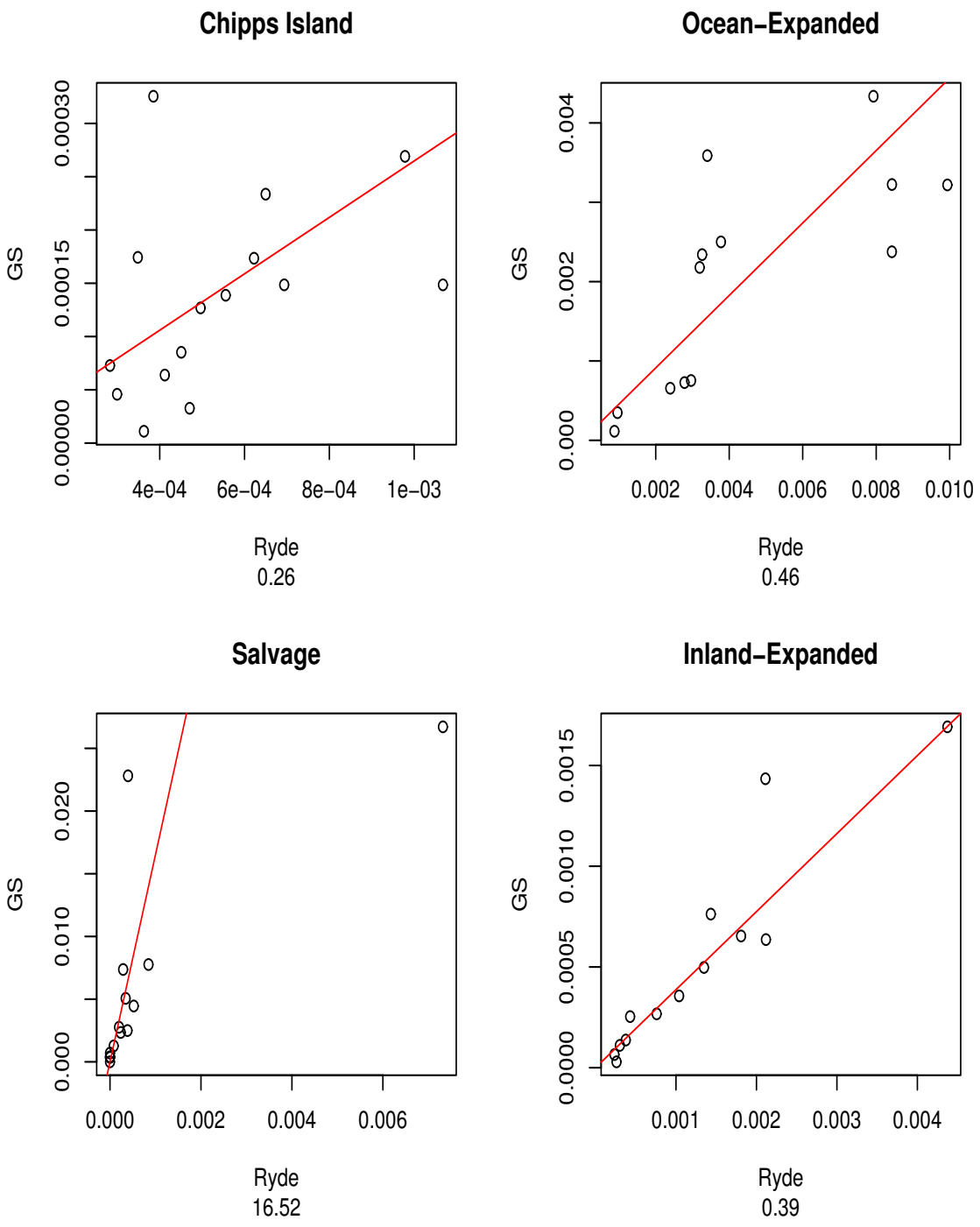


FIGURE 7. DA 8: Estimated fraction of the release that is salvaged at the SWP and CVP fish facilities plotted against the export level (for both Georgiana Slough and Ryde releases). Solid line and dashed line are scatterplot smooths of fraction salvaged for Georgiana Slough and Ryde releases, respectively.

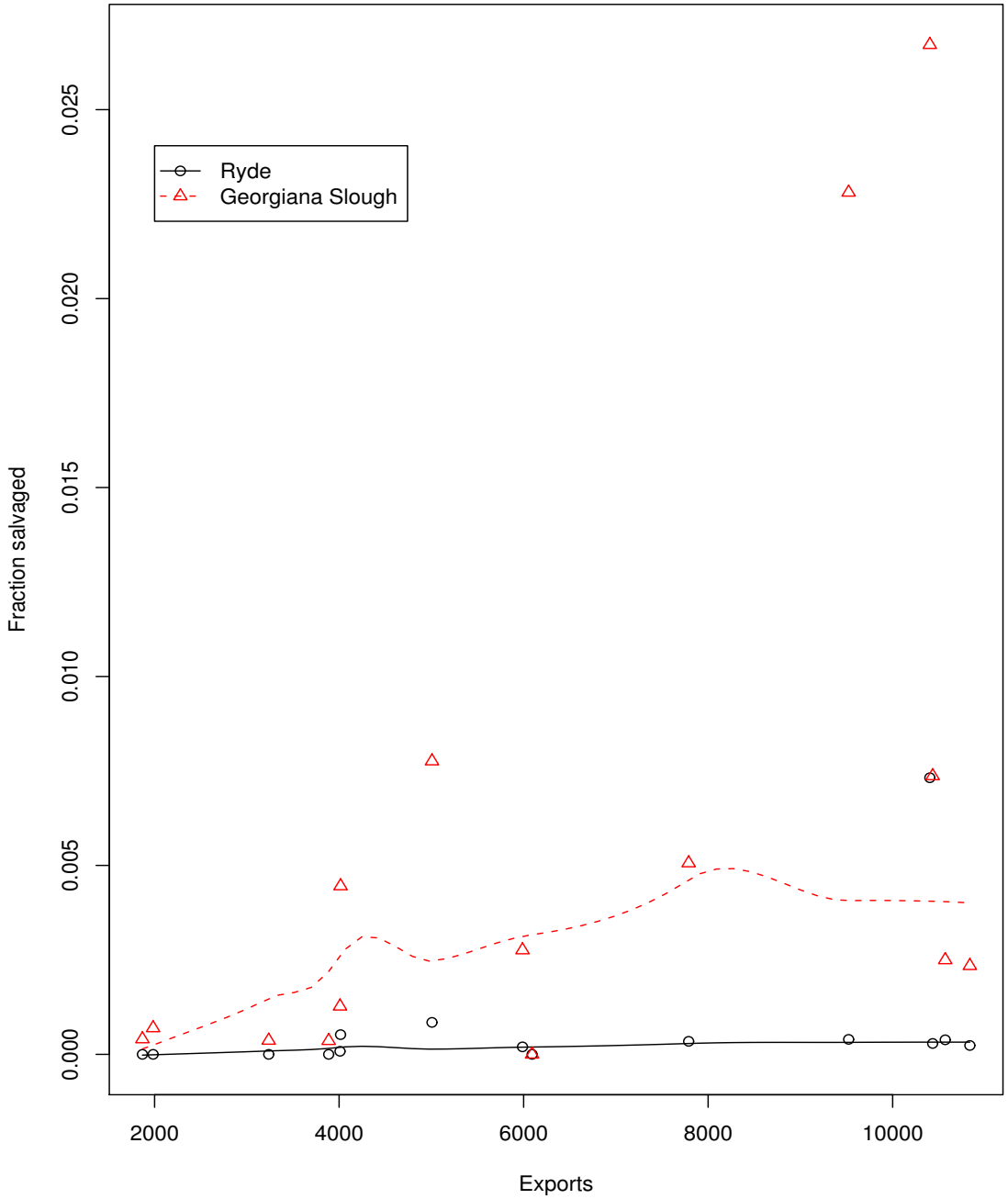


FIGURE 8. VAMP: Combinations of flow and export volumes when the HORB is in and when it is out. The flow and export measurements were those measured or estimated effective near Mossdale.

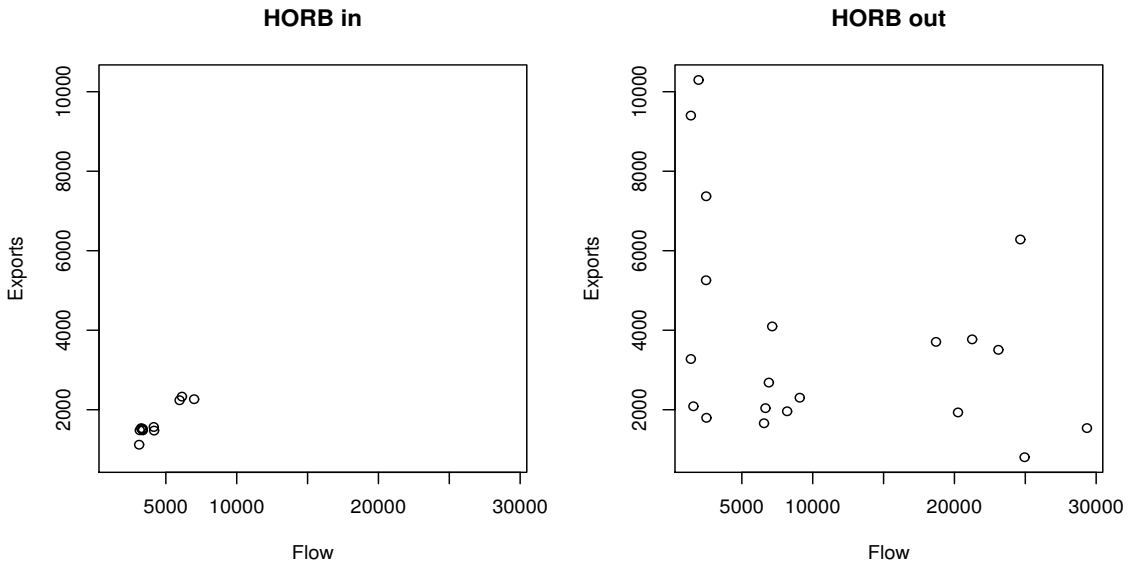


FIGURE 9. VAMP: Recovery fractions by release site; i.e., for release site x, $(y_{x\to Ant} + y_{x\to CI} + y_{x\to Oc})/R_x$.

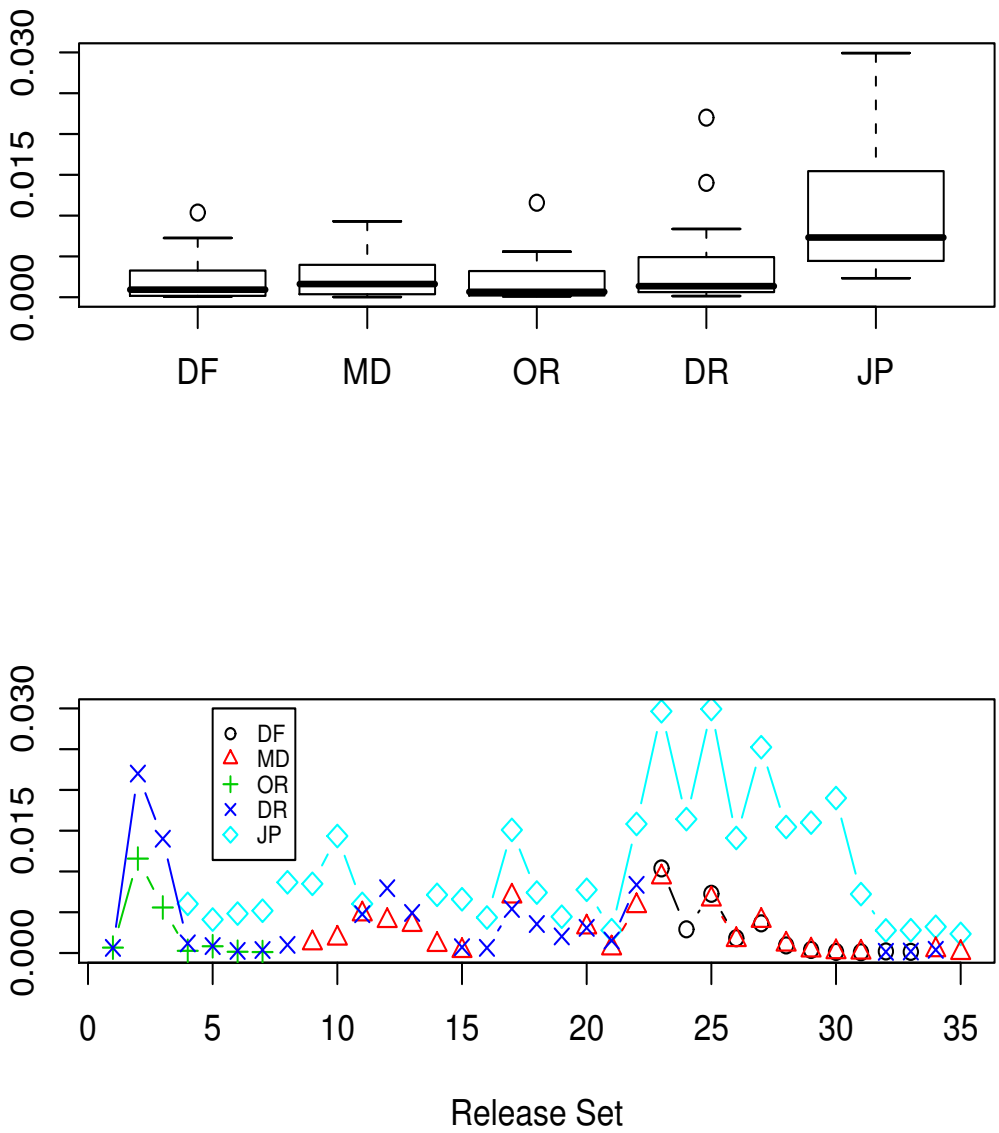


FIGURE 10. VAMP: Estimated fraction of releases salvaged at SWP and CVP fish salvage facilities when the HORB is in or out.

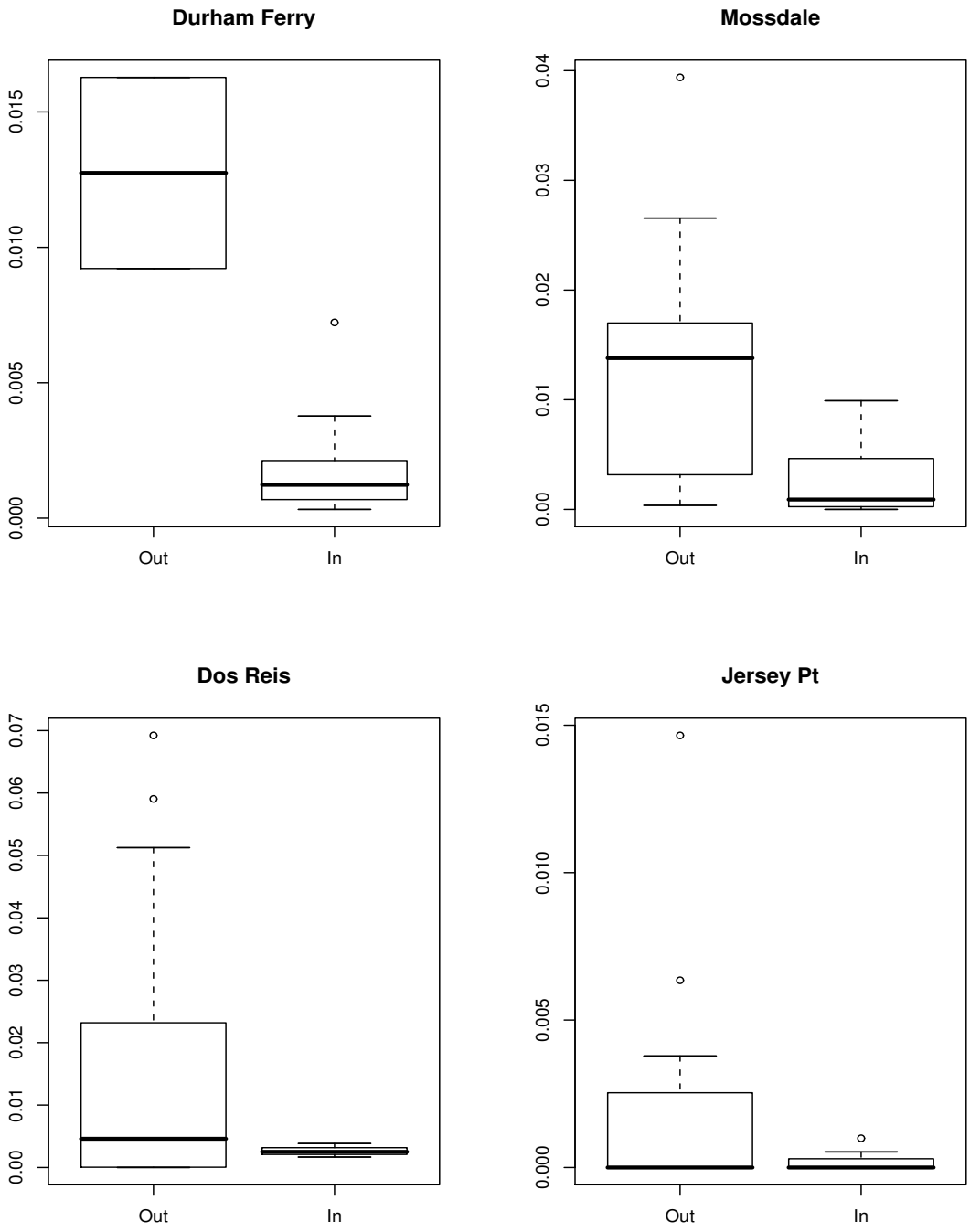


FIGURE 11. VAMP: Adult inland recovery fractions for Durham Ferry, Mossdale, Dos Reis, and Jersey Point releases by release pair.

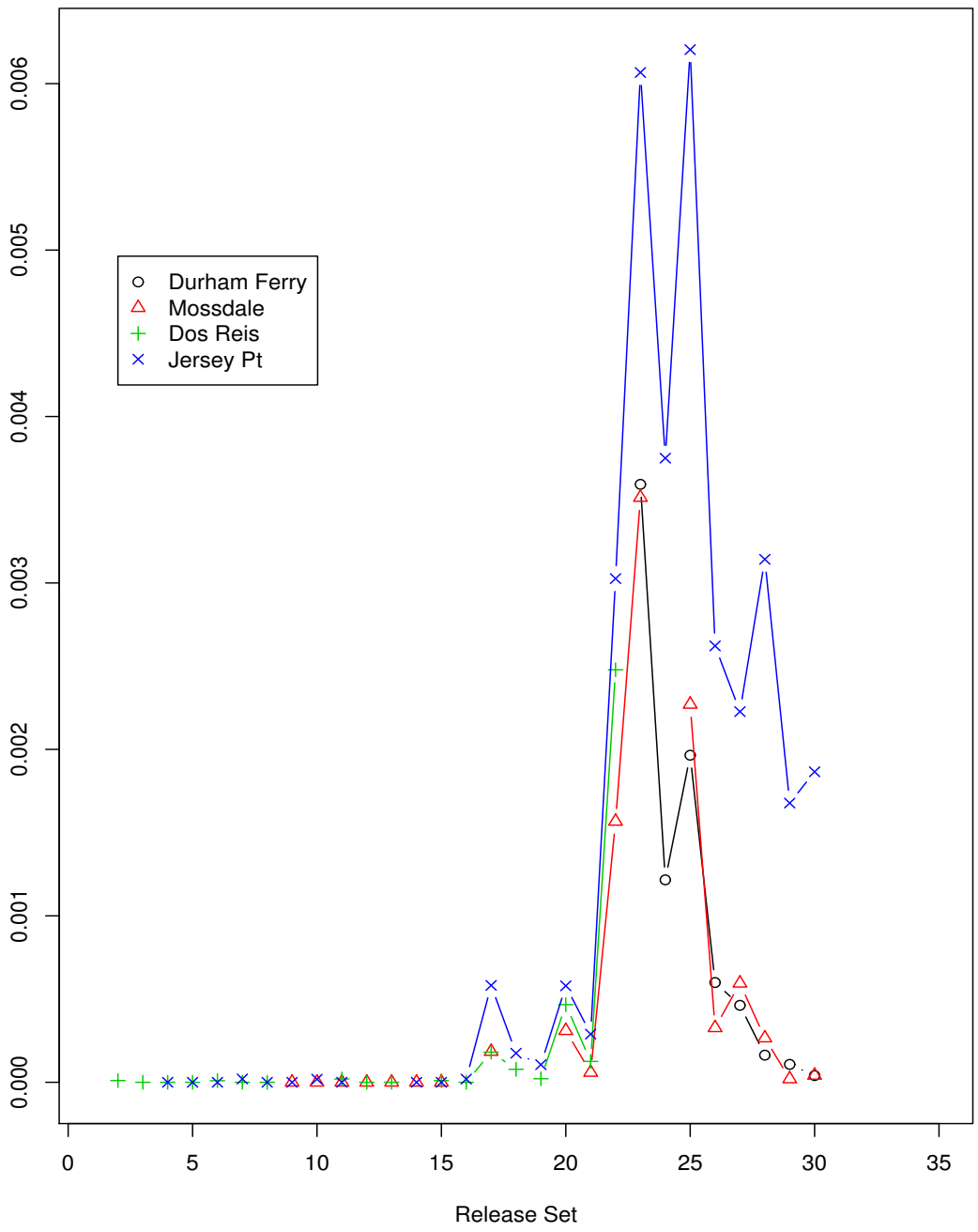


FIGURE 12. CWT recovery pattern by date at Chipps Island for examples taken from DCC, Interior/DA 8, and VAMP studies.

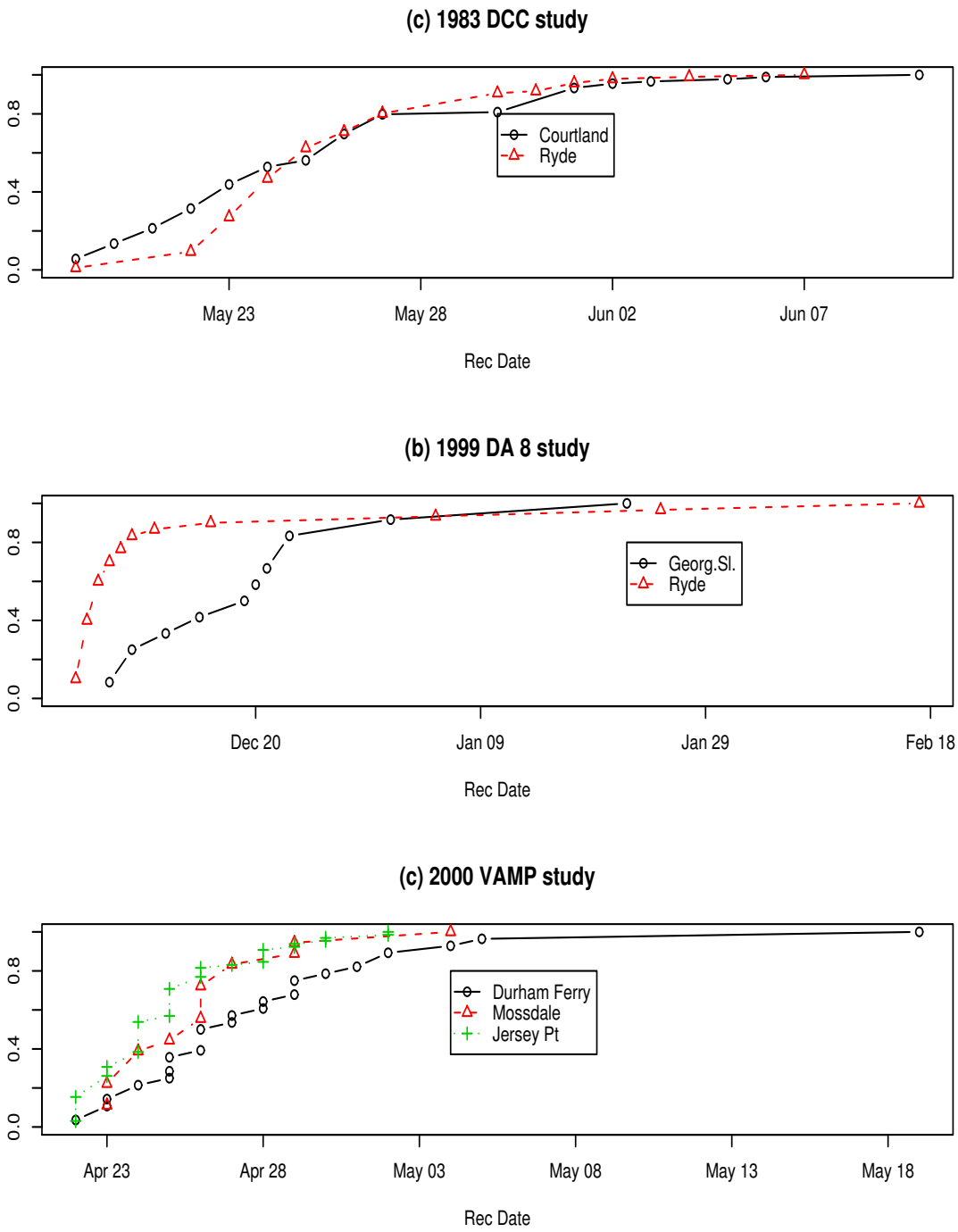


FIGURE 13. DCC: Bootstrap sample (B=10,000) of the estimated ratio, $\widehat{\left(\frac{\mu_{\theta(Open)}}{\mu_{\theta(Closed)}}\right)}$, equation (15). Vertical line marks the point estimate.

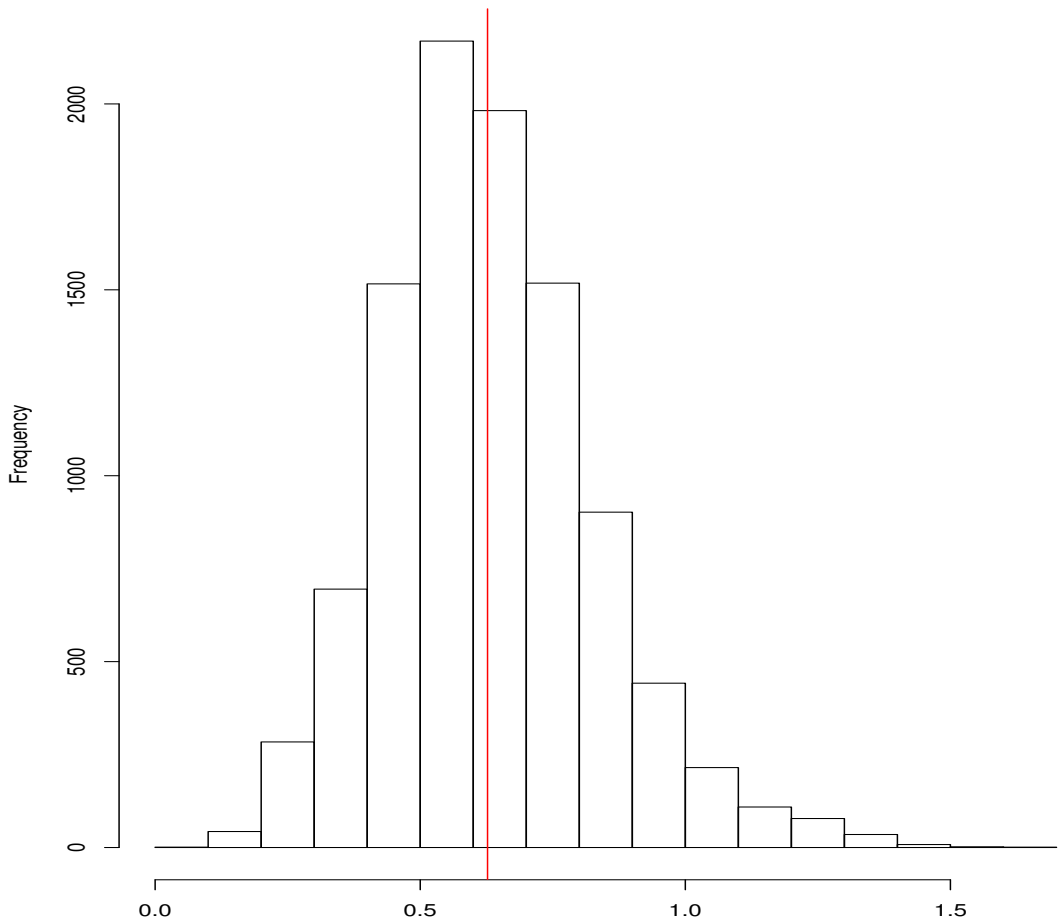


FIGURE 14. DCC: Predicted recoveries at Chipps Island of Ryde releases, $y_{Ry \to CI}$ (red vertical line), and Bayesian P-values.

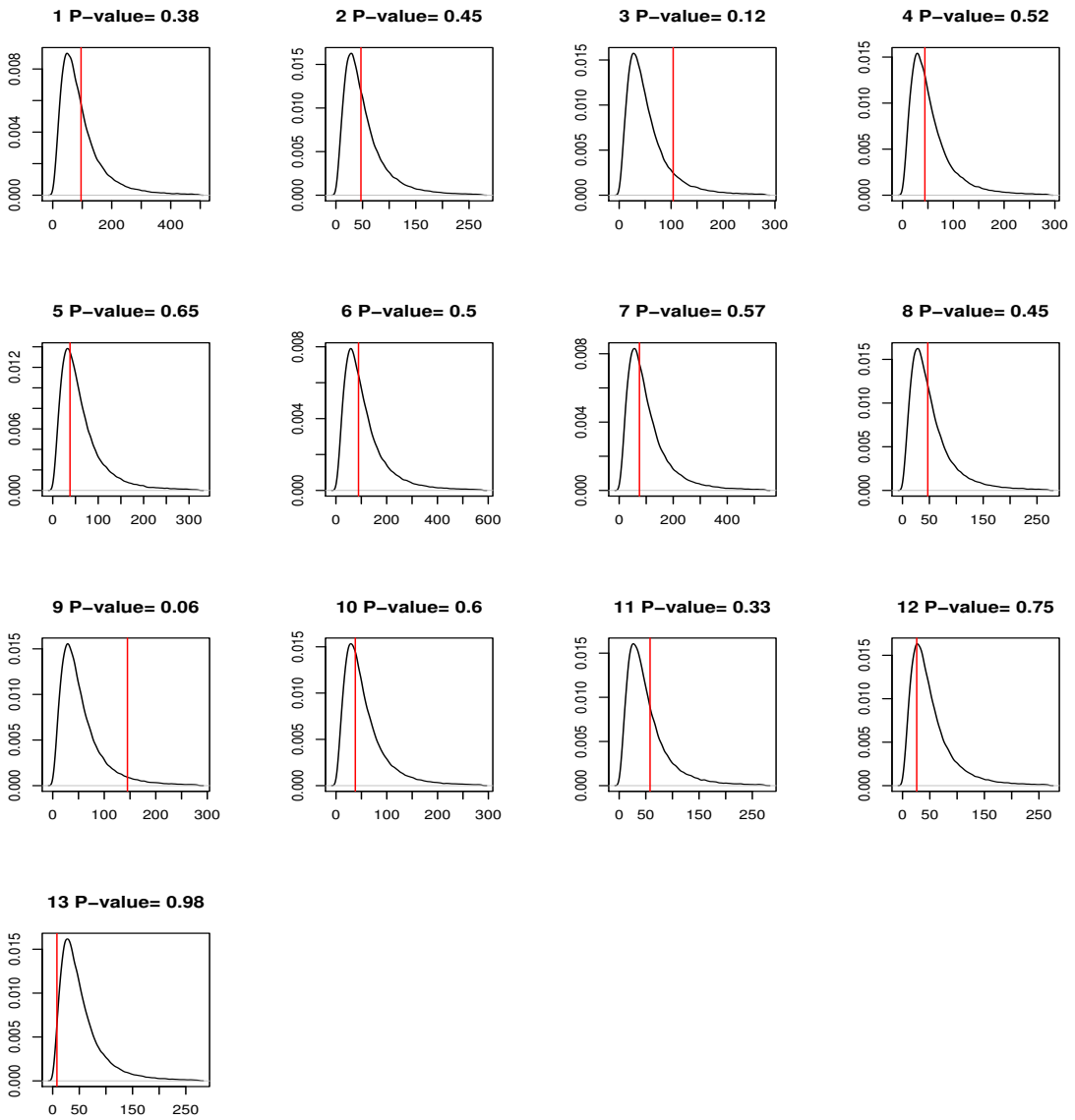


FIGURE 15. DCC: Predicted recoveries in Ocean fisheries of Ryde releases, $\hat{y}_{Ry \to Oc}$ (red vertical line), and Bayesian P-values.

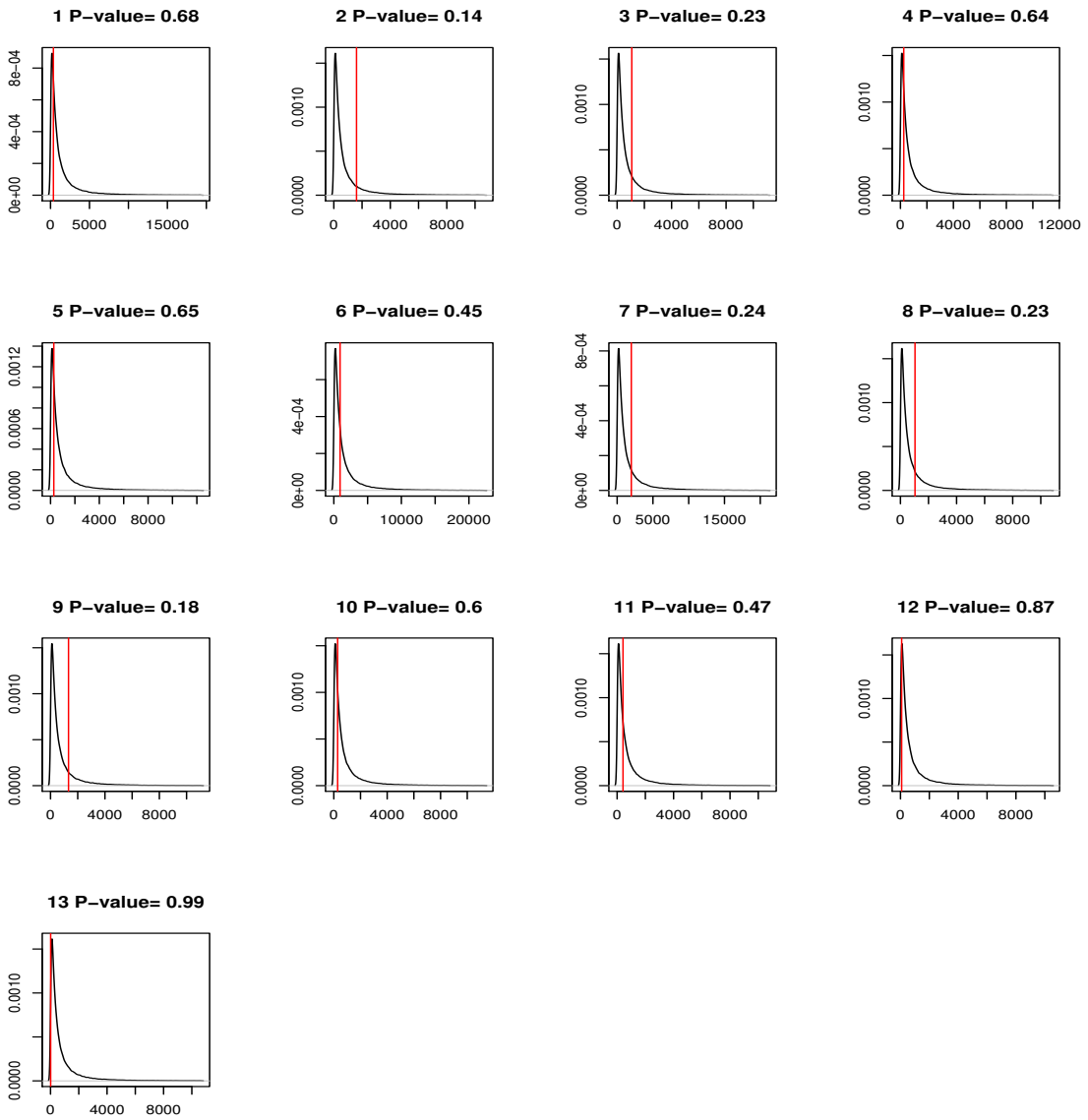


FIGURE 16. DCC: Predicted recoveries at Chipps Island of Courtland releases, $y_{Ct \to CI}$ (red vertical line), and Bayesian P-values.

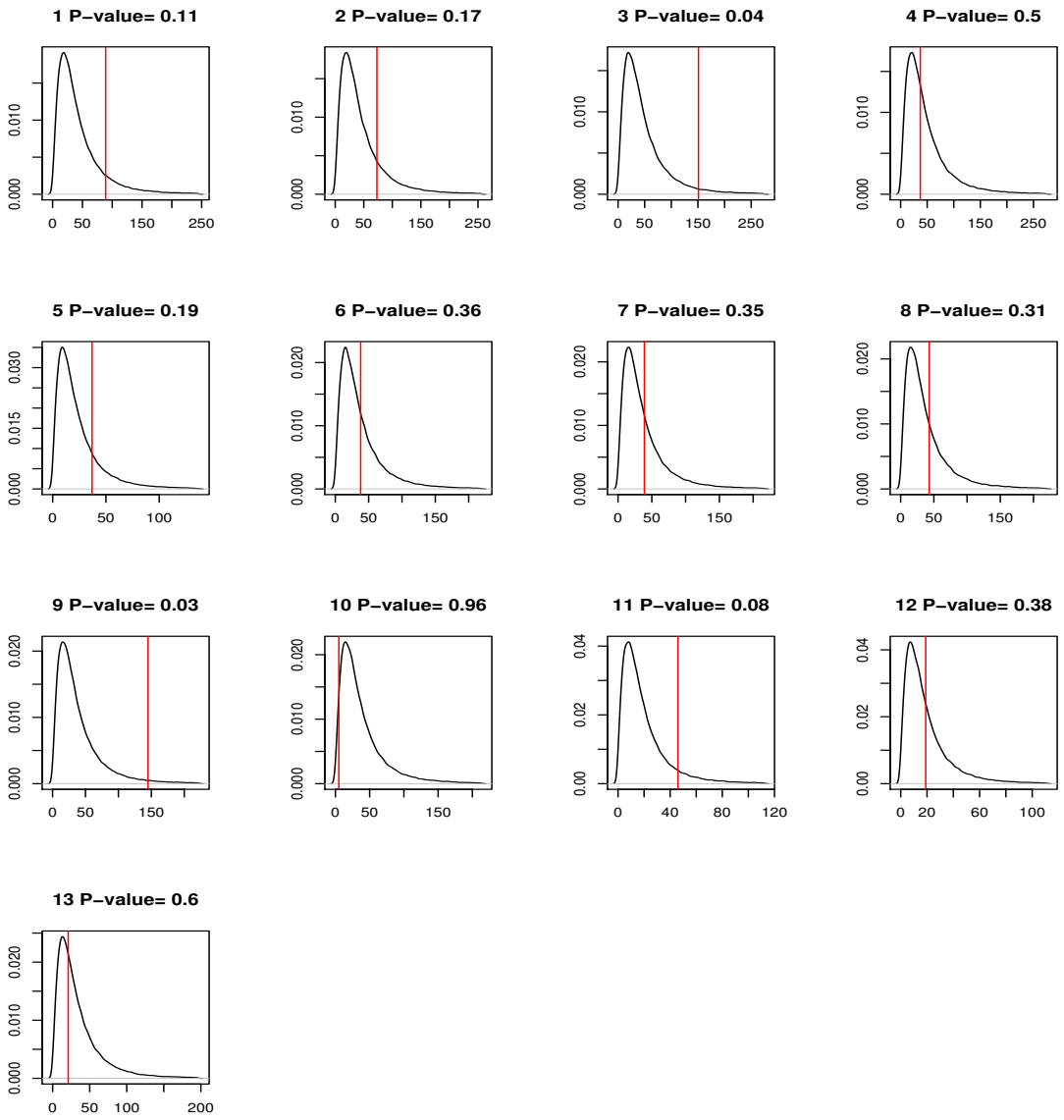


FIGURE 17. DCC: scaled residuals plotted against predicted values.

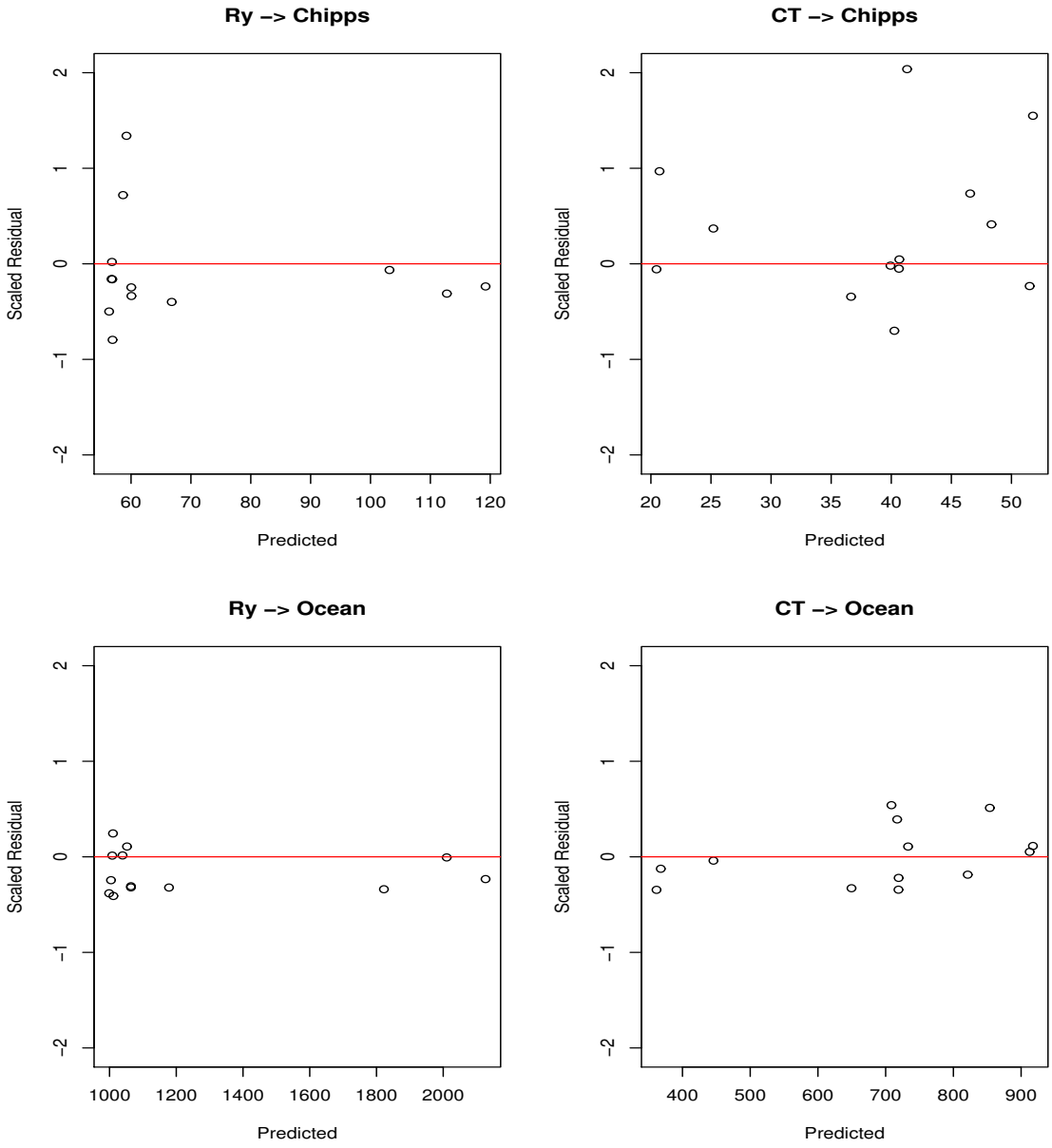


FIGURE 18. DCC: scaled residuals plotted against predicted values for model without random effects.

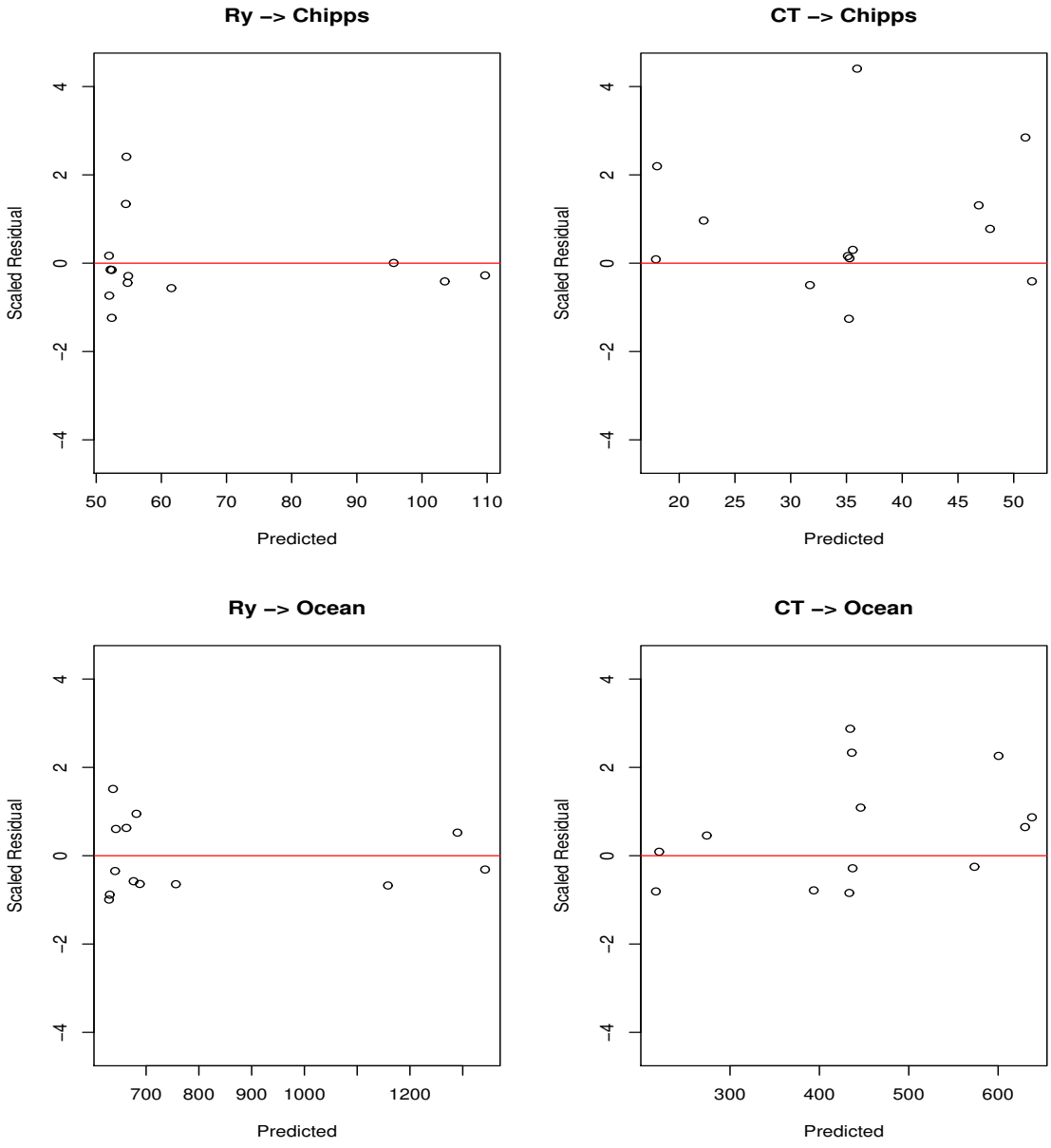


FIGURE 19. Interior: Predicted recoveries at Chipps Island of Ryde releases, $y_{Ry \to CI}$ (red vertical line), and Bayesian P-values.

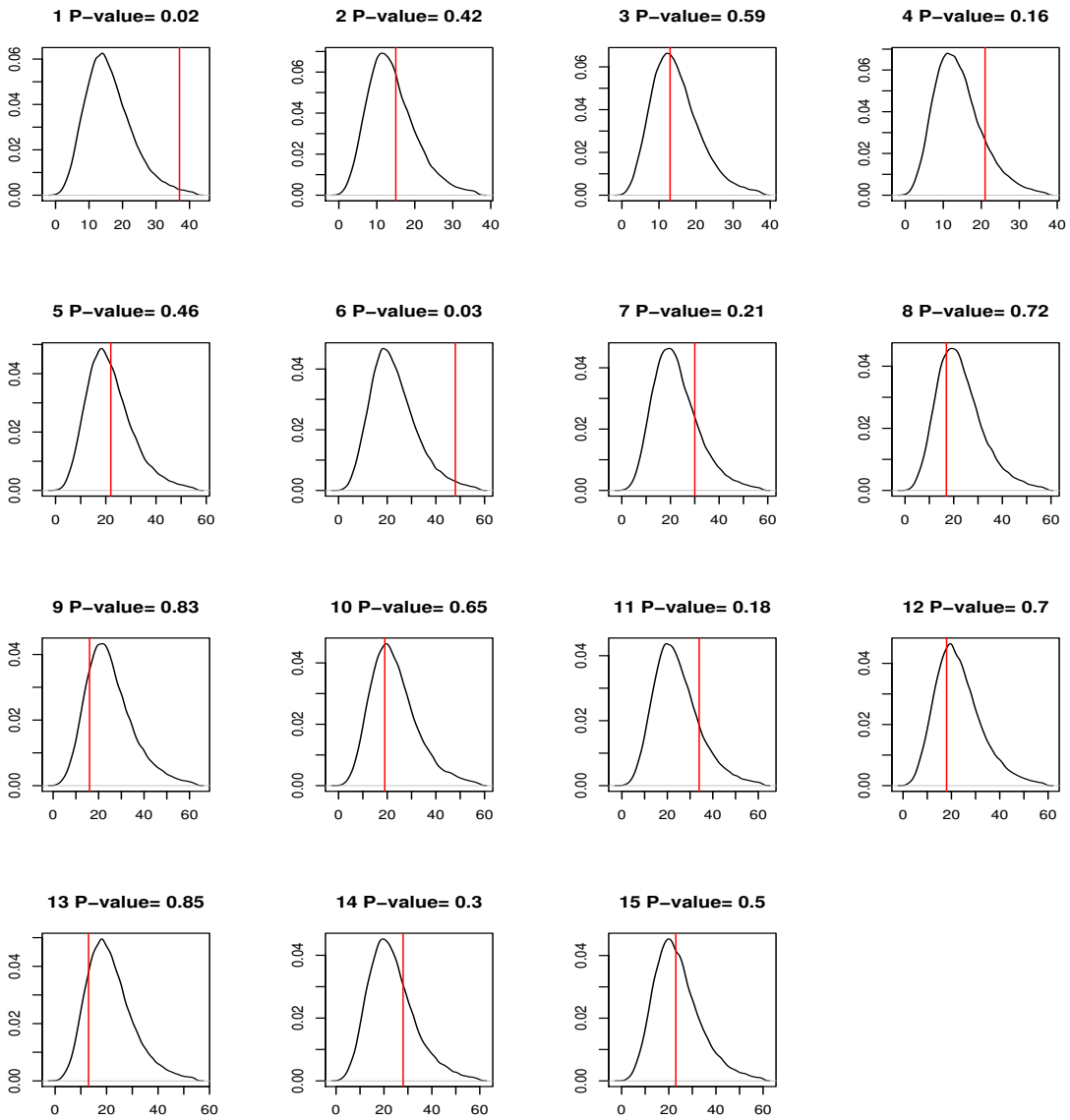


FIGURE 20. Interior: scaled residuals plotted against predicted values.

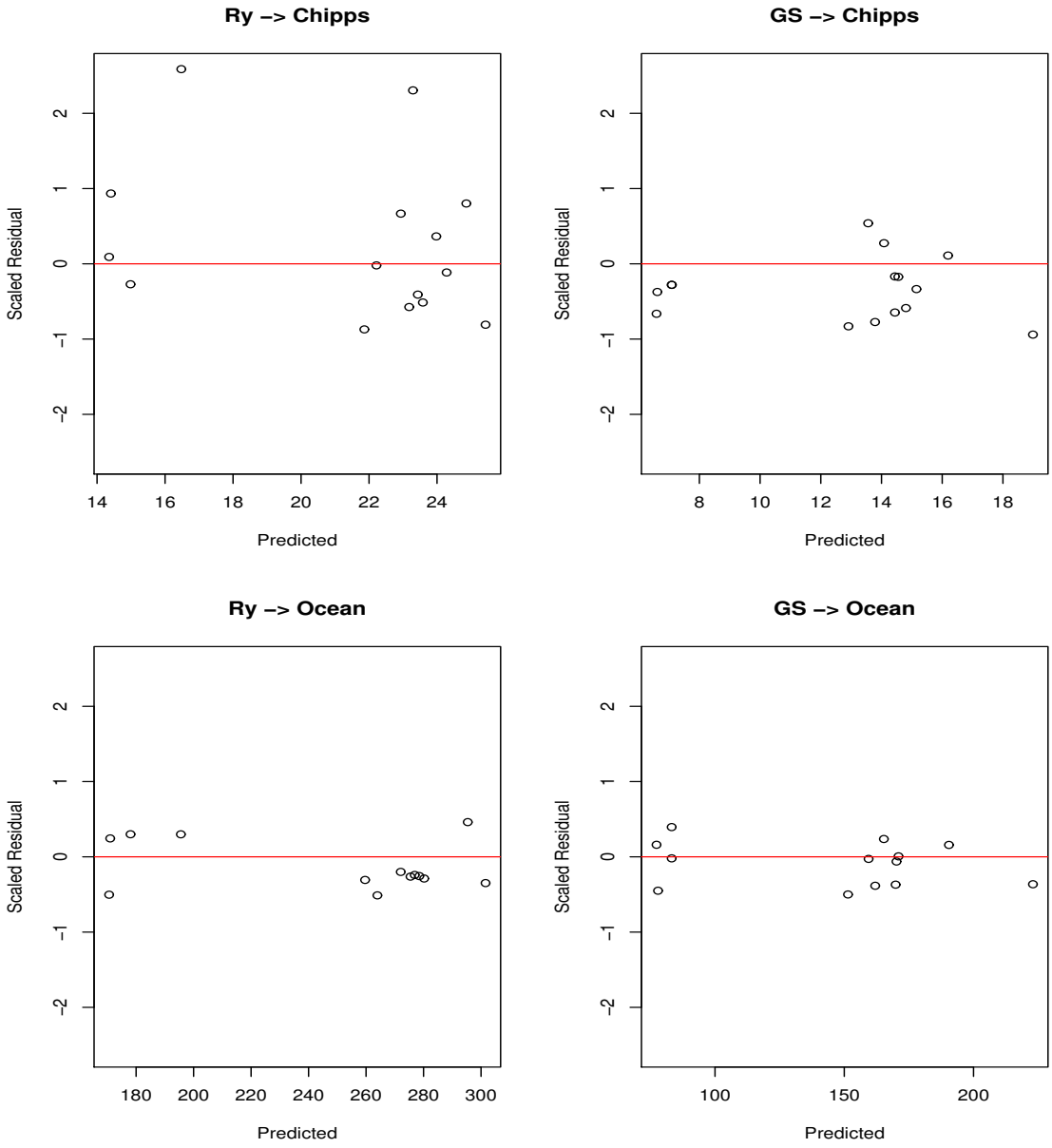


FIGURE 21. Interior: scaled residuals plotted against predicted values for model without random effects.

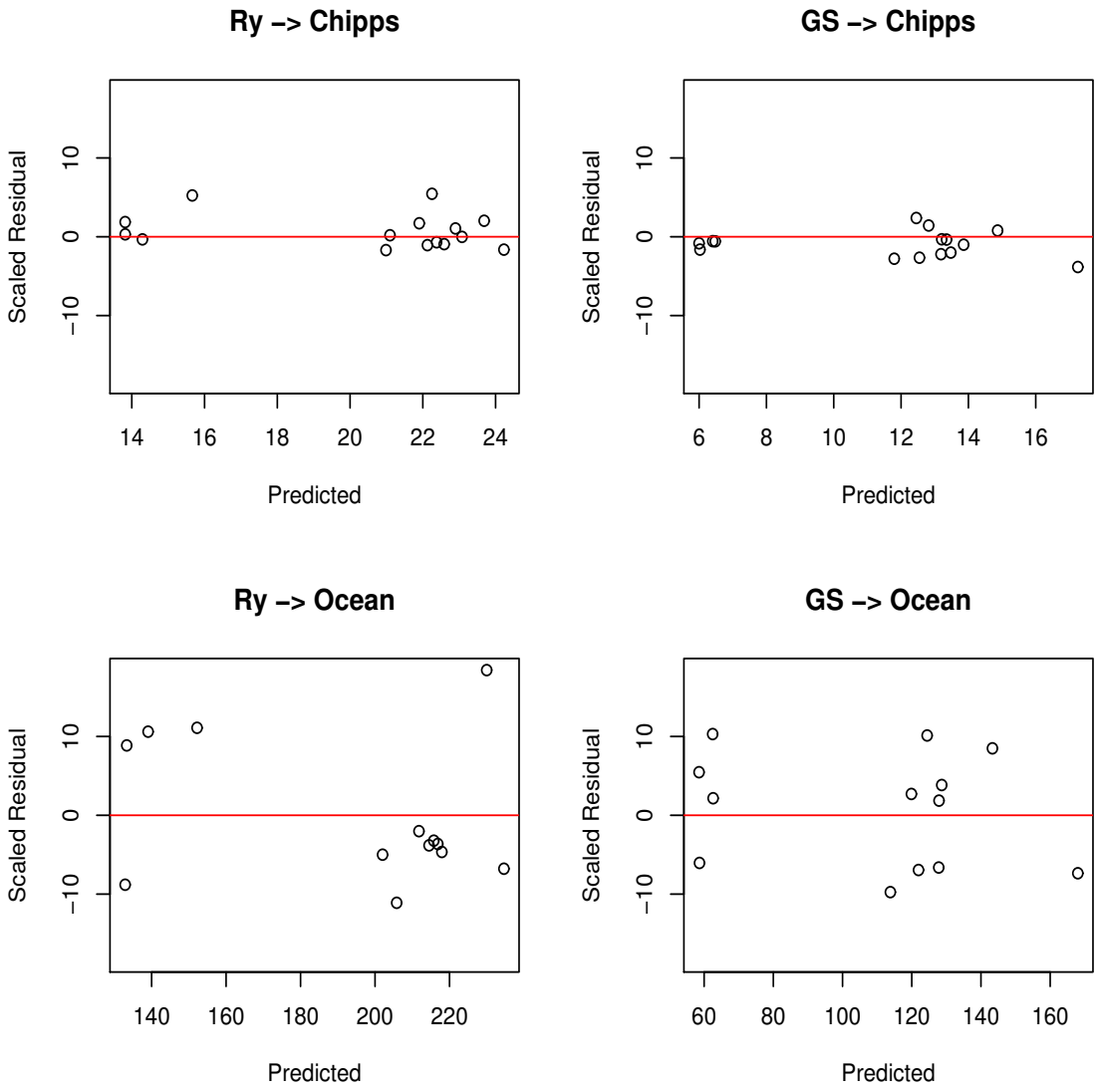
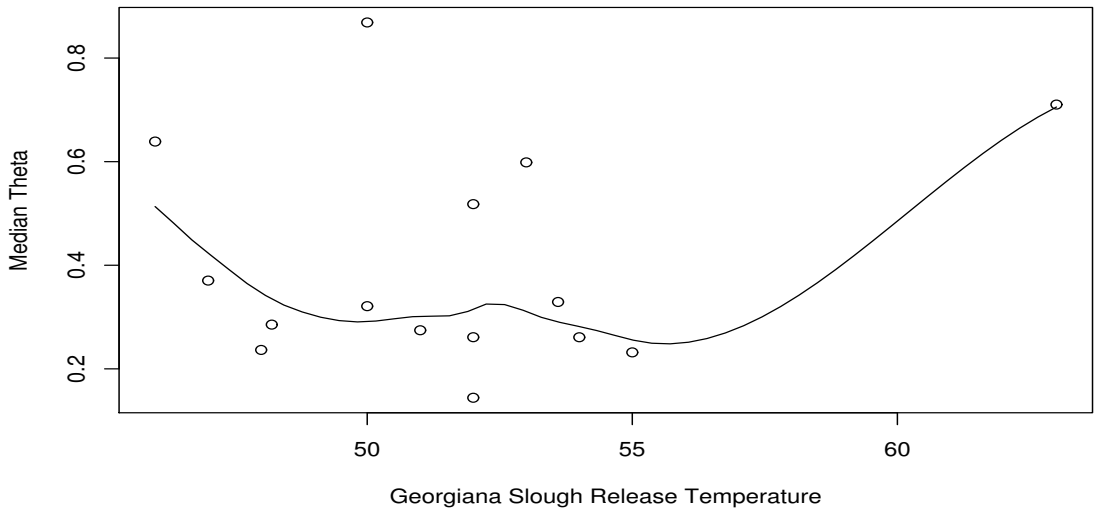


FIGURE 22. Interior: Posterior median θ's plotted against secondary covariates, Georgiana Slough release temperatures and mean fish lengths at time of release.



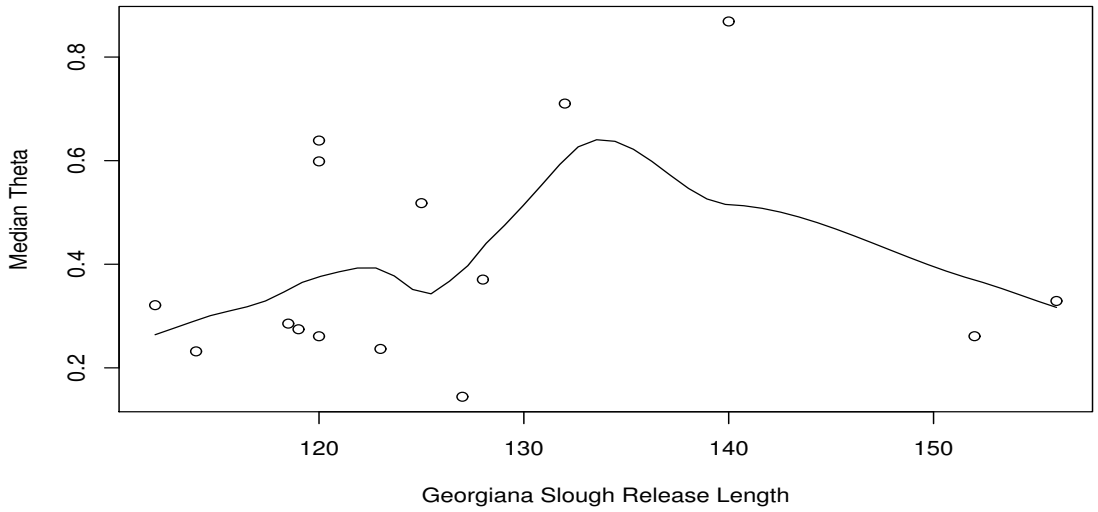


FIGURE 23. DA 8: $\hat{\theta}$ $(=\hat{r}_{GS\rightarrow CI+Oc}/\hat{r}_{Ry\rightarrow CI+Oc})$ plotted against export levels. Vertical lines extend up and down one standard error. Fitted line is a nonparametric weighted regression using the supersmoother function in `R` with weights being the inverse of the standard errors squared.

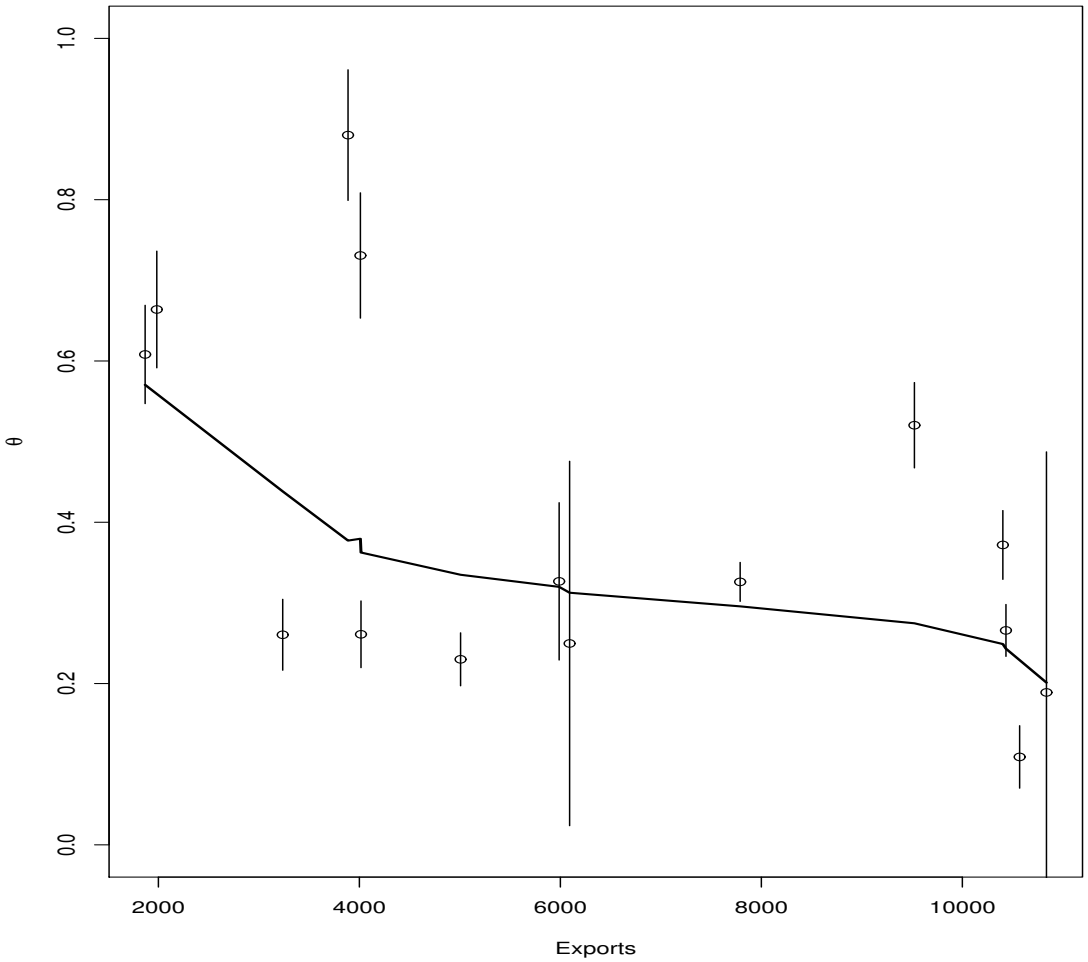


FIGURE 24. DA 8: Posterior means (solid) and medians (dashed line) for θ from the BHM (with log transformed θ and uniform priors on standard deviations of random effects) plotted against export levels. The 2.5% and 97.5% intervals are indicated by vertical lines.

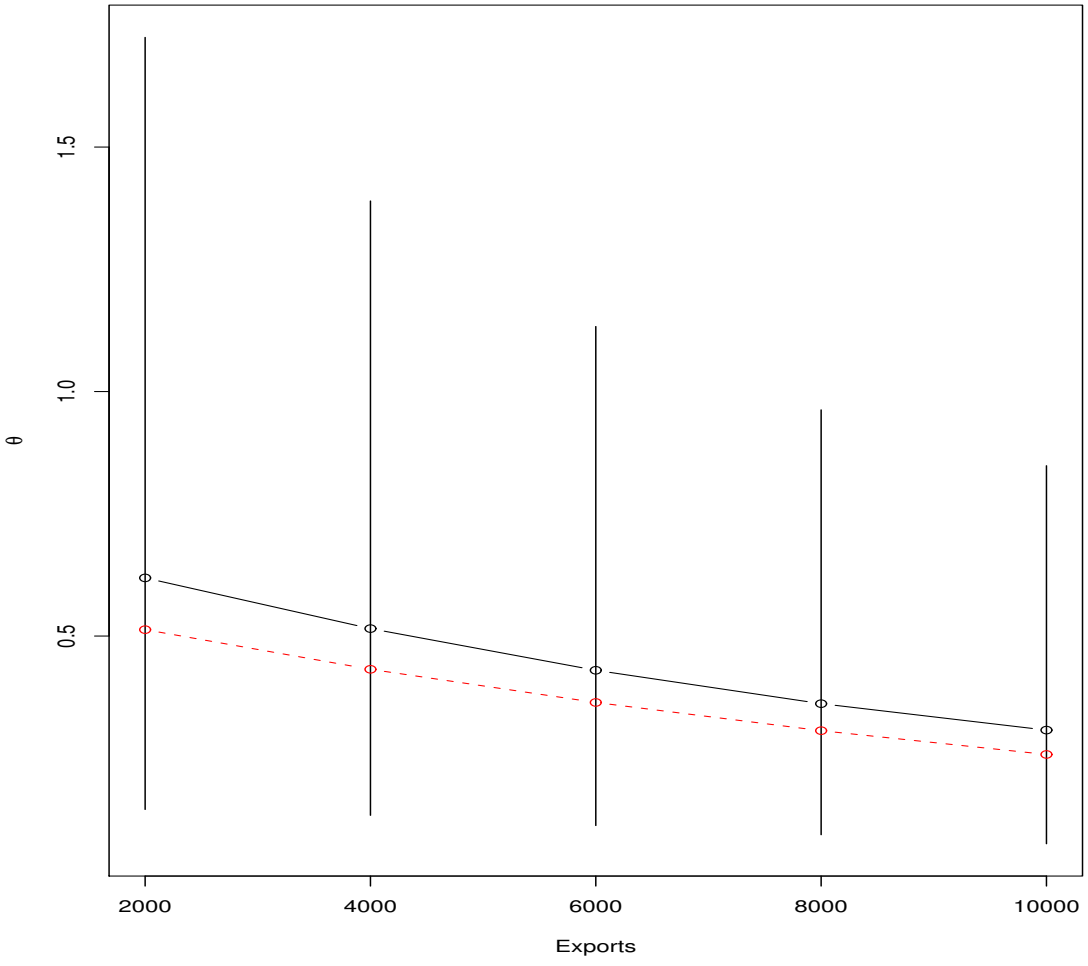


FIGURE 25. DA 8: Predicted θ ($S_{GS\to CI}/S_{Ry\to CI}$) values for different levels of exports for three different models, M1, M2, and M3. M1 is a linear regression of $\hat{r}_{GS\to CI}/\hat{r}_{Ry\to CI}$ on exports. The M2 values are the exponentiated values of a linear regression of $\log(\hat{r}_{GS\to CI+Oc}/\hat{r}_{Ry\to CI+Oc})$ on exports. M3 is a BHM (with log transformed θ and uniform priors on standard deviations of random effects). Also plotted are the non-BHM point estimates $\hat{r}_{GS\to CI+Oc}/\hat{r}_{Ry\to CI+Oc}$ for the individual releases (denoted by X).

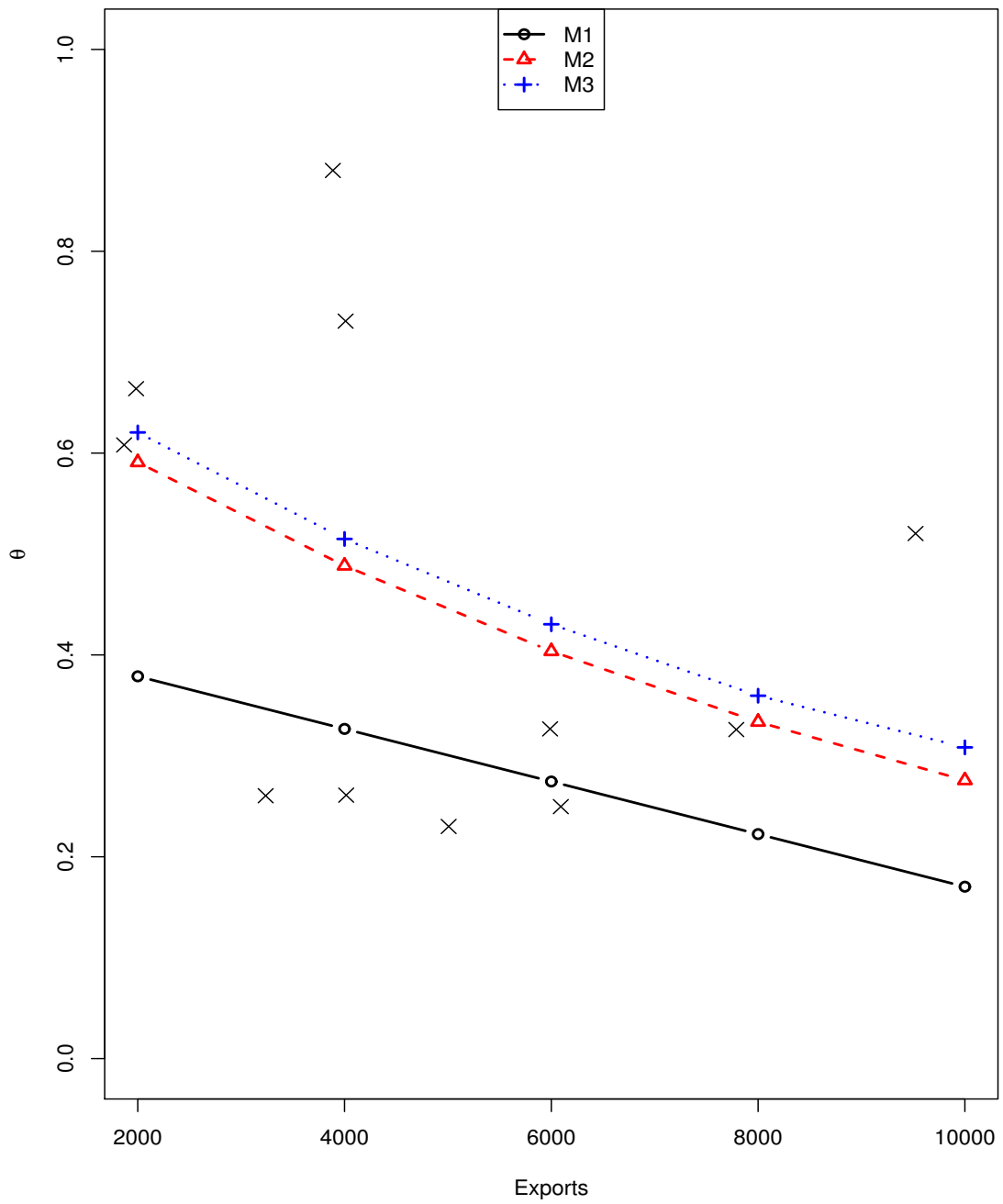


FIGURE 26. VAMP: Histograms of posterior distributions for coefficients, ξ_1, ξ_2, ζ_1, ζ_2, corresponding to flow at Dos Reis and exports following the time of releases from Dos Reis, and flow in Upper Old River and exports following the time of releases from Upper Old River (or Mossdale). (Based on Null.FE.FE model.)

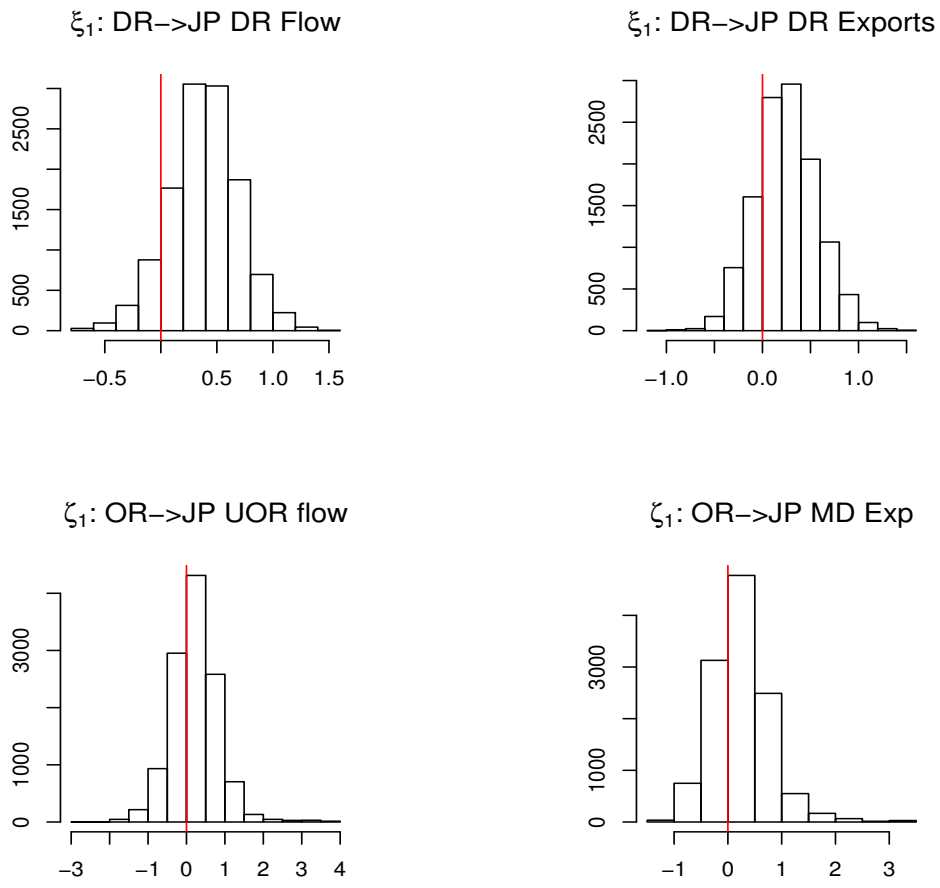


FIGURE 27. VAMP: Posterior mean survival probabilities for each of the release sets through the Dos Reis to Jersey Point reach, the Upper Old River to Jersey Point "reach". Blue vertical bars on x-axis denote when the HORB was in place. (Based on Null.FE.FE model.)

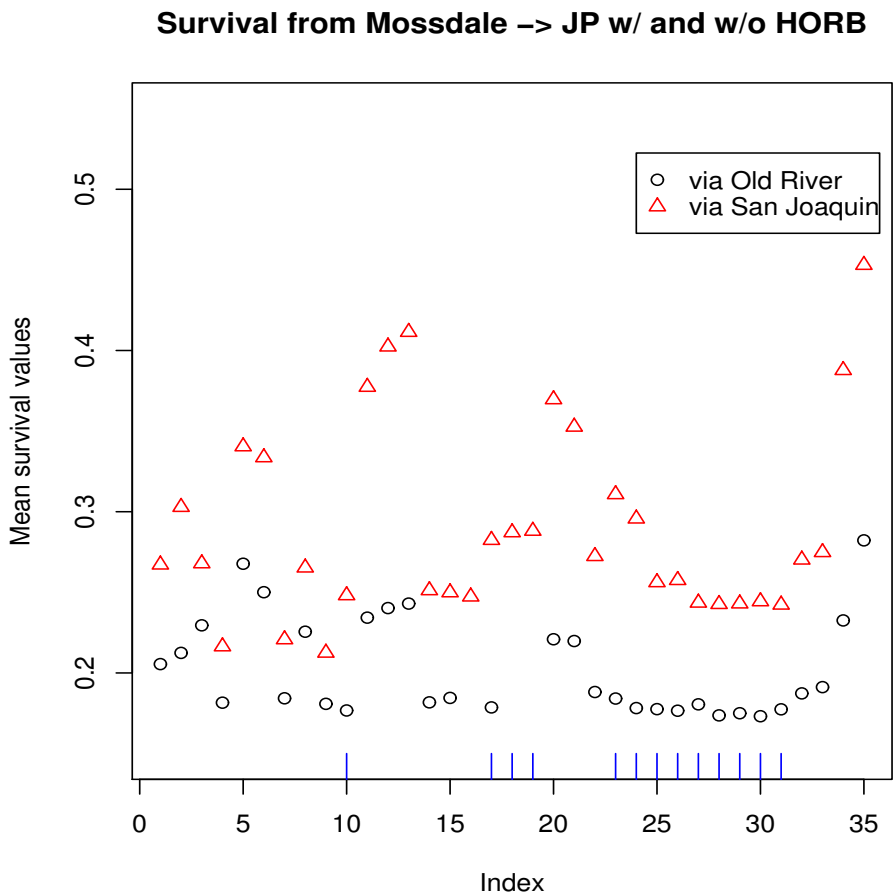


FIGURE 28. VAMP: Posterior predictive distribution and Bayesian P-values for recoveries at Antioch of releases from Mossdale. P-values are the minimum of the two tail probabilities. (Based on Null.FE.FE model.)

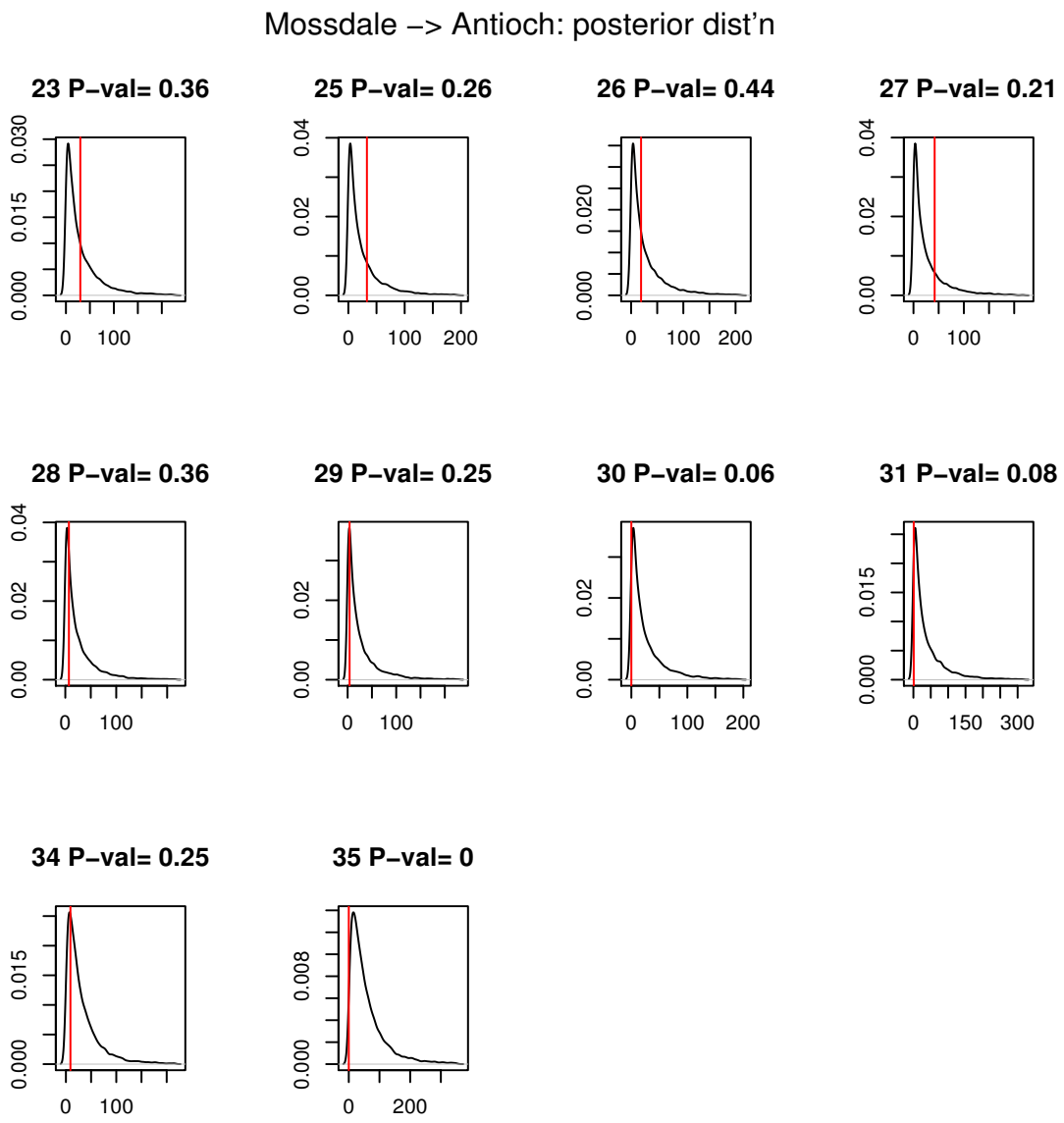


FIGURE 29. VAMP: Scaled residuals versus posterior predictive means. (Based on Null.FE.FE model.)

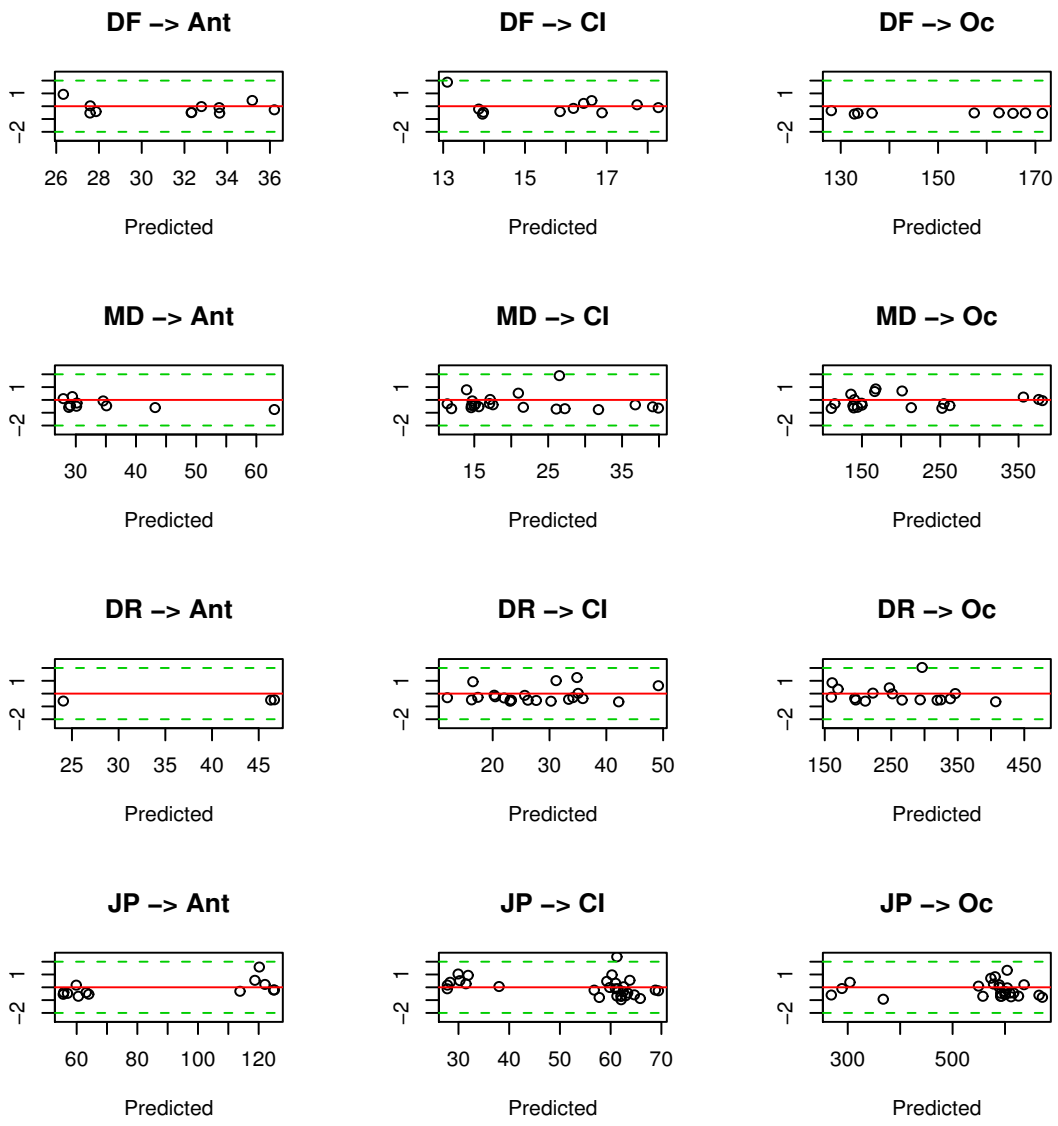


FIGURE 30. VAMP: Random effects residuals, by stream section, for logit of survival plotted against water temperature at release with supersmoother fit superimposed. The effects for Jersey Point are for the logit of Chipps Island recovery rate, either $r_{JP \to Ant \to CI}$ or $r_{JP \to CI}$. (Based on Null.FE.FE model.)

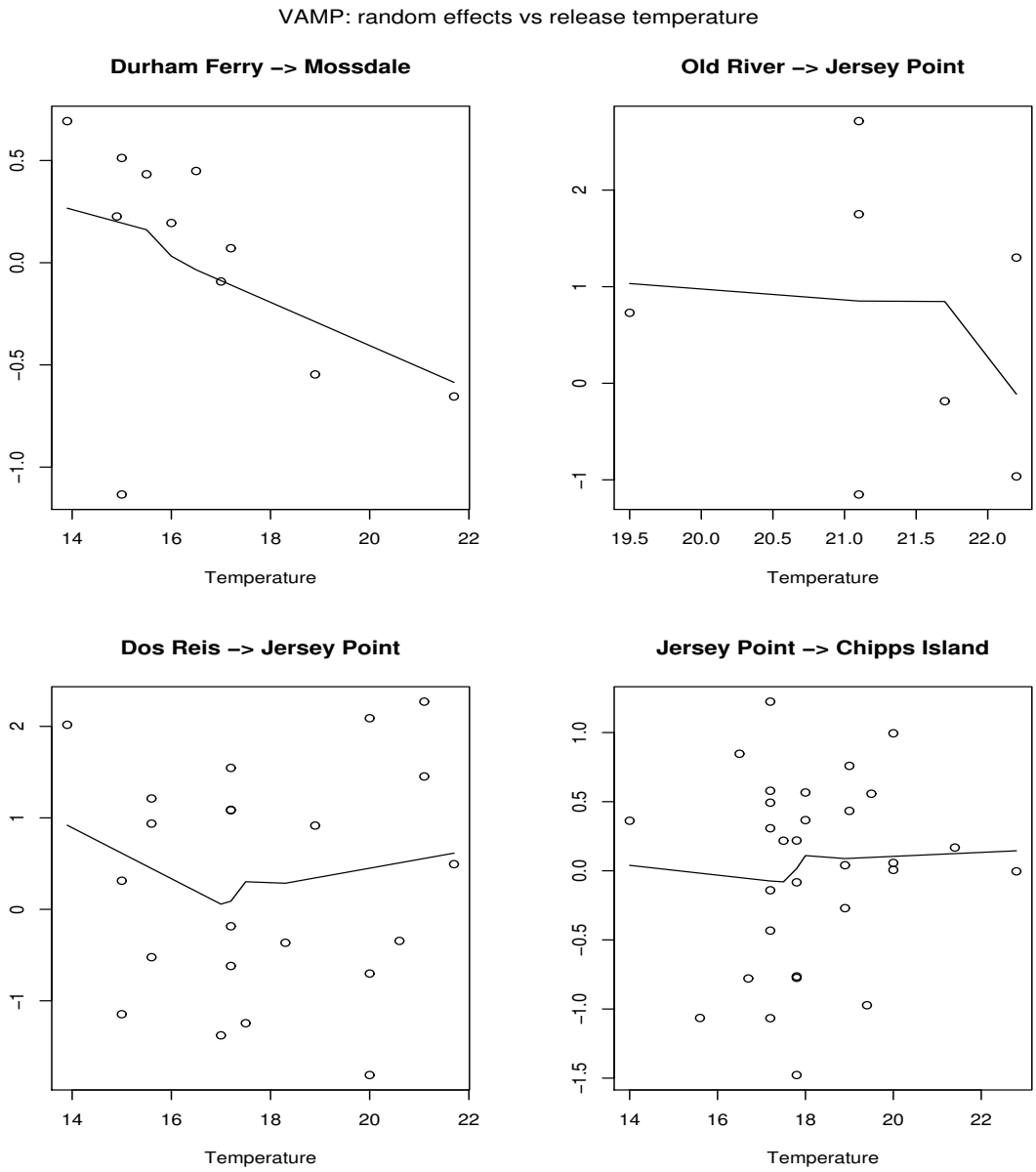


FIGURE 31. VAMP: Random effects residuals, by stream section, for logit of survival plotted against stock origin (FRH=Feather River Hatchery, MRFF=Merced River Fish Facility). The effects for Jersey Point are for the logit of Chipps Island recovery rate, $r_{JP \to CI}$. (Based on Null.FE.FE model.)

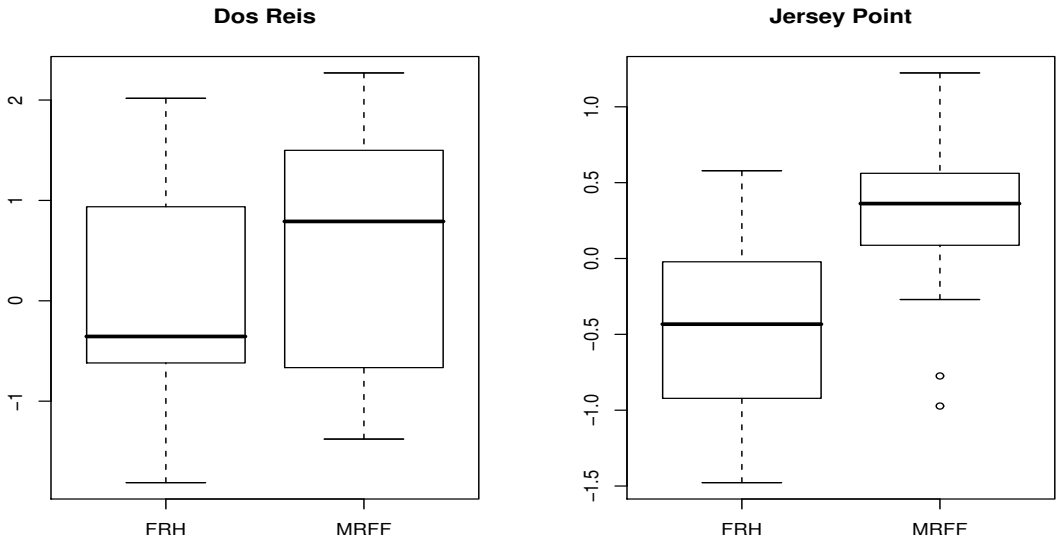


FIGURE 32. VAMP: Random effects residuals, by stream section, for logit of survival plotted against the estimated number of salmon salvaged at the fish facilities at CVP and SWP. The effects for Jersey Point are for the logit of Chipps Island recovery rate, $r_{JP \to CI}$. (Based on Null.FE.FE model.)

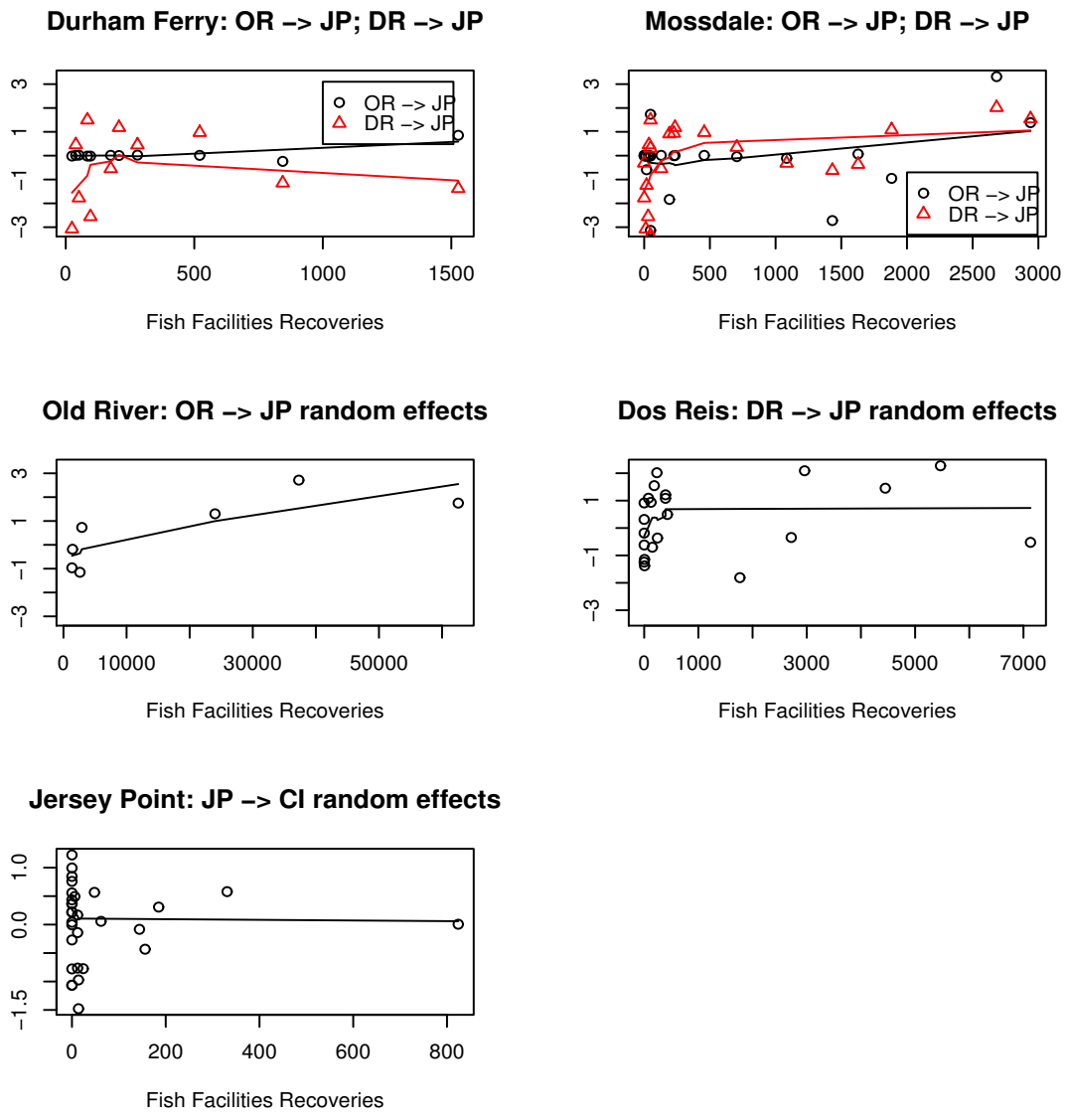


FIGURE 33. DCC: Bootstrap standard errors for $\widehat{\frac{\mu_{\theta(Open)}}{\mu_{\theta(Closed)}}}$ as a function of the number of replications. The number of replications on the x-axis refer to the total number of replications, with half being gates open and half with gates closed; e.g., 10 means 5 experiments with DCC gate open and 5 experiments with DCC gate closed. Number of fish released at each site was fixed at 100,000, R_{Ct}=R_{Ry}=100,000. An extreme value of 62, for n=10 was deleted before plotting.

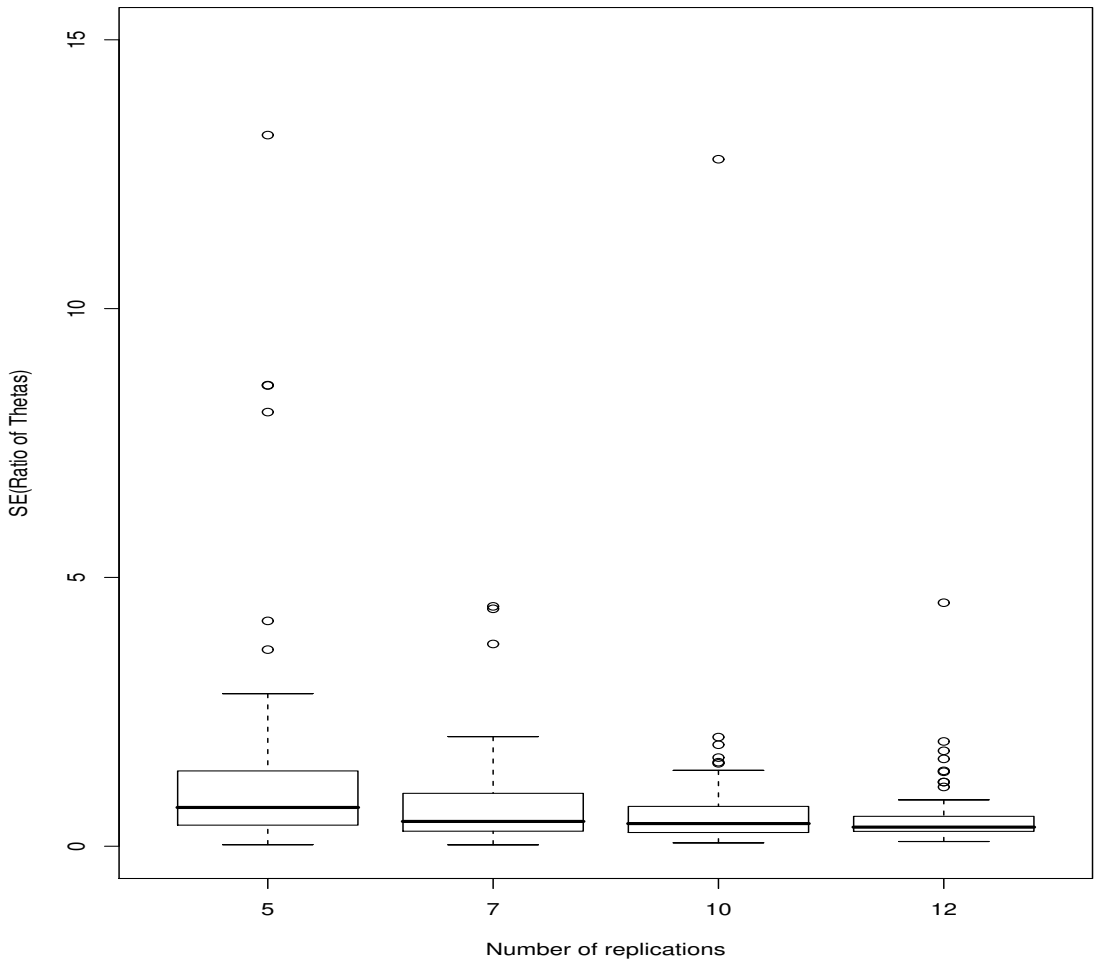
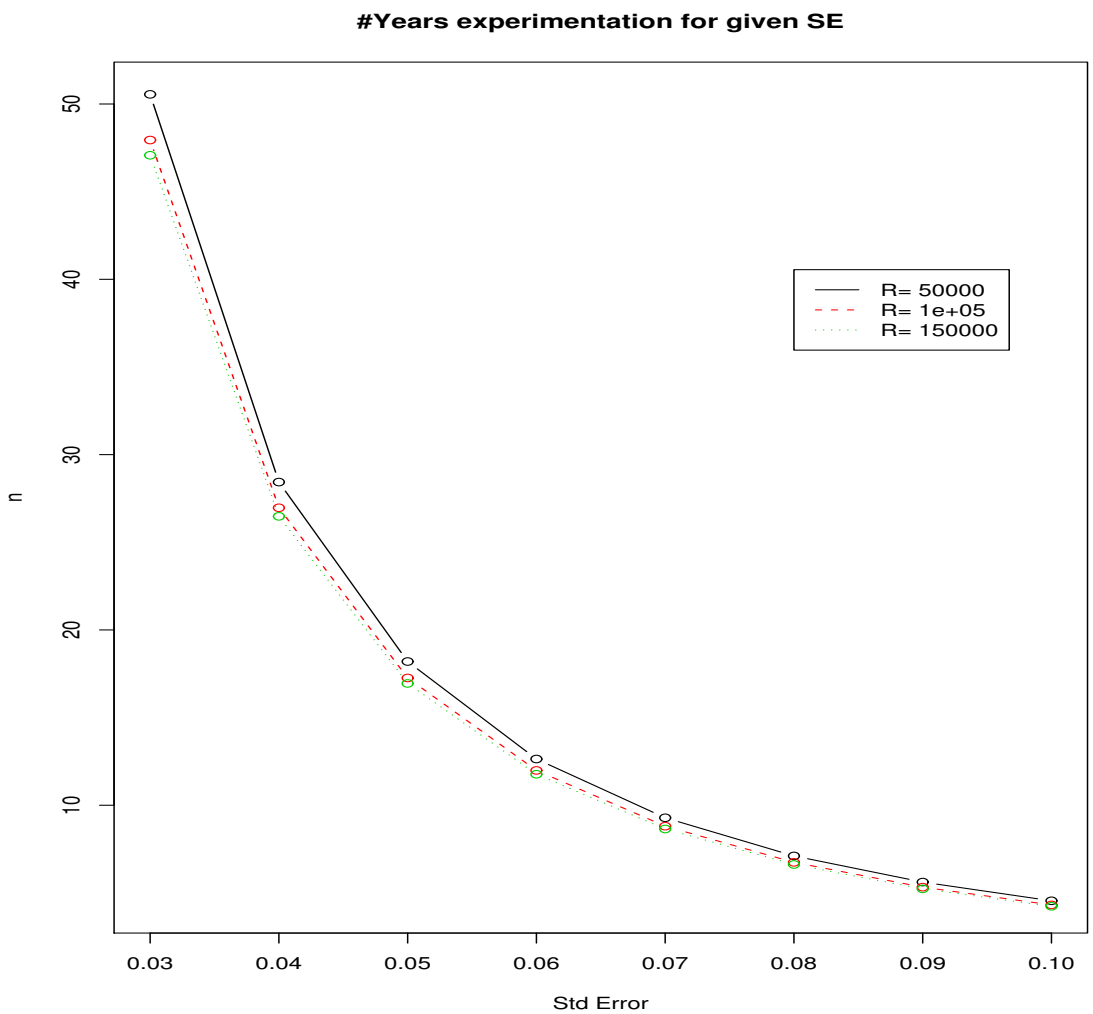


FIGURE 34. Interior: Number of years of experimentation (n) to achieve a specified standard error for $\hat{\mu}_\theta$ for expected numbers of recoveries plotted against observed numbers of recoveries, by release site and recovery location. (μ_θ=0.8.)



APPENDICES

Appendix A. DCC and Interior: Theoretical variance of $\hat{\mu}_\theta$

The expected value of the ratio of the survival probabilities for two "upstream" releases, μ_θ, can be estimated by averaging year specific estimates of θ_t:

$$\begin{aligned}\hat{\mu}_\theta &= \sum_{t=1}^{n} w_t \hat{\theta}_t \\ &= \sum_{t=1}^{n} w_t \frac{(y_{13,t}+y_{14,t})/R_{1t}}{(y_{23,t}+y_{24,t})/R_{2t}},\end{aligned}$$

where w_t are weights, $\sum_{t=1}^{n} w_t = 1$. Variation in this estimate arises from between year variation in the survival and capture probabilities and within year sampling variation. The following standard result from probability theory reflects these two levels of variation and is used to calculate the variance of $\hat{\mu}_\theta$:

$$V(\hat{\mu}_\theta) = E\left[V\left(\hat{\mu}_\theta|\theta_t, S_{23,t}, p_t, \pi_t\right)\right] + V\left[E\left(\hat{\mu}_\theta|\theta_t, S_{23,t}, p_t, \pi_t\right)\right]. \tag{57}$$

A.1. $V[E]$ **calculation.** Regarding the second term on the righthand side of (57), the expectation portion can be written:

$$E[\hat{\mu}_\theta|\theta_t, S_{23,t}, p_t, \pi_t] = \sum_{t=1}^{n} w_t E[\hat{\theta}_t|\theta_t, S_{23,t}, p_t, \pi_t] \approx \sum_{t=1}^{n} w_t \theta_t,$$

assuming that $\hat{\theta}_t$ is unbiased for θ_t. Then

$$V\left[E(\hat{\mu}_\theta|\theta_t, S_{23,t}, p_t, \pi_t)\right] \approx \sum_{t=1}^{n} w_t^2 V(\theta_t) = \sum_{t=1}^{n} w_t^2 \sigma_\theta^2. \tag{58}$$

If each of the yearly estimates of θ are given equal weight (as would be the case with equal release numbers per year), this component reduces to

$$V\left[E(\hat{\mu}_\theta)|\theta_t, S_{23,t}, p_t, \pi_t)\right] \approx \frac{\sigma_\theta^2}{n}.$$

A.2. $E[V]$ **calculation.** For the first term on the righthand side of (57), the delta approximation (Stuart and Ord, 1987, p. 324) is used to calculate $V(\hat{\mu}_\theta|\theta_t, S_{23,t}, p_t, \pi_t)$:

$$V(\hat{\mu}_\theta|\mu_\theta, S_{23,t}, p_t, \pi_t) = \sum_{t=1}^{n} w_t^2 V(\hat{\theta}_t), \tag{59}$$

where

$$\begin{aligned} V(\hat{\theta}_t) &\approx d_1^2\left(v(y_{13,t}) + v(y_{14,t}) + 2cov(y_{13,t}, y_{14,t})\right) + \\ &\quad d_2^2\left(v(y_{23,t}) + v(y_{24,t}) + 2cov(y_{23,t}, y_{24,t})\right), \end{aligned}$$

and

$$\begin{aligned} d_1 &= \frac{R_{2t}}{R_{1t}}\frac{1}{E[y_{23,t}] + E[y_{24,t}]} = \frac{R_{2t}}{R_{1t}}\frac{1}{R_{2t}S_{23,t}(p_t + (1-p_t)\pi_t)} \\ &= \frac{1}{R_{1t}S_{23,t}(p_t + (1-p_t)\pi_t)} \\ v(y_{13,t}) &= R_{1t}\theta_t S_{23,t}p_t\left(1 - \theta_t S_{23,t}p_t\right) \\ v(y_{14,t}) &= R_{1t}\theta_t S_{23,t}(1-p_t)\pi_t\left(1 - \theta_t S_{23,t}(1-p_t)\pi_t\right) \\ cov(y_{13,t}, y_{14,t}) &= -R_{1t}\theta_t S_{23,t}p_t * \theta_t S_{23,t}(1-p_t)\pi_t \\ d_2 &= \frac{R_{2t}}{R_{1t}}\frac{E[y_{13,t}] + E[y_{14,t}]}{(E[y_{23,t}] + E[y_{24,t}])^2} = \frac{\theta_t S_{23,t}(p_t + (1-p_t)\pi_t)}{R_{2t}\left(S_{23,t}(p_t + (1-p_t)\pi_t)\right)^2} \\ v(y_{23,t}) &= R_{2t}S_{23,t}p_t\left(1 - S_{23,t}p_t\right) \\ v(y_{24,t}) &= R_{2t}S_{23,t}(1-p_t)\pi_t\left(1 - S_{23,t}(1-p_t)\pi_t\right) \\ cov(y_{23,t}, y_{24,t}) &= -R_{2t}S_{23,t}p_t * S_{23,t}(1-p_t)\pi_t \end{aligned}$$

The expected value, $E\left[V(\hat{\mu}_\theta)|\theta_t, S_{23,t}, p_t, \pi_t)\right]$, is also approximated using the delta method (with a second order approximation, Stuart and Ord (1987, p 342)[9]). Assuming independence between θ_t and the survival and capture probabilities, the approximation has the following form:

$$\begin{aligned} E\left[V(\hat{\mu}_\theta)|\theta_t, S_{23,t}, p_t, \pi_t)\right] &\approx \sum_{t=1}^{n} w_t^2\, V(\hat{\theta}_t)\Big|_\mu + \\ &\quad 0.5\sum_{t=1}^{n} w_t^2\left[\frac{d^2V}{d\theta_t^2}\bigg|_\mu \sigma_{\theta_t}^2 + \frac{d^2V}{dS_{23,t}^2}\bigg|_\mu \sigma_{S_{23,t}}^2 + \frac{d^2V}{dp_t^2}\bigg|_\mu \sigma_{p_t}^2 + \frac{d^2V}{d\pi_t^2}\bigg|_\mu \sigma_{\pi_t}^2\right] \end{aligned} \tag{60}$$

where μ denotes the expected values μ_θ, $\mu_{S_{23}}$, μ_p, and μ_π.

[9]Note: simply substituting (μ_θ, $\mu_{S_{23}}$, μ_p,μ_π) for ($\theta_t, S_{23,t}, p_t, \pi_t$) into $V(\hat{\theta}_t)$ is relatively inaccurate. Simulations using beta distributions for the survival and capture probabilities indicated that such an approximation was biased low.

Formulae for second derivatives. The formulae for the second derivatives are shown below; to reduce notation the t subscripts have been dropped and $S_{23,t}$ is simply written as S. Furthermore, let

$$\begin{aligned}
N_1 &= \theta p(1-\theta S p) + \theta(1-p)\pi(1-\theta S(1-p)\pi) - 2\theta^2 p S(1-p)\pi \\
N_2 &= \theta^2 p(1-Sp) + \theta^2(1-p)\pi(1-S(1-p)\pi) - 2\theta^2 p S(1-p)\pi \\
D_1 &= R_1 S(p+(1-p)\pi)^2 \\
D_2 &= R_2 S(p+(1-p)\pi)^2
\end{aligned}$$

Then

$$\frac{d^2V}{d\theta^2} = \frac{d^2N_1}{d\theta^2}D_1^{-1} + \frac{d^2N_2}{d\theta^2}D_2^{-1},$$

where

$$\begin{aligned}
\frac{d^2N_1}{d\theta^2} &= -2Sp^2 - 2S(1-p)^2\pi^2 - 4Sp(1-p)\pi \\
\frac{d^2N_2}{d\theta^2} &= 2p - 2Sp^2 + 2(1-p)\pi - 2S(1-p)^2\pi^2 - 4Sp(1-p)\pi
\end{aligned}$$

And

$$\begin{aligned}
\frac{d^2V}{dS^2} = {} & 2\left[\theta^2p^2 + \theta^2(1-p)^2\pi^2 + 2\theta^2p(1-p)\pi\right] D_1^{-2}R_1(p+(1-p)\pi)^2 + \\
& 2N_1D_1^{-3}\left(R_1(p+(1-p)\pi)^2\right)^2 + \\
& 2\left[\theta^2p^2 + \theta^2(1-p)^2\pi^2 + 2\theta^2p(1-p)\pi\right] D_2^{-2}R_2(p+(1-p)\pi)^2 + \\
& 2N_2D_2^{-3}\left(R_2(p+(1-p)\pi)^2\right)^2.
\end{aligned}$$

And

$$\begin{aligned}
\frac{d^2V}{dp^2} = {} & \frac{d^2N_1}{dp^2}D_1^{-1} - 2\frac{dN_1}{dp}D_1^{-2}\frac{dD_1}{dp} + 2N_1D_1^{-3}\left(\frac{dD_1}{dp}\right)^2 - N_1D_1^{-2}R_1S(2-4\pi+2\pi^2) + \\
& \frac{d^2N_2}{dp^2}D_2^{-1} - 2\frac{dN_2}{dp}D_2^{-2}\frac{dD_2}{dp} + 2N_2D_2^{-3}\left(\frac{dD_2}{dp}\right)^2 - N_2D_2^{-2}R_2S(2-4\pi+2\pi^2),
\end{aligned}$$

where

$$\begin{aligned}
\frac{dN_1}{dp} &= \theta - 2\theta^2 Sp - \theta\pi - \theta^2 S(-2+2p)\pi^2 - 2\theta^2 S(1-2p)\pi \\
\frac{d^2N_1}{dp^2} &= -2\theta^2 S - 2\theta^2 S\pi^2 + 4\theta^2 S\pi \\
\frac{dD_1}{dp} &= R_1 S(2p + 2\pi - 4p\pi + (-2+2p)\pi^2) \\
\frac{dN_2}{dp} &= \theta^2 - 2\theta^2 Sp - \theta^2\pi - \theta^2 S(-2+2p)\pi^2 - 2\theta^2 S(1-2p)\pi \\
\frac{d^2N_2}{dp^2} &= -2\theta^2 S - 2\theta^2 S\pi^2 + 4\theta^2 S\pi \\
\frac{dD_2}{dp} &= R_2 S(2p + 2\pi - 4p\pi + (-2+2p)\pi^2).
\end{aligned}$$

Lastly,

$$\begin{aligned}
\frac{d^2V}{d\pi^2} &= \frac{d^2N_1}{d\pi^2}D_1^{-1} - 2\frac{dN_1}{d\pi}D_1^{-2}\frac{dD_1}{d\pi} + 2N_1D_1^{-3}\left(\frac{dD_1}{d\pi}\right)^2 - 2N_1D_1^{-2}R_1S(1-p)^2 + \\
&\quad \frac{d^2N_2}{d\pi^2}D_2^{-1} - 2\frac{dN_2}{d\pi}D_2^{-2}\frac{dD_2}{d\pi} + 2N_2D_2^{-3}\left(\frac{dD_2}{d\pi}\right)^2 - 2N_2D_2^{-2}R_2S(1-p)^2,
\end{aligned}$$

where

$$\begin{aligned}
\frac{dN_1}{d\pi} &= \theta(1-p) - 2\theta^2 S(1-p)^2\pi - 2\theta^2 Sp(1-p) \\
\frac{d^2N_1}{d\pi^2} &= -2\theta^2 S(1-p)^2 \\
\frac{dD_1}{d\pi} &= 2R_1 S(1-p)(p + (1-p)\pi) \\
\frac{dN_2}{d\pi} &= \theta^2(1-p) - 2\theta^2 S(1-p)^2\pi - 2\theta^2 Sp(1-p) \\
\frac{d^2N_2}{d\pi^2} &= -2\theta^2 S(1-p)^2 \\
\frac{dD_2}{d\pi} &= 2R_2 S(1-p)(p + (1-p)\pi).
\end{aligned}$$

Each of the above second derivatives is then evaluated at the expected values for θ_t, $S_{23,t}$, p_t, and π_t.

A.3. **Summary.** Thus equation (57), which is found by adding equations (58) and (60), yields an approximate theoretical variance. This is what is needed for determining sample sizes and making power calculations. One must put in assumed known parameter values, particularly the means and variances of θ_t, $S_{23,t}$, p_t, and π_t. `R` code has been written that calculates the theoretical variance approximation (Appendix D.1).

The quality of the approximation to the theoretical variance was evaluated using simulations. The simulation code (in `R` code) is listed in Appendix D.2. The results based on 30,000 simulations (example code also given in Appendix D.2) are summarized below; R_1=R_2=50,000 in each case and σ_θ was fixed at 0.1, and E[S_{23}]= 0.9 $\sigma_{S_{23}}$=0.15, E[p_3]=0.002, σ_{p_3}=0.0002, E[π]=0.0079, σ_π=0.00627.

θ	n	Theoretical Std Error	Simulated SE Std Error	Relative Error (%)
0.6	5	0.05117	0.05202	-1.7%
0.6	10	0.03618	0.03685	-1.8%
0.8	5	0.05408	0.05663	-4.7%
0.8	10	0.03824	0.03875	-1.3%
0.95	5	0.05646	0.05795	-2.6%
0.95	10	0.03992	0.04092	-2.5%

The theoretical standard error approximation appears to be biased low, with a negative bias from 1 and 5%.

Appendix B. DCC and Interior: Bootstrap estimate of variance of $\hat{\mu}_\theta$

To calculate confidence intervals or carry out hypothesis tests in practice, the standard error must be calculated using the data, not hypothesized values for the parameters. Estimates of unknown parameters can be substituted in some cases, but the calculations can be involved. A simpler approach is to use a bootstrap procedure. The general procedure for bootstrapping hierarchical models is described by Davison and Hinkley (1997, pp 100-102).

The gist of the bootstrap procedure is to mimic the original data generation procedure: first, generate samples of the "annual" studies, then generate observations within each generated study. To generate samples of the studies, the release pairs are resampled with replacement; this then reflects between release pair variation. To generate observations, samples are generated from trinomial distributions for recoveries using the observed recovery *rates* for each sampled group. Thus the recoveries within a group are resampled with replacement. An alternative is to sample without replacement, however, with large release numbers the results will be essentially equivalent.

Bootstrap code has been written in `R` (Appendix D.3) that is applicable to the Interior studies and the problem of estimating μ_θ. The quality of the bootstrap standard errors, and 95% confidence intervals based on $\pm$ 2 standard errors, was evaluated by simulation study. The bootstrap standard errors compared favorably to empirical standard errors and the confidence intervals were reasonably accurate for the values of μ_θ tried. For example, with θ=0.6, R_1=R_2=50,000, the median bootstrap standard error was 0.03808 compared to an empirical standard error of 0.03641. The percentage of bootstrap based 95% confidence intervals that included μ_θ was 95.16%, thus accurate coverage.

Appendix C. Interior: Sample size determination

There are two sample sizes that can be manipulated to achieve a specified level of precision (standard error) and these are n, the number of replications of paired releases, and R_1 and R_2, the number of fish released. The variance formula for $\hat{\mu}_\theta$ given in Appendix A can be used to solve for R_1, R_2, and n to achieve a specified standard error. For any given standard error there are multiple combinations of R_1, R_2, and n that will work. For simplicity assume that R_1=R_2=R and that the annual weights, w_t, are thus $1/n$. The variance formula (see equations (59) and (60)) can be written:

$$V[\hat{\mu}_\theta] \approx \frac{\sigma_\theta^2}{n} + \frac{1}{n}\left[V(\hat{\theta}_t) + 0.5\left(\left.\frac{d^2V}{d\theta_t^2}\right|_\mu \sigma_{\theta_t}^2 + \left.\frac{d^2V}{dS_{23,t}^2}\right|_\mu \sigma_{S_{23,t}}^2 + \left.\frac{d^2V}{dp_t^2}\right|_\mu \sigma_{p_t}^2 + \left.\frac{d^2V}{d\pi_t^2}\right|_\mu \sigma_{\pi_t}^2\right)\right] \tag{61}$$

The term $V(\hat{\theta}_t)$ and the second derivative terms each have release number, R, in the denominator and the variance formula can be rewritten as:

$$V[\hat{\mu}_\theta] \approx \frac{\sigma_\theta^2}{n} + \frac{1}{n}\left[\frac{A}{R} + 0.5\frac{B}{R}\right] \tag{62}$$

where A and B are constants involving the means and standard deviations of θ_t, $S_{23,t}$, p_t, and π_t (as in equation (61)). One can then solve for n given $V[\hat{\mu}_\theta]$ and R, or for R given n and $V[\hat{\mu}_\theta]$:

$$\begin{aligned} n &= \frac{\sigma_\theta^2 + \frac{1}{R}[A + 0.5B]}{V[\hat{\mu}_\theta]} \\ R &= \frac{A + 0.5B}{nV[\hat{\mu}_\theta] - \sigma_\theta^2}. \end{aligned}$$

`R` code has been written for both of these cases (Appendix D.5).

Appendix D. R code

D.1. **Interior: Theoretical variance calculation.** The R function, `theory.exp.var`, estimates the variance of $\hat{\mu_\theta}$ (the non-Bayesian estimate, see Equation (57)) based on number released, number of replicates (years of experimentation), and parameter values.

```
theory.exp.var <- function(R1,R2,n,mu.theta,sigma2.theta,mu.S,sigma2.S,
  mu.p,sigma2.p,mu.pi,sigma2.pi) {
  # Calculates variance of mu.theta.hat using double variance formula
  # Var() = E[V] + V[E]
  # - delta approximations used for conditional variance and unconditional
  #   expectation

  # Input parameters:
  #  R1, R2   = number released in each group (group 1 is the "upstream" grp)
  #  n        = number of years of experimentation
  #  mu.theta = expected value of theta, the ratio of survival rates
  # sigma2.theta = variance of theta
  #  mu.S        = expected value of S_{23}, survival from location 2 to 3
  # sigma2.S     = variance of S_{23}
  #  mu.p        = expected probability of capture at location 3
  # sigma2.p     = variance of p
  #  mu.pi       = expected probability of recovery (S_{34}*p_4) at loc. 4
  # sigma2.pi    = variance of pi

  theta <- mu.theta; S<-mu.S; p <- mu.p; opi <- mu.pi #saves typing

  N1 <- theta*p*(1-theta*S*p)+theta*(1-p)*opi*
        (1-theta*S*(1-p)*opi)-2*theta^2*p*S*(1-p)*opi

  D1 <- R1*S*(p+(1-p)*opi)^2

  N2 <- theta^2*p*(1-S*p)+theta^2*(1-p)*opi*
        (1-S*(1-p)*opi)-2*theta^2*p*S*(1-p)*opi

  D2 <- R2*S*(p+(1-p)*opi)^2

  #-------- 2nd Derivative wrt Theta -------------
  d2N1     <- -2*S*p^2 - 2*S*(1-p)^2*opi^2- 4*S*p*(1-p)*opi
  d2N2     <- 2*p-2*S*p^2+2*(1-p)*opi- 2*S*(1-p)^2*opi^2- 4*S*p*(1-p)*opi
  d2.theta <- d2N1*D1^(-1) + d2N2*D2^(-1)
```

```
  #-------- 2nd Derivative wrt S_{23} -------------
  d1N1     <- d1N2 <-
              -theta^2*p^2-theta^2*(1-p)^2*opi^2- 2*theta^2*p*(1-p)*opi
  d1D1     <- R1*(p+(1-p)*opi)^2
  d1D2     <- R2*(p+(1-p)*opi)^2
  d2.S23   <- -2*d1N1*D1^(-2)*d1D1 + 2*N1*D1^(-3)*d1D1^2 +
              -2*d1N2*D2^(-2)*d1D2 + 2*N2*D2^(-3)*d1D2^2

  #-------- 2nd Derivative wrt p -------------
  d1N1    <- theta - 2*theta^2*S*p - theta*opi -
              theta^2*S*(-2+2*p)*opi^2 - 2*theta^2*S*(1-2*p)*opi
  d1N2    <- theta^2 - 2*theta^2*S*p - theta^2*opi -
              theta^2*S*(-2+2*p)*opi^2 - 2*theta^2*S*(1-2*p)*opi
  d2N1    <- d2N2  <- -2*theta^2*S*(1+opi^2-2*opi)
  d1D1    <- R1*S*(2*p+2*opi-4*p*opi+(-2+2*p)*opi^2)
  d1D2    <- R2/R1*d1D1

  d2.p     <- (d2N1 * D1^(-1) - 2*d1N1*D1^(-2)*d1D1 +
               2*N1*D1^(-3)*d1D1^2 - N1*D1^(-2)*R1*S*(2-4*opi+2*opi^2))  +
              (d2N2 * D2^(-1) - 2*d1N2*D2^(-2)*d1D2 +
               2*N2*D2^(-3)*d1D2^2 - N2*D2^(-2)*R2*S*(2-4*opi+2*opi^2))

  #-------- 2nd Derivative wrt pi -------------
  d1N1     <- theta*(1-p)   - 2*theta^2*S*(1-p)^2*opi - 2*theta^2*S*p*(1-p)
  d1N2     <- theta^2*(1-p) - 2*theta^2*S*(1-p)^2*opi - 2*theta^2*S*p*(1-p)
  d2N1     <- d2N2 <- -2*theta^2*S*(1-p)^2
  d1D1     <- R1*S*2*(1-p)*(p+(1-p)*opi)
  d1D2     <- R2/R1*d1D1

  d2.pi     <- (d2N1*D1^(-1) - 2*d1N1*D1^(-2)*d1D1 + 2*N1*D1^(-3)*d1D1^2 -
                2*N1*D1^(-2)*R1*S*(1-p)^2) +
               (d2N2*D2^(-1) - 2*d1N2*D2^(-2)*d1D2 + 2*N2*D2^(-3)*d1D2^2 -
                2*N2*D2^(-2)*R2*S*(1-p)^2)

 #----output ----------
 out       <-  (N1/D1+N2/D2) +
                0.5*(d2.theta*sigma2.theta + d2.S23*sigma2.S +
                     d2.p*sigma2.p         + d2.pi*sigma2.pi)
 SE        <- sqrt((1/n)*(out + sigma2.theta))
 return(SE)
}}
```

D.2. **Interior: Simulation of hierarchical recovery model.** The `R` function, `two.grp.sim`, simulates the recoveries from paired releases for a specified number of years of study, `numyrs`. The other input parameters are the number of fish released in each group (`R1` and `R2`) and the expected values and standard deviations of the parameters, θ, S_{23}, p, and π.

```
#-----------------------------------------------------------------------
# --- Pgm to simulate the hierarchical processes of between year variation
# and within year variation in survival, capture, and then estimate
# expected ratio of survival probabilities (mu.theta)

two.grp.sim <- function(numyrs,R1,R2,mu.theta,sig.theta,mu.S23,sig.S23,
                  mu.p,sig.p,mu.pi,sig.pi) {

  temp <- alpha.beta(mu.theta,sig.theta)
  theta <- rbeta(numyrs,temp$alpha,temp$beta)

  temp <- alpha.beta(mu.S23,sig.S23)
  S23  <- rbeta(numyrs,temp$alpha,temp$beta)

  temp <- alpha.beta(mu.p,sig.p)
  p    <- rbeta(numyrs,temp$alpha,temp$beta)

  temp <- alpha.beta(mu.pi,sig.pi)
  pi.o <- rbeta(numyrs,temp$alpha,temp$beta)

  # recoveries from group 1
  y13 <- rbinom(numyrs,R1,theta*S23*p)
  y14 <- rbinom(numyrs,R1-y13,theta*S23*(1-p)*pi.o/(1-theta*S23*p))
  # recoveries from group 2
  y23 <- rbinom(numyrs,R2,S23*p)
  y24 <- rbinom(numyrs,R2-y23,S23*(1-p)*pi.o/(1-S23*p))

  theta.hat <- ((y13+y14)/R1)/((y23+y24)/R2)
  output <- list(theta.hat=theta.hat,y13=y13,y14=y14,y23=y23,y24=y24)
  return(output)
}
```

An example demonstrating use of `two.grp.sim`, along with output, is shown below.

```
two.grp.sim(numyrs=10,R1=60000,R2=75000,mu.theta=0.8,sig.theta=0.12,mu.S23=0.85,sig.S23=0.10,
    mu.p=0.002,sig.p=0.0003,mu.pi=0.008,sig.pi=0.005)
```

```
#$theta.hat
# [1] 0.8438486 0.8993476 0.7716049 0.7328767 0.7480971 0.9375000 0.4288026
# [8] 0.9076545 0.8216946 0.7474530
#
#$y13
# [1]  89  63 100  71  81 124  41  90 115  67
#
#$y14
# [1] 339 709 100 143 548  59  65 427 238 696
#
#$y23
# [1] 139  81 165 111 171 143 122  97 179 136
#
#$y24
# [1]  495  992  159  254  880  101  187  615  358 1140
```

Below is `R` code that uses `two.grp.sim` for 30,000 simulations, estimating θ in each case, calculates the empirical standard error of $\hat{\theta}$, and then compares this standard error to the theoretical approximation.

```
set.seed(201)
numsims <- 30000
numyrs.opt <- 10
numrel.opt <- 50000
mu.theta <- 0.6;     sig.theta <- 0.1
mu.S     <- 0.9;     sig.S23   <- 0.15
mu.p     <- 0.002;   sig.p     <- 0.0002
mu.pi    <- 0.0079;  sig.pi    <- 0.00627   #based on Ctland, DCC recoveries

mean.theta.vector  <- numeric(numsims)
for(i in 1:numsims) {
 out <- two.grp.sim(numyrs=numyrs.opt,R1=numrel.opt,R2=numrel.opt,
  mu.theta=mu.theta,sig.theta=sig.theta,mu.S=mu.S,sig.S23=sig.S23,
  mu.p=mu.p,sig.p=sig.p,mu.pi=mu.pi,sig.pi=sig.pi)$theta.hat
 mean.theta.vector[i] <- mean(out)
 }
empirical.se <- sd(mean.theta.vector)

#--- theoretical variance approximation
out <- theory.exp.var(R1=numrel.opt,R2=numrel.opt,n=numyrs.opt,
  mu.theta=mu.theta,sigma2.theta=sig.theta^2,mu.S=mu.S,sigma2.S=sig.S23^2,
  mu.p=mu.p,sigma2.p=sig.p^2,mu.pi=mu.pi,sigma2.pi=sig.pi^2)
```

```
#--- 95% confidence intervals, using theoretical SE
lb <- mean.theta.vector-2*out
ub <- mean.theta.vector+2*out
performance <- rep(FALSE,numsims)
performance[lb <= mu.theta & mu.theta <= ub] <- TRUE

#print output
cat("Empirical SE=",empirical.se,"\n",
    "Theoretical SE=",out,"rel err=",1-empirical.se/out,"\n",
    "CI coverage=",sum(performance)/numsims,"\n")

# Empirical SE= 0.03685179
# Theoretical SE= 0.03618268 rel err= -0.01849254
# CI coverage= 0.9508667
```

D.3. **Interior: Bootstrap estimate of variance of $\hat{\mu}_\theta$.** The `R` function, `two.grp.boot`, estimates the variance of $\hat{\mu}_\theta$ (the non-Bayesian estimate, see Equation 57 in Appendix A) using `B` bootstrap samples. Other inputs are number of release pairs (`numyrs`), number released from each group, and number of recoveries from each group. Conceptually, one can view locations 1, 2, 3, and 4 as a spatial sequence with 1 furthest upstream and 4 furthest downstream; `y13` is the number recovered from the first release group at "downstream" recovery location 3, below release location 2, and `y14` is the number recovered at downstream recovery location 4, below recovery location 4.

```
two.grp.boot <- function(B,numyrs,R1,R2,y13,y14,y23,y24,wts=NULL,wt.opt=FALSE) {
  #K. Newman, 3 October 2006
  # Modified 7 August 2007 to calculate weighted estimate
  #  Computes a bootstrap estimate of the SE of the estimated
  #    avg. ratio of upstream survival to downstream survival (mu.theta)
  #    given multiple years of paired release and recovery data.

  #    Uses a hierarchical bootstrap:
  #     (1) resample the release pairs (between year variation)
  #     (2) resample the recoveries (within year variation)

  #Not yet computationally efficient....
  mu.theta.star <- numeric(B)
  if(wt.opt) wts <- wts/sum(wts)  #scale to sum to 1.0
  for(b in 1:B) {
    #resample the pairs of release groups first
    n.star   <- sample(1:numyrs,numyrs,replace=TRUE)
    R1.star  <- R1[n.star]
    R2.star  <- R2[n.star]
    p13.star <- y13[n.star]/R1.star
    p14.star <- y14[n.star]/R1.star
    p23.star <- y23[n.star]/R2.star
    p24.star <- y24[n.star]/R2.star

    #next "resample" within each selected release group pairs

    # recoveries from group 1
    y13.star <- rbinom(numyrs,R1.star,p13.star)
    y14.star <- rbinom(numyrs,R1.star-y13.star,p14.star/(1-p13.star))
    # recoveries from group 2
    y23.star <- rbinom(numyrs,R2.star,p23.star)
    y24.star <- rbinom(numyrs,R2.star-y23.star,p24.star/(1-p23.star))
```

```
    theta.hat.star <- ((y13.star+y14.star)/R1.star)/
                      ((y23.star+y24.star)/R2.star)

    #Bootstrap estimate of mu.theta
    if(wt.opt) {
      mu.theta.star[b] <- sum(wts*theta.hat.star)
    } else {
     mu.theta.star[b] <- mean(theta.hat.star)
    }
  }
  boot.se <- sd(mu.theta.star)
  return(boot.se)
}
```

D.4. **DCC: Simulating effect of sample sizes on estimate of DCC effect.** The R code simulates the survival and recapture processes when the DCC is either open or closed and outputs a bootstrap estimate of the ratio of expected ratios of DCC closed to DCC open.

```
#DCC sample size determination
#  Based on underlying hierarchical model with multinomial dist'n
#  "True" parameter values based on results from Bayesian analysis
#  For specified b0 and b1 and var(theta)
#    DCC closed: for n/2 times (and R_1 = R_2)
#   (1) generate logit(theta_closed)
#   (2) generate r_{Ry -> CI}, r_{Ry -> Oc}
#   (3) generate observations
#    DCC open: for n/2 times (and R_1 = R_2)
#   (4) generate logit(theta_open)
#   (5) generate r_{Ry -> CI}, r_{Ry -> Oc}
#   (6) generate observations
#   then (7) estimate ratio of means
#   then bootstrap a SE for this ratio....
#    ..repeat the above

#WinBUGS results with last year deleted
b0 <- 0.83; b1 <- 2.29; sig2.theta   <- 7.44
mu.r.Ry.CI <- -6.98;    sig2.r.Ry.CI <- 0.39
mu.r.Ry.Oc <- -4.62;    sig2.r.Ry.Oc <- 0.97

R.Ct <- R.Ry <- 100000
num.reps.seq <- c(5,7,10,12); num.outer <- length(num.reps.seq)
numsims <- 100
ratio.matrix <- se.matrix <- matrix(NA,num.outer,numsims)
dimnames(ratio.matrix) <- dimnames(se.matrix) <- list(2*num.reps.seq,1:numsims)

for(rep in 1:num.outer) {
 num.reps.open <- num.reps.closed <- num.reps.seq[rep]
 print(c("Number of reps=",num.reps.open))
 for(i in 1:numsims) {
  #Simulating the gate-closed group
  theta.closed <- inv.logit(rnorm(num.reps.closed,b0+b1,sqrt(sig2.theta)))
  r.Ry.CI      <- inv.logit(rnorm(num.reps.closed,mu.r.Ry.CI, sqrt(sig2.r.Ry.CI)))
  r.Ry.Oc      <- inv.logit(rnorm(num.reps.closed,mu.r.Ry.Oc, sqrt(sig2.r.Ry.Oc)))
  y.Ct.CI.c    <- rbinom(num.reps.closed,R.Ct,theta.closed*r.Ry.CI)
  y.Ct.Oc.c    <- rbinom(num.reps.closed,R.Ct-y.Ct.CI.c,
                     theta.closed*r.Ry.Oc/(1-theta.closed*r.Ry.CI))
  y.Ry.CI.c    <- rbinom(num.reps.closed,R.Ry, r.Ry.CI)
```

```
y.Ry.Oc.c    <- rbinom(num.reps.closed,R.Ry-y.Ry.CI.c, r.Ry.Oc/(1-r.Ry.CI))
thetac.hat   <- ((y.Ct.CI.c+y.Ct.Oc.c)/R.Ct)/
                ((y.Ry.CI.c+y.Ry.Oc.c)/R.Ry)

#Now the gate-open group
theta.open   <- inv.logit(rnorm(num.reps.open,b0,sqrt(sig2.theta)))
r.Ry.CI      <- inv.logit(rnorm(num.reps.open,mu.r.Ry.CI, sqrt(sig2.r.Ry.CI)))
r.Ry.Oc      <- inv.logit(rnorm(num.reps.open,mu.r.Ry.Oc, sqrt(sig2.r.Ry.Oc)))
y.Ct.CI.o    <- rbinom(num.reps.open,R.Ct,theta.open*r.Ry.CI)
y.Ct.Oc.o    <- rbinom(num.reps.open,R.Ct-y.Ct.CI.c,
                   theta.open*r.Ry.Oc/(1-theta.open*r.Ry.CI))
y.Ry.CI.o    <- rbinom(num.reps.open,R.Ry, r.Ry.CI)
y.Ry.Oc.o    <- rbinom(num.reps.open,R.Ry-y.Ry.CI.c, r.Ry.Oc/(1-r.Ry.CI))
thetao.hat   <- ((y.Ct.CI.o+y.Ct.Oc.o)/R.Ct)/
                ((y.Ry.CI.o+y.Ry.Oc.o)/R.Ry)

ratio.pt.est <-  mean(thetao.hat)/mean(thetac.hat)
ratio.matrix[rep,i] <- ratio.pt.est

#--- bootstrap se for the ratio estimate
B <- 10000
ratio.boot <- numeric(B)

for(b in 1:B) {
    #resample the pairs of release groups first
    nc.star   <- sample(1:num.reps.closed,num.reps.closed,replace=TRUE)
    no.star   <- sample(1:num.reps.open,  num.reps.open,  replace=TRUE)

    p13c.star <- y.Ct.CI.c[nc.star]/R.Ct
    p14c.star <- y.Ct.Oc.c[nc.star]/R.Ct
    p23c.star <- y.Ry.CI.c[nc.star]/R.Ry
    p24c.star <- y.Ry.CI.c[nc.star]/R.Ry

    p13o.star <- y.Ct.CI.o[no.star]/R.Ct
    p14o.star <- y.Ct.Oc.o[no.star]/R.Ct
    p23o.star <- y.Ry.CI.o[no.star]/R.Ry
    p24o.star <- y.Ry.CI.o[no.star]/R.Ry

    #next "resample" within each selected release group pairs
    y13c.star <- rbinom(num.reps.closed,R.Ct,p13c.star)
    y14c.star <- rbinom(num.reps.closed,R.Ct-y13c.star,p14c.star/(1-p13c.star))
    y23c.star <- rbinom(num.reps.closed,R.Ry,p23c.star)
    y24c.star <- rbinom(num.reps.closed,R.Ry-y23c.star,p24c.star/(1-p23c.star))
    thetac.hat.star <- ((y13c.star+y14c.star)/R.Ct)/
```

```
                        ((y23c.star+y24c.star)/R.Ry)

      y13o.star <- rbinom(num.reps.open,R.Ct,p13o.star)
      y14o.star <- rbinom(num.reps.open,R.Ct-y13o.star,p14o.star/(1-p13o.star))
      y23o.star <- rbinom(num.reps.open,R.Ry,p23o.star)
      y24o.star <- rbinom(num.reps.open,R.Ry-y23o.star,p24o.star/(1-p23o.star))
      thetao.hat.star <- ((y13o.star+y14o.star)/R.Ct)/
                        ((y23o.star+y24o.star)/R.Ry)

      ratio.boot[b] <- mean(thetao.hat.star)/mean(thetac.hat.star)
    }
    boot.se <- sd(ratio.boot)
    se.matrix[rep,i] <- boot.se
    print(c("iter=",i,"pt est of ratio=",round(ratio.pt.est,2),"se =",round(boot.se,2)))
  }
}
```

D.5. **Interior: Sample size determination.** The `R` function, `sampsize.interior`, outputs either the release number `R` or the number of release pairs `n` required to achieve a specified standard error `targSE` for $\hat{\mu}_\theta$.

```
sampsize.interior <- function(nopt=TRUE,Ropt=FALSE, targSE,
   mu.theta,sigma2.theta,mu.S,sigma2.S,
   mu.p,sigma2.p,mu.pi,sigma2.pi) {
  # Sample size determination
  # Based on theory.exp.var() R function.

  #set nopt=TRUE and Ropt=R to achieve target SE
  #set nopt=n and Ropt=TRUE to achieve target SE

  if(nopt) R <- Ropt
  if(Ropt) n <- nopt
  R1 <- R2 <- R

  theta <- mu.theta; S<-mu.S; p <- mu.p; opi <- mu.pi #saves typing

  N1 <- theta*p*(1-theta*S*p)+theta*(1-p)*opi*
        (1-theta*S*(1-p)*opi)-2*theta^2*p*S*(1-p)*opi

  D1 <- R1*S*(p+(1-p)*opi)^2

  N2 <- theta^2*p*(1-S*p)+theta^2*(1-p)*opi*
        (1-S*(1-p)*opi)-2*theta^2*p*S*(1-p)*opi

  D2 <- R2*S*(p+(1-p)*opi)^2

  #-------- 2nd Derivative wrt Theta -------------
  d2N1     <- -2*S*p^2 - 2*S*(1-p)^2*opi^2- 4*S*p*(1-p)*opi
  d2N2     <- 2*p-2*S*p^2+2*(1-p)*opi- 2*S*(1-p)^2*opi^2- 4*S*p*(1-p)*opi
  d2.theta <- d2N1*D1^(-1) + d2N2*D2^(-1)

  #-------- 2nd Derivative wrt S_{23} -------------
  d1N1     <- d1N2 <-
              -theta^2*p^2-theta^2*(1-p)^2*opi^2- 2*theta^2*p*(1-p)*opi
  d1D1     <- R1*(p+(1-p)*opi)^2
  d1D2     <- R2*(p+(1-p)*opi)^2
  d2.S23   <- -2*d1N1*D1^(-2)*d1D1 + 2*N1*D1^(-3)*d1D1^2 +
              -2*d1N2*D2^(-2)*d1D2 + 2*N2*D2^(-3)*d1D2^2

  #-------- 2nd Derivative wrt p -------------
```

```
  d1N1    <- theta - 2*theta^2*S*p - theta*opi -
              theta^2*S*(-2+2*p)*opi^2 - 2*theta^2*S*(1-2*p)*opi
  d1N2    <- theta^2 - 2*theta^2*S*p - theta^2*opi -
              theta^2*S*(-2+2*p)*opi^2 - 2*theta^2*S*(1-2*p)*opi
  d2N1    <- d2N2  <- -2*theta^2*S*(1+opi^2-2*opi)
  d1D1    <- R1*S*(2*p+2*opi-4*p*opi+(-2+2*p)*opi^2)
  d1D2    <- R2/R1*d1D1

  d2.p     <- (d2N1 * D1^(-1) - 2*d1N1*D1^(-2)*d1D1 +
               2*N1*D1^(-3)*d1D1^2 - N1*D1^(-2)*R1*S*(2-4*opi+2*opi^2))  +
              (d2N2 * D2^(-1) - 2*d1N2*D2^(-2)*d1D2 +
               2*N2*D2^(-3)*d1D2^2 - N2*D2^(-2)*R2*S*(2-4*opi+2*opi^2))

  #-------- 2nd Derivative wrt pi -------------
  d1N1     <- theta*(1-p)   - 2*theta^2*S*(1-p)^2*opi - 2*theta^2*S*p*(1-p)
  d1N2     <- theta^2*(1-p) - 2*theta^2*S*(1-p)^2*opi - 2*theta^2*S*p*(1-p)
  d2N1     <- d2N2 <- -2*theta^2*S*(1-p)^2
  d1D1     <- R1*S*2*(1-p)*(p+(1-p)*opi)
  d1D2     <- R2/R1*d1D1

  d2.pi     <- (d2N1*D1^(-1) - 2*d1N1*D1^(-2)*d1D1 + 2*N1*D1^(-3)*d1D1^2 -
                2*N1*D1^(-2)*R1*S*(1-p)^2) +
               (d2N2*D2^(-1) - 2*d1N2*D2^(-2)*d1D2 + 2*N2*D2^(-3)*d1D2^2 -
                2*N2*D2^(-2)*R2*S*(1-p)^2)

 A       <-  R*(N1/D1+N2/D2)
 B       <-  R*(d2.theta*sigma2.theta + d2.S23*sigma2.S +
                     d2.p*sigma2.p    + d2.pi*sigma2.pi)

 if(nopt) {
  n <- (sigma2.theta+ (1/R)*(A+0.5*B))/targSE^2
  return(n)
  }
 else {
  R <- (A+0.5*B)/(n*targSE^2-sigma2.theta)
  return(R)
 }
}
```

Demonstration of usage:

```
mu.theta <- 0.8;     sig.theta <- 0.1
```

```
mu.S     <- 0.9;     sig.S23   <- 0.15
mu.p     <- 0.002;   sig.p     <- 0.0002
mu.pi    <- 0.0079;  sig.pi    <- 0.00627

sampsize(nopt=TRUE,Ropt=50000, targSE=0.05,
   mu.theta=mu.theta,sigma2.theta=sig.theta^2,
   mu.S=mu.S,sigma2.S=sig.S23^2,
   mu.p=mu.p,sigma2.p=sig.p^2,
   mu.pi=mu.pi,sigma2.pi=sig.pi^2)

#[1] 5.8491
```

Thus need 5.85 or 6 years of paired releases, each of size 50,000, to achieve a standard error of 0.05.

D.6. **DA 8: Simulating the effect of sample size on the precision of β_1.**

```
#--- Simulating hierarchical model and indirect fitting procedure
#  for Delta Action 8 experiments
#  and then calculating the Std Deviation of the estimates
b0    <- -0.4; b1 <- -0.57; sig.theta <- sqrt(0.79)
mu.rc <- -7.71;  sig.rc <- sqrt(0.1)
mu.ro <- -5.63;  sig.ro <- sqrt(0.64)

R.set <- c(50000, 100000, 150000); n.R <- length(R.set)
n.set <- c(15,20,25)     ; n.n <- length(n.set)
sd.mat.b1 <- mean.mat.b1 <- matrix(NA,n.R,n.n)
dimnames(sd.mat.b1) <- dimnames(mean.mat.b1) <-
         list(paste("R=",R.set),paste("n=",n.set))
numsims <- 1000
b1.vec  <- numeric(numsims)

inv.logit <- function(x) exp(x)/(1+exp(x))

for(i in 1:n.R) {
  R <- R.set[i]
  for(j in 1:n.n) {
    n <- n.set[j]
    cat("R=",R,"n=",n,"\n")
    for(k in 1: numsims) {
       #simulate parameters
       exports <- runif(n,1500,11000)
       std.exports <- (exports-6058)/3158
       temp    <- rnorm(n,b0+b1*std.exports,sig.theta)
       theta   <- inv.logit(temp)
       temp    <- rnorm(n,mu.rc,sig.rc)
       rc      <- inv.logit(temp)
       temp    <- rnorm(n,mu.ro,sig.ro)
       ro      <- inv.logit(temp)

       #simulate recoveries
       y.gs.ci <- rbinom(n,R,theta*rc)
       y.gs.oc <- rbinom(n,R-y.gs.ci,(theta*ro)/(1-theta*rc))
       y.ry.ci <- rbinom(n,R,rc)
       y.ry.oc <- rbinom(n,R-y.ry.ci,ro/(1-ro))

       #estimate theta's (divisions by R cancel)
       theta.hat <- (y.gs.ci+y.gs.oc)/(y.ry.ci+y.ry.oc)
```

```
      logit.theta.hat <- logit(theta.hat)
      miss <- is.na(logit.theta.hat) | is.infinite(logit.theta.hat)

      #regress theta.hats on exports
      temp <- lm(logit.theta.hat[!miss] ~ std.exports[!miss])
      b1.vec[k] <- coef(temp)[[2]]
    }
  sd.mat.b1[i,j] <- sd(b1.vec,na.rm=TRUE)
  mean.mat.b1[i,j] <- mean(b1.vec,na.rm=TRUE)
  }
}
```

D.7. **VAMP: Simulating effect of sample size on precision of parameter estimates.**

```
#--- Simulating hierarchical model and indirect fitting procedure
#  for VAMP experiments and then calculating the IQR of the estimates

numsims <- 10000

# Utility function
iqr <- function(x) {
 out <- diff(quantile(x,prob=c(0.25,0.75),na.rm=TRUE))
 return(out)
}

# Durham Ferry to Mossdale Section: function of flow
b0    <- -2.5 ; b1 <- 1.0; sig.df.md <- 1/sqrt(0.1)

# Mossdale to Dos Reis Section: function of flow, HORB, exports*(1-HORB)
g0 <- -1.5;  g1 <- 0.32; g2 <- 5;  g4 <- -1.4; sig.md.dr <- 1/sqrt(0.14)

# Dos Reis to Jersey Point Section: function of flow, HORB, exports
xi0   <- -1.5; xi1 <- 0.71; xi2 <- 5; xi3 <- -0.5; sig.dr.jp <- 1/sqrt(0.79)

# Jersey Point to Antioch, Chipps Island, and the Ocean
mu.jp.ant <- -6.34; sig.jp.ant <- 1/sqrt(2.4)
mu.jp.ci  <- -6.48; sig.jp.ci  <- 1/sqrt(12.4)
mu.jp.oc  <- -4.61; sig.jp.oc  <- 1/sqrt(0.7)

R.set <- c(50000, 100000, 150000); n.R <- length(R.set)
n.set <- seq(15,25,by=5)     ; n.n <- length(n.set)

iqr.mat.b1 <- median.mat.b1 <- matrix(NA,n.R,n.n)
iqr.mat.g1 <- median.mat.g1 <- iqr.mat.g2 <- median.mat.g2 <-
iqr.mat.g4 <- median.mat.g4 <- matrix(NA,n.R,n.n)
iqr.mat.xi1 <- median.mat.xi1 <- iqr.mat.xi2 <- median.mat.xi2 <- iqr.mat.xi3 <-
    median.mat.xi3 <- matrix(NA,n.R,n.n)

dimnames(iqr.mat.b1)  <- dimnames(median.mat.b1)  <-
dimnames(iqr.mat.g1)  <- dimnames(median.mat.g1)  <-
dimnames(iqr.mat.g2)  <- dimnames(median.mat.g2)  <-
dimnames(iqr.mat.g4)  <- dimnames(median.mat.g4)  <-
dimnames(iqr.mat.xi1) <- dimnames(median.mat.xi1) <-
dimnames(iqr.mat.xi2) <- dimnames(median.mat.xi2) <-
dimnames(iqr.mat.xi3) <- dimnames(median.mat.xi3) <-
```

```
        list(paste("R=",R.set),paste("n=",n.set))

b1.vec  <- g1.vec <- g2.vec <- g4.vec <- xi1.vec <-
  xi2.vec <- xi3.vec <-  numeric(numsims)

for(i in 1:n.R) {
  R <- R.set[i]
  for(j in 1:n.n) {
    n <- n.set[j]
    cat("R=",R,"n=",n,"\n")
    for(k in 1: numsims) {
       #simulate parameters
       flow        <- rgamma(n,1.4,0.00013)
       std.flow    <- (flow-10400)/8800
       exports     <- rgamma(n,3.62,0.0016)
       std.exports <- (exports-2200)/1150
       HORB        <- numeric(n)
       barrier     <- rbinom(sum(flow<=7000),1,0.5)
       HORB[flow <= 7000] <- barrier

       temp    <- rnorm(n,b0+b1*std.flow,sig.df.md)
       df.md   <- inv.logit(temp)

       temp    <- rnorm(n,g0+g1*std.flow + g2*HORB +
                   g4*std.exports*(1-HORB), sig.md.dr)
       md.dr   <- inv.logit(temp)

       temp    <- rnorm(n,xi0+xi1*std.flow+xi2*HORB + xi3*std.exports, sig.dr.jp)
       dr.jp   <- inv.logit(temp)

       temp    <- rnorm(n,mu.jp.ant,sig.jp.ant)
       ra      <- inv.logit(temp)

       temp    <- rnorm(n,mu.jp.ci,sig.jp.ci)
       rc      <- inv.logit(temp)

       temp    <- rnorm(n,mu.jp.oc,sig.jp.oc)
       ro      <- inv.logit(temp)

       #simulate recoveries at Antioch, Chipps Island, and Ocean
       temp <- df.md*md.dr*dr.jp; p1 <- temp*ra; p2 <- temp*rc; p3 <- temp*ro
       y.df.ant <- rbinom(n,R,p1)
       y.df.ci  <- rbinom(n,R-y.df.ant,p2/(1-p1))
       y.df.oc  <- rbinom(n,R-y.df.ant-y.df.ci,p3/(1-p2-p3))
```

```
temp <- temp/df.md; p1 <- temp*ra; p2 <- temp*rc; p3 <- temp*ro
y.md.ant <- rbinom(n,R,p1)
y.md.ci  <- rbinom(n,R-y.md.ant,p2/(1-p1))
y.md.oc  <- rbinom(n,R-y.md.ant-y.md.ci,p3/(1-p1-p2))

temp <- temp/md.dr; p1 <- temp*ra; p2 <- temp*rc; p3 <- temp*ro
y.dr.ant <- rbinom(n,R,p1)
y.dr.ci  <- rbinom(n,R-y.dr.ant,p2/(1-p1))
y.dr.oc  <- rbinom(n,R-y.dr.ant-y.dr.ci,p3/(1-p1-p2))

y.jp.ant <- rbinom(n,R,ra)
y.jp.ci  <- rbinom(n,R,rc)
y.jp.oc  <- rbinom(n,R,ro)

#estimate theta's (divisions by R cancel)
theta.df.md <- (y.df.ant+y.df.ci+y.df.oc)/(y.md.ant+y.md.ci+y.md.oc)
theta.df.md[theta.df.md >= 1 | is.infinite(theta.df.md)] <- 0.999
theta.df.md[theta.df.md <= 0] <- 0.001
miss.df <- is.na(theta.df.md)
logit.theta.df.md <- logit(theta.df.md[!miss.df])

theta.md.dr <-  (y.md.ant+y.md.ci+y.md.oc)/(y.dr.ant+y.dr.ci+y.dr.oc)
theta.md.dr[theta.md.dr >= 1 | is.infinite(theta.md.dr)] <- 0.999
theta.md.dr[theta.md.dr <= 0] <- 0.001
miss.md <- is.na(theta.md.dr)
logit.theta.md.dr <- logit(theta.md.dr[!miss.md])

theta.dr.jp <- (y.dr.ant+y.dr.ci+y.dr.oc)/(y.jp.ant+y.jp.ci+y.jp.oc)
theta.dr.jp[theta.dr.jp >= 1 | is.infinite(theta.dr.jp)] <- 0.999
theta.dr.jp[theta.dr.jp <= 0] <- 0.001
miss.dr <- is.na(theta.dr.jp)
logit.theta.dr.jp <- logit(theta.dr.jp[!miss.dr])

#regress theta.hats
# survival from Durham Ferry to Mossdale
temp <- lm(logit.theta.df.md ~ std.flow[!miss.df])
b1.vec[k] <- coef(temp)[[2]]

# survival from Mossdale to Dos Reis
temp <- lm(logit.theta.md.dr ~ std.flow[!miss.md] +
           HORB[!miss.md] + (std.exports*(1-HORB))[!miss.md])
g1.vec[k] <- coef(temp)[[2]]
g2.vec[k] <- coef(temp)[[3]]
```

```
      g4.vec[k] <- coef(temp)[[4]]

      # survival from Dos Reis to Jersey Point
      temp <- lm(logit.theta.dr.jp ~ std.flow[!miss.dr] + HORB[!miss.dr] +
               std.exports[!miss.dr])
      xi1.vec[k]<- coef(temp)[[2]]
      xi2.vec[k]<- coef(temp)[[3]]
      xi3.vec[k]<- coef(temp)[[4]]

    }
  iqr.mat.b1[i,j]   <- iqr(b1.vec)
  median.mat.b1[i,j] <- median(b1.vec,na.rm=TRUE)
  iqr.mat.g1[i,j]   <- iqr(g1.vec)
  median.mat.g1[i,j] <- median(g1.vec,na.rm=TRUE)
  iqr.mat.g2[i,j]   <- iqr(g2.vec)
  median.mat.g2[i,j] <- median(g2.vec,na.rm=TRUE)
  iqr.mat.g4[i,j]   <- iqr(g4.vec)
  median.mat.g4[i,j] <- median(g4.vec,na.rm=TRUE)

  iqr.mat.xi1[i,j]  <- iqr(xi1.vec)
  median.mat.xi1[i,j]<- median(xi1.vec,na.rm=TRUE)
  iqr.mat.xi2[i,j]  <- iqr(xi2.vec)
  median.mat.xi2[i,j]<- median(xi2.vec,na.rm=TRUE)
  iqr.mat.xi3[i,j]  <- iqr(xi3.vec)
  median.mat.xi3[i,j]<- median(xi3.vec,na.rm=TRUE)
  }
}
```

Appendix E. WinBUGS code with R interface

E.1. **DCC hierarchical model.** Negative binomial distribution for Level 1, logit transformation of θ for Level 2, gamma priors for precision for Level 3.

R code frontend to WinBUGS

```
library(R2WinBUGS)

input.data <- list(
 R.Ct     = c(96706, 100302, 107249, 106901, 62604, 100626,
         98866, 100919, 102480, 99827, 51211, 50659, 90720),
 R.Ryde=c(92693,    51103,   52741,  53961,  59998, 107161, 101320,
         51008,   53238, 53942, 51046, 50601, 51134),
 y.ct.ci = c(89, 73, 151, 37, 37, 38, 39, 43, 145, 5, 46, 19, 21),
 y.ct.oc = c(428, 1981, 1188, 1037, 399, 313, 1692, 1434, 936, 70, 240, 41, 84),
 y.ry.ci = c(96, 47, 104, 44, 38, 89, 75, 47, 145, 38, 58, 26, 8),
 y.ry.oc = c(368, 1607, 1076, 252, 268, 926, 1979, 1039, 1324, 285, 417, 82, 10),
 gate.pos=c(1,1,1,1,0,0,0,0,0,0,0,0,0), n=13)
n  <- input.data$n

init.val.generator <- function(n) {
   eps.theta   <- rnorm(n,0,0.1); eps.rc      <- rnorm(n,0,0.1)
   eps.ro      <- rnorm(n,0,0.1); sigma.theta <- runif(1,0,20)
   sigma.rc    <- runif(1,0,20);  sigma.ro    <- runif(1,0,20)
   b0          <- rnorm(1,-9,1);  b1          <- rnorm(1,-2,1)
   mu.rc       <- rnorm(1,-1,0.5);mu.ro       <- rnorm(1,-1,0.5)
   k.ci        <- sample(1:100,1);k.oc        <- sample(1:100,1)

   out <- list( b0 = b0,b1=b1,mu.rc=mu.rc, mu.ro= mu.ro,
     k.ci=k.ci,k.oc=k.oc)

   return(out)
}

init.values <- list(init.val.generator(n),
        init.val.generator(n), init.val.generator(n))

params <- c("b0","b1","mu.rc","mu.ro","sigma.theta","sigma.rc","sigma.ro",
    "k.ci","k.oc")

out.DCC.negbin <- bugs(data=input.data, inits=init.values,
  parameters.to.save=params, model.file=
  "C:/Documents and Settings/Ken Newman/Desktop/CalFed_Pat/Model_DCC_NegBin.txt",
 n.chains=3, n.iter=50000, n.burnin=10000,n.thin=10,debug=TRUE)
```

WinBUGS model code

```
# Code for DCC analysis of gate position effect on Courtland
#    releases'recovery rate (relative to Ryde releases) that are later recovered at
#    Chipps Island, and in the Ocean fisheries.

model {

    #Priors
       b0          ~ dnorm(0,1.0E-6); b1          ~ dnorm(0,1.0E-6)
       mu.rc       ~ dnorm(0,1.0E-6); mu.ro       ~ dnorm(0,1.0E-6)
       sigma.theta ~ dunif(0,20);     sigma.rc    ~ dunif(0,20)
       sigma.ro    ~ dunif(0,20)
       k.ci        ~ dunif(0,1000);   k.oc        ~ dunif(0,1000)
       tau.theta   <- 1/(sigma.theta*sigma.theta)
       tau.rc      <- 1/(sigma.rc*sigma.rc)
       tau.ro      <- 1/(sigma.ro*sigma.ro)

    for(i in 1:n) {

      # random effects
      eps.theta[i]      ~ dnorm(0.0, tau.theta)
      eps.rc[i]         ~ dnorm(0.0, tau.rc)
      eps.ro[i]         ~ dnorm(0.0, tau.ro)

     # rc = recovery probability at Chipps Island
     # ro = recovery probability in Ocean fisheries
     # theta is the ratio of Courtland survival probability to Ryde survival probability
      log(theta[i])      <- b0 + b1*gate.pos[i] + eps.theta[i]
      logit(rc[i])       <- mu.rc + eps.rc[i]
      logit(ro[i])       <- mu.ro + eps.ro[i]

      p.ct.ci[i]         <- k.ci/(R.Ct[i]*theta[i]*rc[i]+k.ci)
      p.ct.oc[i]         <- k.oc/(R.Ct[i]*theta[i]*ro[i]+k.oc)
      p.ry.ci[i]         <- k.ci/(R.Ry[i]*rc[i]+k.ci)
      p.ry.oc[i]         <- k.oc/(R.Ry[i]*ro[i]+k.oc)

      y.ct.ci[i]         ~ dnegbin(p.ct.ci[i],k.ci)
      y.ct.oc[i]         ~ dnegbin(p.ct.oc[i],k.oc)
      y.ry.ci[i]         ~ dnegbin(p.ry.ci[i],k.ci)
      y.ry.oc[i]         ~ dnegbin(p.ry.oc[i],k.oc)
   }
  }
```

E.2. **DCC hierarchical model with multivariate Level 2 distribution.** The `WinBUGS` model code is shown below.

```
model {

    #Priors
      b0          ~ dnorm(0, 1.0E-6)
      b1          ~ dnorm(0, 1.0E-6)
      mu.rc       ~ dnorm(0,1.0E-6)
      mu.ro       ~ dnorm(0,1.0E-6)
      Omega[1:3,1:3] ~ dwish(R[,],4)
      Sigma[1:3,1:3] <- inverse(Omega[,])


    for(i in 1:n) {

      #Mean structure
      mu[i,1] <- b0 + b1*gate.pos[i]
      mu[i,2] <- mu.rc
      mu[i,3] <- mu.ro

      #Correlated random effects
      Y[i,1:3] ~ dmnorm(mu[i,],Omega[,])

      theta[i] <- exp(Y[i,1])/(1+exp(Y[i,1]))
      rc[i]    <- exp(Y[i,2])/(1+exp(Y[i,2])+exp(Y[i,3]))
      ro[i]    <- exp(Y[i,3])/(1+exp(Y[i,2])+exp(Y[i,3]))


      p13[i]             <- theta[i] * rc[i]
      p14[i]             <- theta[i] * ro[i]
      condp14[i]         <- p14[i]/(1-p13[i])
      p23[i]             <- rc[i]
      p24[i]             <- ro[i]
      condp24[i]         <- p24[i]/(1-p23[i])

      #Two trinomial distributions for the recoveries
      y.ct.ci [i]        ~ dbin(p13[i], R.Ct[i])
      condR.Ct[i]        <- R.Ct[i]-y.ct.ci [i]
      y.ct.oc[i]         ~ dbin(condp14[i], condR.Ct[i])
      y.ry.ci[i]         ~ dbin(p23[i], R.Ryde[i])
      condR.Ryde[i]      <- R.Ryde[i]-y.ry.ci[i]
      y.ry.oc[i]         ~ dbin(condp24[i], condR.Ryde[i])

  }
}
```

E.3. **Interior hierarchical model.** Multinomial distribution for Level 1; logit (or log) transformation of θ for Level 2, uniform priors on σ for Level 3.

R code frontend to WinBUGS

```
 #  Georgiana Slough and Ryde releases

library(R2WinBUGS)

input.data <- list(
   R.gs= c( 33668, 31532, 31328, 33670, 61276, 66893, 69180,
                  68843, 65517, 64515, 77053, 55173, 68703, 72082,70414),
   R.ry= c(  34650, 30220, 31557, 30281, 46756, 49059, 48207, 48804, 53426,
                  49341, 52327, 49629,45981, 50397,51017),
   y.gs.ci= c(  5 ,4,2,5,2,18,12,12,3,21,18,1,5,10, 6),
   y.gs.oc= c( 80,11,101,146,7,240,173,150,43,151,248,68,50,NA, NA),
   y.ry.ci= c( 37,15 ,13 ,21,22,48,30,17,16,19,34,18,13,28, 23),
   y.ry.oc= c(292,29,266,240,41,167,182,156,128,161,520,147,128,NA, NA),
   n=15)

init.val.generator <- function(n) {
  eps.theta   <- rnorm(n,0,0.1); eps.rc      <- rnorm(n,0,0.1)
  eps.ro      <- rnorm(n,0,0.1); sigma.theta <- runif(1,1,2)
  sigma.rc    <- runif(1,1,2);   sigma.ro    <- runif(1,1,2)
  mu.theta    <- rnorm(1,-5,0.5);mu.rc       <- rnorm(1,-5,0.5)
  mu.ro       <- rnorm(1,-5,0.5)
  out <- list(eps.theta = eps.theta,eps.rc = eps.rc, eps.ro = eps.ro,
     mu.theta=mu.theta,mu.rc=mu.rc, mu.ro= mu.ro,
      sigma.theta = sigma.theta,sigma.rc = sigma.rc, sigma.ro = sigma.ro)
     # tau.theta = rgamma(1,0.1,0.1), tau.rc = rgamma(1,0.1,0.1), tau.ro  = rgamma(1,0.1,0.1))
  return(out)
}

init.values <- list(init.val.generator(n),
   init.val.generator(n), init.val.generator(n))
params <- c("mu.theta","mu.rc","mu.ro","sigma.theta","sigma.rc","sigma.ro")

out.int.multinom <- bugs(data=input.data, inits=init.values,
  parameters.to.save=params, model.file=
  "C:/Documents and Settings/Ken Newman/Desktop/CalFed_Pat/Model_Interior_Multinomial.txt",
 n.chains=3, n.iter=100000, n.burnin=50000,n.thin=1,debug=TRUE)
```

WinBUGS model code

```
model {
    #Priors for the Parameters in the logistic models
      mu.theta    ~ dnorm(0,1.0E-6)
      mu.rc       ~ dnorm(0,1.0E-6)
      mu.ro       ~ dnorm(0,1.0E-6)
      sigma.theta ~ dunif(0,20)
      sigma.rc    ~ dunif(0,20)
      sigma.ro    ~ dunif(0,20)
      tau.theta   <- 1/(sigma.theta*sigma.theta)
      tau.rc      <- 1/(sigma.rc*sigma.rc)
      tau.ro      <- 1/(sigma.ro*sigma.ro)

   for(i in 1:n) {
      eps.theta[i]     ~ dnorm(0.0, tau.theta)
      eps.rc[i]        ~ dnorm(0.0, tau.rc)
      eps.ro[i]        ~ dnorm(0.0, tau.ro)
      #logit(theta[i])     <- mu.theta + eps.theta[i]
      log(theta[i])     <- mu.theta + eps.theta[i]
      logit(rc[i])      <- mu.rc + eps.rc[i]
      logit(ro[i])      <- mu.ro + eps.ro[i]

      r.gs.ci[i]        <- theta[i] * rc[i]
      r.gs.oc[i]        <- theta[i] * ro[i]
      cond.gs.ro.rc[i]  <- r.gs.oc[i]/(1-r.gs.ci[i])
      cond.ro.rc[i]     <- ro[i]/(1-rc[i])
    }

   for(i in 1:(n-2)) {
      #Two trinomial distributions for the recoveries
      y.gs.ci[i]        ~ dbin(r.gs.ci[i], R.gs[i])
      cond.R.gs[i]      <- R.gs[i]-y.gs.ci[i]
      y.gs.oc[i]        ~ dbin(cond.gs.ro.rc[i], cond.R.gs[i])

      y.ry.ci[i]        ~ dbin(rc[i], R.ry[i])
      cond.R.ry[i]      <- R.ry[i]-y.ry.ci[i]
      y.ry.oc[i]        ~ dbin(cond.ro.rc[i], cond.R.ry[i])
  }

 #handling the missing ocean data in the last year
 for(i in (n-1):n) {
   y.gs.ci[i]        ~ dbin(r.gs.ci[i], R.gs[i])
   y.ry.ci[i]        ~ dbin(rc[i], R.ry[i])
 }
}
```

E.4. **DA 8 hierarchical model.** Multinomial distribution for Level 1; logit (or log) transformation of θ for Level 2; gamma priors for precision (or uniform for σ's) for Level 3.

R code frontend to WinBUGS

```
# Code for DA 8 analysis of exports effects on Georgiana Slough releases
#   that are later recovered Chipps Island, and in the Ocean fisheries.

library(R2WinBUGS)

exports.raw <- c(10434,5988,10403,9523,10570,3887,1868,1984,3237,4010,7789,5007,4016,6092,10837)
exports <- as.vector(scale(exports.raw))

input.data <- list(
   R.gs= c( 33668, 31532, 31328, 33670, 61276, 66893, 69180,
                  68843, 65517, 64515, 77053, 55173, 68703, 72082,70414),
   R.ry= c(  34650, 30220, 31557, 30281, 46756, 49059, 48207, 48804, 53426,
                  49341, 52327, 49629,45981, 50397,51017),
   y.gs.ci= c(  5 ,4,2,5,2,18,12,12,3,21,18,1,5,10, 6),
   y.gs.oc= c( 80,11,101,146,7,240,173,150,43,151,248,49,50,NA, NA),
   y.ry.ci= c( 37,15 ,13 ,21,22,48,30,17,16,19,34,18,13,28, 24),
   y.ry.oc= c(292,29,266,240,41,167,182,156,128,161,520,147,128,NA, NA),
   exports= exports, n=15)

n  <- input.data$n
init.val.generator <- function(n) {
 eps.theta <- rnorm(n,0,0.1); eps.rc    <- rnorm(n,0,0.1)
 eps.ro    <- rnorm(n,0,0.1)
 b0        <- rnorm(1,-9,1);  b1        <- rnorm(1,-2,1)
 mu.rc     <- rnorm(1,-1,0.5);mu.ro <- rnorm(1,-1,0.5)
 sigma.theta <- runif(1,0,20);sigma.rc <- runif(1,0,20);sigma.ro <- runif(1,0,20)
 out <- list(eps.theta = eps.theta,eps.rc = eps.rc, eps.ro = eps.ro,
     b0 = b0,b1=b1,mu.rc=mu.rc, mu.ro= mu.ro,
     sigma.theta = sigma.theta,sigma.rc = sigma.rc, sigma.ro = sigma.ro)
     #tau.theta = rgamma(1,0.1,0.1), tau.rc = rgamma(1,0.1,0.1), tau.ro  = rgamma(1,0.1,0.1))
 return(out)
}
init.values <- list(init.val.generator(n),init.val.generator(n),
   init.val.generator(n))

params <- c("b0","b1","mu.rc","mu.ro","sigma.theta","sigma.rc","sigma.ro","theta")

out.DA8.multinom <- bugs(data=input.data, inits=init.values,
  parameters.to.save=params, model.file=
  "C:/Documents and Settings/Ken Newman/Desktop/CalFed_Pat/Model_DA8_Multinomial.txt",
   n.chains=3, n.iter=200000, n.burnin=50000,n.thin=10,debug=TRUE)
```

WinBUGS model code

```
model {

    #Level 3: Priors for the Parameters in the logistic models
     b0          ~ dnorm(0, 1.0E-6)
     b1          ~ dnorm(0, 1.0E-6)
     mu.rc       ~ dnorm(0,1.0E-6)
     mu.ro       ~ dnorm(0,1.0E-6)
     sigma.theta ~ dunif(0,20);          tau.theta   <- 1/(sigma.theta*sigma.theta)
     sigma.rc    ~ dunif(0,20);          tau.rc      <- 1/(sigma.rc*sigma.rc)
     sigma.ro    ~ dunif(0,20);          tau.ro      <- 1/(sigma.ro*sigma.ro)

   #Level 2: Generating random effects and probabilities
   for(i in 1:n) {
      eps.theta[i]     ~ dnorm(0.0, tau.theta)
      eps.rc[i]        ~ dnorm(0.0, tau.rc)
      eps.ro[i]        ~ dnorm(0.0, tau.ro)

      log(theta[i])     <- b0 + b1*exports[i] + eps.theta[i]
      logit(rc[i])      <- mu.rc + eps.rc[i]
      logit(ro[i])      <- mu.ro + eps.ro[i]

      r.gs.ci[i]        <- theta[i] * rc[i]
      r.gs.oc[i]        <- theta[i] * ro[i]
      cond.gs.ro.rc[i]  <- r.gs.oc[i]/(1-r.gs.ci[i])
      cond.ro.rc[i]     <- ro[i]/(1-rc[i])
     }

   #Level 1: Obs'ns
   for(i in 1:(n-2)) {
      #Two trinomial distributions for the recoveries
      y.gs.ci[i]        ~ dbin(r.gs.ci[i], R.gs[i])
      cond.R.gs[i]      <- R.gs[i]-y.gs.ci[i]
      y.gs.oc[i]        ~ dbin(cond.gs.ro.rc[i], cond.R.gs[i])

      y.ry.ci[i]        ~ dbin(rc[i], R.ry[i])
      cond.R.ry[i]      <- R.ry[i]-y.ry.ci[i]
      y.ry.oc[i]        ~ dbin(cond.ro.rc[i], cond.R.ry[i])
   }

   #handling the missing ocean data in the last two years
   for(i in (n-1):n) {
     y.gs.ci[i]        ~ dbin(r.gs.ci[i], R.gs[i])
     y.ry.ci[i]        ~ dbin(rc[i], R.ry[i])
    }
 }
```

E.5. **VAMP hierarchical model.** Multinomial distribution for Level 1; logit transformation of θ for Level 2; uniform priors on σ's for Level 3.

R code frontend to WinBUGS

Creating input file.

```
#Flow at Durham Ferry: 2 day avg (day of and day after release) at Vernalis from DAYFLOW
DF.flow.raw <- c(rep(NA,22),6690,5665,4125,4135,3165,3356,3430,3370,3170,8250,8940,NA,NA)
DF.flow <- as.vector(scale(DF.flow.raw))
DF.flow[is.na(DF.flow)] <- -99

#Flow at Mossdale: 2 day avg (day of and day after release) at Vernalis from DAYFLOW
 MD.flow.raw <- c(2475,7140,2480,2500,1945,1400,1400,NA,1580, 3115,18700,21250,23100,6665,6565,NA,6135,
            NA, NA, 24950, 20250,  6905,
           6995, 5969, 4170,4145,3255,3356,3345,3370,3160,
         8195, 9085,  29350, 24650)
MD.flow <- as.vector(scale(MD.flow.raw))
MD.flow[is.na(MD.flow)] <- -99

#Exports at Mossdale: 2 day avg (day of and day after release)
  MD.exp.raw <-   c(5257,4096,7370,1797,10295,9400,3276,7610, 2087,1120,3707,3770, 3507,2040,1660,NA,2330,
         NA,NA, 805,1932,2683,
       2265,2238,1475,1566,1536,1523,1494,1481,1483,
        1961,2303,1538,6283)
MD.exp <- as.vector(scale(MD.exp.raw))
MD.exp[is.na(MD.exp)] <- -99

#Flow at Dos Reis: 2 Day average (day of and day after release) at Dos Reis
DR.flow.raw <- c(384,2492,391,677,-17,48,431,-49,
       466, 2891, 8267, 9316,  9545, 3296, 3113, 3113, 4709, 4709,4740,9645,
       8447, 3180,
       5918, 5062,   3630,    3610,2671,2814, 2904,   3017,  2831,
       3743, 4147, 10756, 10018)
DR.flow <-   as.vector( scale(DR.flow.raw))

#Exports at time of release at Dos Reis
DR.exp.raw <- c(5794,5626,5856,1798,
        10211.5,9597,2353,5990,1725,1598, 3684,3958,4209,1614,1629,1629,
       2329, 2329,2410,1722,1926,3105,
       2366, 2196,1482, 1495,1532,1507,1497,1479,1483,
       2293, 2300,1544,6046)
DR.exp <- as.vector(scale(DR.exp.raw))

#Flow at Upper Old River: median of 5 days, day of release + next 4 days
UOR.flow.raw <- c(1928,4842,2057,1522,2049,1060,934,796,1018,0,
```

```
     9192,9801,10066,3499,3378,3378,284,284,268,10356,9404,3429,
     296,560,687,654,549,570,297,299,297,
     3934,4529,11130,10423)
UOR.flow <- as.vector(scale(UOR.flow.raw))

#Temperatures at release
DR.temp <- c(21.1,20.0,21.1,21.7,20.6,20.0,20.0,15.6,NA,NA,13.9,17.2,18.3,NA,17.2,17.2,15.6,15.6,17.2,15.0,
        18.9,17.2,rep(NA,9),17.0,15.0,17.5,NA)
UOR.temp <- c(21.1,21.1,22.2,21.7,19.5,21.1,22.2,rep(NA,28))
JP.temp  <- c(rep(NA,3),20.0,17.8,17.2,20.0,17.2,17.8,17.2,15.6,NA,NA,16.7,17.8,18.9,17.2,17.8,19.4,17.2,18.9,
    17.2,17.8,17.2,20.0,22.8,18.0,17.5,16.5,14.0,21.4,18.0,19.0,19.0,19.5)
MD.temp <- c(rep(NA,8),17.2,15.6,13.9,16.7,17.2,15.6,17.8,NA,16.1,NA,NA,13.9,18.9,16.7,13.3,NA,19.4,21.1,13.9,
    17.5,15.2,15.7,17.0,NA,NA,18.0,19.5)
DF.temp <- c(rep(NA,22),13.9,17.2,21.7,18.9,15.0,17.0,15.0,16.5,15.5,16.0,14.9,NA,NA)

 #Stock origin
stock.origin <- c(rep("MRFF",4),rep("FRH",11),"MRFF","FRH",rep("MRFF",3),"FRH",rep("MRFF",14))
stock <- rep(1,length(stock.origin))
stock[stock.origin=="FRH"] <- 0

#Year of release
VAMP.Year <- c(85,86,87,89,89,90,90,91,94,94,rep(95,3),rep(96,3),rep(97,3),98,98,
  99,100,100,101,101,102,102,103,103,104,105,105,106,106)+1900

# Indicator variable for Head of Old River Barrier, 1=In  and 0=Out
HORB  <- c(rep(0,4),0, 0,0,0, 0,1, 0, 0,0, 0,  0, 0,1,1,1, 0, 0, 0,
            1, 1,1,1,1, 1, 1,1, 1,
            0, 0, 0, 0)

#proportion down Old River = 1-(San Joaquin/Vernalis);
# used some eq'n for 1985-1989, and used some model for 1990-2006
 p.OR <- c(0.81, 0.73, 0.90, 0.66,
        1.04, 1.19, 0.84, 1.26, 0.67, 0.11, 0.55, 0.58,0.59,0.53, 0.52,
        0.52,0.16,0.16,0.21,0.6,0.57,0.55,0.18,0.11,0.12,0.12,0.19,0.20,0.07,0.11,0.11,
        0.56, 0.55, 0.61, 0.59)

# 1989-1999,  MD, OR, DR, and JP releases; CI and Oc recoveries; 22 groups of releases
# 2000-2004, no Dos Reis releases, Antioch, Chipps Island, and Ocean recoveries, 9 groups of releases
# 2005-2006, no Ocean recoveries, 4 release groupings
n1 <- 22;   n2 <- 9;     n3 <- 4

 #-------------------------------------------------------------------------------------------------------------
 #Durham Ferry Release and Recovery Data
   R.DF  <- c(rep(NA,22),
       72094, 74001, 68192,  71744, 97318,  98082,  74377, 74491,   91867,
       93833, 91563, NA,NA)
```

```
  DF.index.2 <- 23:31; DF.index.3 <- 32:33
  y.DF   <- cbind(c(rep(NA,22), 27, 31, 76,29, 63,18, 6, 0, 2,6,  7,NA,NA),
                  c(rep(NA,22), 28, 22, 53, 9, 21,15, 3, 0, 3,12, 6,NA,NA),
                  c(rep(NA,22),693,162,366,92,270,58,19,10, 3,NA,NA,NA,NA),
                  c(rep(NA,22),521,279, 84, 39, 207,175,51,24,96,1527,844,NA,NA))

#-----------------------------------------------------------------------------------------------------------------
 #Mossdale Release and Recovery Data
  R.MD <- c(rep(NA,8),51084,50726,100969,102562,104125,100742,99656,  NA,
        48730, NA, NA, 77430,  33800, 74646,
        46111, NA, 44923, 48888,  50411,  48924,  49827, 48317,  73258,
        NA, NA, 48828, 73764)

  MD.index.1 <-  c(9:15,17,20:22); MD.index.2 <- c(23,25:31); MD.index.3<- 34:35
  y.MD    <-  cbind(c(rep(NA,22),30,NA,33,19, 42, 7, 4, 0, 1,NA,NA,9,0),
                    c(rep(NA,8), 0, 2,20, 13, 8, 2, 1, NA,10,NA,NA, 88, 7, 36,
                      18, NA,  31, 8, 13, 5, 5, 1, 3,NA,NA,9,2),
                    c(rep(NA,8),62,89,461,392,353,100,26,NA,329,NA,NA,157,13,395,
                      381, NA,232,52,145,40, 8, 5,2,rep(NA,4)),
                    c(rep(NA,8),705,0,2682,1883,1628,1084,1432,NA,226,NA,NA,48,
                     192,2940,457,NA,48,36,234,129,0,12,30,NA,NA,18,48))
#-----------------------------------------------------------------------------------------------------------------
 #Dos Reis Release and Recovery Data
  R.DR     = c(149968,95595,92612,76073,
    52962,105742,103533,102999,NA,NA, 50848,52097,  51665,
    NA,98638, 107961,49784,102431,46682,77180,47874, 49636,
    NA,NA,NA,NA,NA,NA,NA,NA,NA,
    69125, 68646,25463, NA)

  DR.index.1<-  c(1:8,11:13,15:22); DR.index.2 <- NULL;DR.index.3 <- 32:34
  y.DR <-  cbind(c(rep(NA,22),rep(NA,9),7,7,3,NA),
                c(94, 36, 79, 12,
                 11, 4, 4,17, NA,NA, 8, 21, 9, NA,3,10, 10, 16, 5, 93,17, 39,rep(NA,9),
                  3,6,7,NA),
                 c(NA, 2068, 1219, 78,
                 34,23,34,86,NA,NA,234,393,245,NA,67,58,259,348,90,145,56,376,rep(NA,9),
                  rep(NA,4)),
                 c(4450,2960,5469,428,2714,1766,150,7130,NA,NA,234,393,245,NA,0,0,125,394,
                    78,0,0,185,rep(NA,9),7,6,0,NA))
 #-----------------------------------------------------------------------------------------------------------------
 #Old River Release and Recovery Data
  R.OR     <- c(150048, 100181,92612, 74341,51972,106267,103595, rep(NA,28))
  OR.index.1 <- 1:7
  y.OR <- cbind(rep(NA,35),
                c(99,  21, 17, 4, 5, 2, 1,rep(NA,28)),
                c(NA,1139,500,16,38,14,11,rep(NA,28)),
                c(37299,62564,24019,1439,2916,2613,1346,rep(NA,28)))
```

```
#-----------------------------------------------------------------------------------------------------------------
 #Jersey Point Release and Recovery Data
 R.JP<- c(rep(NA,3),56233,
   56816, 52962, 50143, 52139,50689, 53810,50779, NA, NA,  50041, 50820,
  51737, 49815,    51540,  47208, 50050, 31091, 48907,
  51098, 49871, 49161, 51107,  48496,  46469,  24441, 25732,  22708,
  22767, 23231, 26113, 24757)


 JP.index.1<- c(4:11,14:22); JP.index.2 <- 23:31; JP.index.3 <- 32:35
 y.JP <- cbind(c(rep(NA,22),97,152, 329, 96,190, 75, 71, 35, 22,
                31,27,26,14),
               c(NA,NA,NA,56,53, 32, 56 ,94, 10, 16, 26,NA,NA, 25, 24, 39, 55, 27, 18,187,40, 59,
                65, 78, 111, 44, 83, 46, 57, 39, 25,
                32,38,58,44),
               c(NA,NA,NA,283,180,224,204,358,420,756,280,NA,NA,332,311,186,697,355,192,201,47,715,
                 1353,589,1031,581,951,597,263,415,117,
                 rep(NA,4)),
               c(NA,NA,NA,824,144,156,62,331,14,0,0,NA,NA,0,12,0,12,24,14,0,0,185,0,6,0,0,48,0,0,0,
                12,0,0,0,0))

#---Creating an input.data object for input to WinBUGS  ----------------------------------------
input.data <- list(
  n1=n1,n2=n2,n3=n3,
  R.DF = R.DF, n.DF.2=length(DF.index.2),n.DF.3=length(DF.index.3),
               DF.index.2=DF.index.2,DF.index.3=DF.index.3,
  y.DF.Ant=y.DF[,1],y.DF.CI=y.DF[,2],y.DF.Oc=y.DF[,3],

  R.MD = R.MD, n.MD.1 = length(MD.index.1),n.MD.2=length(MD.index.2),n.MD.3=length(MD.index.3),
         MD.index.1=MD.index.1,MD.index.2=MD.index.2,MD.index.3=MD.index.3,
         y.MD.Ant = y.MD[,1], y.MD.CI = y.MD[,2], y.MD.Oc = y.MD[,3],

  R.DR = R.DR, n.DR.1 = length(DR.index.1), n.DR.3 = length(DR.index.3),
    DR.index.1=DR.index.1,DR.index.3=DR.index.3,
   y.DR.Ant=y.DR[,1],y.DR.CI=y.DR[,2],y.DR.Oc=y.DR[,3],

  R.OR = R.OR, n.OR.1 = length(OR.index.1), OR.index.1=OR.index.1,
        y.OR.CI=y.OR[,2],y.OR.Oc=y.OR[,3],

  R.JP = R.JP, n.JP.1 = length(JP.index.1),n.JP.2=length(JP.index.2),n.JP.3=length(JP.index.3),
        JP.index.1=JP.index.1,JP.index.2=JP.index.2,JP.index.3=JP.index.3,
        y.JP.Ant=y.JP[,1],y.JP.CI=y.JP[,2],y.JP.Oc=y.JP[,3],
   MD.exp=MD.exp,
   DR.flow=DR.flow,
   DR.exp=DR.exp,
   # stock=stock
```

```
    #DF.flow=DF.flow
    #MD.flow=MD.flow,
    UOR.flow=UOR.flow
   )

 if(branch) {
  input.data[[length(input.data)+1]] <- p.OR
  names(input.data)[length(input.data)] <- "p.OR"
  input.data$p.OR[p.OR>1] <- 1
  input.data$p.OR[HORB==1] <- 0
  } else {
  input.data[[length(input.data)+1]] <- HORB
  names(input.data)[length(input.data)] <- "HORB"
  }
```

Sourcing the input file and calling `WinBUGS`.

```
library(R2WinBUGS)
#source the input data
branch <- TRUE
source("C:/Documents and Settings/Ken Newman/Desktop/CalFed_Pat/VAMP_inputdata.r")


 #---Creating a list of 3 lists of initial values for input to WinBUGS
n <- input.data$n1+input.data$n2+input.data$n3
init.val.generator <- function(n) {
  eps.df.md <- rnorm(n,0,1); eps.dr.jp <- rnorm(n,0,1); eps.or.jp <- rnorm(n,0,1)
  eps.jp.ant<- rnorm(n,0,0.1);eps.jp.ci<- rnorm(n,0,0.1);eps.jp.oc<- rnorm(n,0,0.1)
  b0 <- rnorm(1,-1,1)
  xi0<- rnorm(1,1,1); xi1 <- rnorm(1,0,0.1); xi2<- rnorm(1,0,0.1)  #xi3=rnorm(1,0,0.1)
  z0 <- rnorm(1,1,1); z1  <- rnorm(1,1,1);   z2 <- rnorm(1,1,1)
  mu.jp.ant <- rnorm(1,-4,1); mu.jp.ci <- rnorm(1,-4,1); mu.jp.oc <- rnorm(1,-4,1)
  sigma.df.md <- runif(1); sigma.dr.jp <- runif(1); sigma.or.jp <- runif(1)
  sigma.jp.ant <-runif(1); sigma.jp.ci <- runif(1); sigma.jp.oc <- runif(1)

  out <- list(eps.df.md = eps.df.md,eps.dr.jp = eps.dr.jp, eps.or.jp = eps.or.jp,
              eps.jp.ant=eps.jp.ant,eps.jp.ci = eps.jp.ci, eps.jp.oc = eps.jp.oc,
              b0 = b0,xi0=xi0,xi1=xi1,xi2=xi2,
              z0 = z0,z1=z1,z2=z2,
              mu.jp.ant=mu.jp.ant, mu.jp.ci=mu.jp.ci, mu.jp.oc=mu.jp.oc,
              sigma.df.md=sigma.df.md, sigma.dr.jp=sigma.dr.jp, sigma.or.jp=sigma.or.jp,
              sigma.jp.ant=sigma.jp.ant,sigma.jp.ci=sigma.jp.ci,sigma.jp.oc=sigma.jp.oc)
  return(out)
}

init.values <- list(init.val.generator(n),init.val.generator(n),
   init.val.generator(n))

#-----  Parameters for which MCMC samples are wanted
params <- c("b0","xi0", "xi1",  "xi2", #"xi3",
       "z0",  "z1", "z2",
      "mu.jp.ant","mu.jp.ci","mu.jp.oc",
      "sigma.df.md", "sigma.dr.jp","sigma.or.jp","sigma.jp.ant",
      "sigma.jp.ci", "sigma.jp.oc",
      "fit.MD.CI.1","fit.MD.Oc.1","fit.MD.CI.2","fit.MD.Oc.2",
      "fit.MD.CI.3","fit.MD.Oc.3")

#call to WinBUGS vi bugs() function
temp <- bugs(data=input.data, inits=init.values,
  parameters.to.save=params, model.file=
  "C:/Documents and Settings/Ken Newman/Desktop/CalFed_Pat/Model_VAMP_Branch.txt",
  n.chains=3, n.iter=250000, n.burnin=50000,n.thin=10,debug=TRUE)
```

WinBUGS model code

```
# Example Code for branching model used for VAMP data.
# Admittedly clunky use of conditional binomials instead of multinomial.

# Model:  DF->MD  = constant + noise
#         MD->DR  = constant
#         DR->JP  = f(Flow,Exports)+noise
#         OR->JP  = f(Flow,Exports)+noise

#*****************************************************************************************************
#Branching Model

model {

    #Priors for the Parameters in the logistic models
    # DF -> MD
    b0           ~ dnorm(0, 1.0E-6)

    # MD -> DR
    #g0           ~ dnorm(0, 1.0E-6)

    # DR -> JP
    xi0          ~ dnorm(0, 1.0E-6); xi1          ~ dnorm(0, 1.0E-6)
    xi2          ~ dnorm(0, 1.0E-6);

    # OR -> JP
    z0           ~ dnorm(0, 1.0E-6); z1          ~ dnorm(0, 1.0E-6)
    z2          ~ dnorm(0, 1.0E-6)

    # JP -> Ant, CI, Oc
    # chi        ~ dnorm(0, 1.0E-6)
    mu.jp.ant    ~ dnorm(0,1.0E-6);  mu.jp.ci     ~ dnorm(0,1.0E-6);
    mu.jp.oc     ~ dnorm(0,1.0E-6)

    sigma.df.md    ~ dunif(0,20); tau.df.md      <- 1/(sigma.df.md*sigma.df.md)
    #sigma.md.dr    ~ dunif(0,20); tau.md.dr      <- 1/(sigma.md.dr*sigma.md.dr)
    sigma.dr.jp    ~ dunif(0,20); tau.dr.jp      <- 1/(sigma.dr.jp*sigma.dr.jp)
    sigma.or.jp    ~ dunif(0,20); tau.or.jp      <- 1/(sigma.or.jp*sigma.or.jp)
    sigma.jp.ant   ~ dunif(0,20); tau.jp.ant     <- 1/(sigma.jp.ant*sigma.jp.ant)
    sigma.jp.ci    ~ dunif(0,20); tau.jp.ci      <- 1/(sigma.jp.ci*sigma.jp.ci)
    sigma.jp.oc    ~ dunif(0,20); tau.jp.oc      <- 1/(sigma.jp.oc*sigma.jp.oc)

    #-----------------------------------------------------------------------------------------
    # Random effects generation; some unnecessary: early Antioch and recent ocean
    for(i in 1:(n1+n2+n3)) {
      eps.df.md[i]  ~ dnorm(0.0, tau.df.md)
```

```
  eps.dr.jp[i]  ~ dnorm(0.0, tau.dr.jp)
  eps.jp.ant[i] ~ dnorm(0.0,tau.jp.ant)
  eps.jp.ci[i]  ~ dnorm(0.0, tau.jp.ci)
  eps.jp.oc[i]  ~ dnorm(0.0, tau.jp.oc)
  eps.or.jp[i]  ~ dnorm(0.0, tau.or.jp)

 #Mossdale to Dos Reis survival
 # logit(S.md.dr[i]) <- g0 + eps.md.dr[i]
 S.md.dr[i] <- 1.0

 #Old River to Jersey Point survival
 #logit(S.or.jp[i]) <-  z0+   eps.or.jp[i]
 #logit(S.or.jp[i]) <-  z0+ z1*UOR.flow[i] + eps.or.jp[i]
 #logit(S.or.jp[i]) <-  z0+ z2*MD.exp[i]+  eps.or.jp[i]
 logit(S.or.jp[i]) <-  z0+ z1*UOR.flow[i] + z2*MD.exp[i]+  eps.or.jp[i]

 #Dos Reis to Jersey Point survival
 #logit(S.dr.jp[i]) <- xi0 +   eps.dr.jp[i]
 #logit(S.dr.jp[i]) <- xi0 + xi1*DR.flow[i]  + eps.dr.jp[i]
 logit(S.dr.jp[i]) <- xi0 + xi1*DR.flow[i] + xi2*DR.exp[i] + eps.dr.jp[i]

 #Mossdale to Jersey Point survival: a combination of probabilities
 S.md.jp[i] <- p.OR[i]*S.or.jp[i] + (1-p.OR[i])*S.md.dr[i]*S.dr.jp[i]

 logit(r.jp.ant[i])   <- mu.jp.ant + eps.jp.ant[i]
 logit(r.jp.ci[i])    <- mu.jp.ci  + eps.jp.ci[i]
 logit(r.jp.oc[i])    <- mu.jp.oc  + eps.jp.oc[i]
 #logit(r.jp.ant[i])   <- mu.jp.ant + chi*stock[i] + eps.jp.ant[i]
 #logit(r.jp.ci[i])    <- mu.jp.ci  + chi*stock[i] + eps.jp.ci[i]
 #logit(r.jp.oc[i])    <- mu.jp.oc  + chi*stock[i] + eps.jp.oc[i]

}

#-----------------------------------------------------------------------------------------
# Modeling the  Recoveries

# 1985-1999,  MD, DR, and JP releases; CI and Oc recoveries; 18 groups  ----------------


# Mossdale recoveries for 1989-1999 (11 releases)
for(j in 1:n.MD.1) {

   p1.MD1[j]      <- S.md.jp[MD.index.1[j]]*r.jp.ci[MD.index.1[j]]
   p2.MD1[j]      <- p1.MD1[j]*r.jp.oc[MD.index.1[j]]/r.jp.ci[MD.index.1[j]]

   cond.p2.MD1[j] <- p2.MD1[j]/(1-p1.MD1[j])
```

```
      y.MD.CI[MD.index.1[j]]   ~ dbin(p1.MD1[j] , R.MD[MD.index.1[j]])
      temp1[j]                 <- R.MD[MD.index.1[j]]  - y.MD.CI[MD.index.1[j]]
      y.MD.Oc[MD.index.1[j]]   ~ dbin(cond.p2.MD1[j], temp1[j])

      fit.MD.CI.1[j] <- R.MD[MD.index.1[j]]*p1.MD1[j]
      fit.MD.Oc.1[j] <- R.MD[MD.index.1[j]]*p2.MD1[j]
    }

   #Dos Reis recoveries for 1985-1999 (15 releases)
   #1985 has only CI recs
   p1.DR1[1]                 <- S.dr.jp[DR.index.1[1]]*r.jp.ci[DR.index.1[1]]
   y.DR.CI[DR.index.1[1]]    ~ dbin(p1.DR1[1],R.DR[DR.index.1[1]])

   for(j in 2:n.DR.1) {
     p1.DR1[j]                 <- S.dr.jp[DR.index.1[j]]*r.jp.ci[DR.index.1[j]]
     p2.DR1[j]                 <- S.dr.jp[DR.index.1[j]]*r.jp.oc[DR.index.1[j]]
     cond.p2.DR1[j]            <- p2.DR1[j]/(1-p1.DR1[j])
     y.DR.CI[DR.index.1[j]]    ~ dbin(p1.DR1[j],R.DR[DR.index.1[j]])
     temp2[j]                  <- R.DR[DR.index.1[j]]-y.DR.CI[DR.index.1[j]]
     y.DR.Oc[DR.index.1[j]]    ~ dbin(cond.p2.DR1[j], temp2[j])
    }

   #Old River recoveries for 1985-1999 (7 releases)
   #1985 has only CI recs
   p1.OR1[1]               <- S.or.jp[OR.index.1[1]]*r.jp.ci[OR.index.1[1]]
   y.OR.CI[OR.index.1[1]]  ~ dbin(p1.OR1[1], R.OR[OR.index.1[1]])

   for(j in 2:n.OR.1) {
     p1.OR1[j]               <- S.or.jp[OR.index.1[j]]*r.jp.ci[OR.index.1[j]]
     p2.OR1[j]               <- S.or.jp[OR.index.1[j]]*r.jp.oc[OR.index.1[j]]
     cond.p2.OR1[j]          <- p2.OR1[j]/(1-p1.OR1[j])
     y.OR.CI[OR.index.1[j]]  ~ dbin(p1.OR1[j], R.OR[OR.index.1[j]])
     temp.2a[j]              <- R.OR[OR.index.1[j]]-y.OR.CI[OR.index.1[j]]
     y.OR.Oc[OR.index.1[j]]  ~ dbin(cond.p2.OR1[j],temp.2a[j])
   }

   #Jersey Point recoveries for 1985-1999 (16 releases)
   for(j in 1:n.JP.1) {
     cond.p2.JP1[j]          <- r.jp.oc[JP.index.1[j]]/(1-r.jp.ci[JP.index.1[j]])
     y.JP.CI[JP.index.1[j]]  ~ dbin(r.jp.ci[JP.index.1[j]],R.JP[JP.index.1[j]])
     temp3[j]                <- R.JP[JP.index.1[j]]-y.JP.CI[JP.index.1[j]]
     y.JP.Oc[JP.index.1[j]]  ~ dbin(cond.p2.JP1[j], temp3[j])
   }

 #------
 # -----   2000-2004,  DF, MD,  and JP releases; Antioch, CI and Oc recoveries; n2=9 groups ----
 # -----     loop from 19 to 27
```

```
#Durham Ferry recoveries for 2000-2004 (9 releases)
for(j in 1:n.DF.2) {
  logit(S.df.md.DF2[j])       <- b0 +  eps.df.md[DF.index.2[j]]
  p1.DF2[j]  <-    S.df.md.DF2[j]*S.md.jp[DF.index.2[j]]*r.jp.ant[DF.index.2[j]]
  p2.DF2[j]      <- p1.DF2[j]*r.jp.ci[DF.index.2[j]]/r.jp.ant[DF.index.2[j]]
  p3.DF2[j]      <- p1.DF2[j]*r.jp.oc[DF.index.2[j]]/r.jp.ant[DF.index.2[j]]

  cond.p2.DF2[j] <- p2.DF2[j]/(1-p1.DF2[j])
  cond.p3.DF2[j] <- p3.DF2[j]/(1-p1.DF2[j]-p2.DF2[j])

  y.DF.Ant[DF.index.2[j]]   ~ dbin(p1.DF2[j], R.DF[DF.index.2[j]])
  temp4[j]                  <- R.DF[DF.index.2[j]]  - y.DF.Ant[DF.index.2[j]]
  y.DF.CI[DF.index.2[j]]    ~ dbin(cond.p2.DF2[j], temp4[j])
  temp5[j]                  <- temp4[j] - y.DF.CI[DF.index.2[j]]
  y.DF.Oc[DF.index.2[j]]    ~ dbin(cond.p3.DF2[j],temp5[j])
}

#Mossdale recoveries for 2000-2004 (8 releases)
for(j in 1:n.MD.2) {
  p1.MD2[j]   <- S.md.jp[MD.index.2[j]]* r.jp.ci[MD.index.2[j]]
  p2.MD2[j]    <- p1.MD2[j]*r.jp.ci[MD.index.2[j]]/r.jp.ant[MD.index.2[j]]
  p3.MD2[j]    <- p1.MD2[j]*r.jp.oc[MD.index.2[j]]/r.jp.ant[MD.index.2[j]]

  cond.p2.MD2[j]            <- p2.MD2[j]/(1-p1.MD2[j])
  cond.p3.MD2[j]            <- p3.MD2[j]/(1-p1.MD2[j]-p2.MD2[j])

  y.MD.Ant[MD.index.2[j]]   ~ dbin(p1.MD2[j], R.MD[MD.index.2[j]])
  temp6[j]                  <- R.MD[MD.index.2[j]]  - y.MD.Ant[MD.index.2[j]]
  y.MD.CI[MD.index.2[j]]    ~ dbin(cond.p2.MD2[j], temp6[j])
  temp7[j]                  <- temp6[j] - y.MD.CI[MD.index.2[j]]
  y.MD.Oc[MD.index.2[j]]    ~ dbin(cond.p3.MD2[j],temp7[j])

  fit.MD.CI.2[j] <- R.MD[MD.index.2[j]]*p1.MD2[j]
  fit.MD.Oc.2[j] <- R.MD[MD.index.2[j]]*p2.MD2[j]
}


#Jersey Point recoveries for 2000-2004 (9 releases)
for(j in 1:n.JP.2) {
  cond.p2.JP2[j]            <- r.jp.ci[JP.index.2[j]]/(1-r.jp.ant[JP.index.2[j]])
  cond.p3.JP2[j]            <- r.jp.oc[JP.index.2[j]]/(1-r.jp.ant[JP.index.2[j]]-r.jp.ci[JP.index.2[j]])

  y.JP.Ant[JP.index.2[j]]   ~ dbin(r.jp.ant[JP.index.2[j]], R.JP[JP.index.2[j]])
  temp8[j]                  <- R.JP[JP.index.2[j]]  - y.JP.Ant[JP.index.2[j]]
  y.JP.CI[JP.index.2[j]]    ~ dbin(cond.p2.JP2[j], temp8[j])
  temp9[j]                  <- temp8 [j]-  y.JP.CI[JP.index.2[j]]
```

```
  y.JP.Oc[JP.index.2[j]]    ~ dbin(cond.p3.JP2[j], temp9[j])
 }

# -----
# -----   2005-2006,  DF, MD,  DR and JP releases; Antioch, CI  recoveries; n3=4 groups   -------

#Durham Ferry recoveries (2 releases)
for(j in 1:n.DF.3) {
  logit(S.df.md.DF3[j])   <- b0 +  eps.df.md[DF.index.3[j]]
  p1.DF3[j]               <-    S.df.md.DF3[j]* S.md.jp[DF.index.3[j]]*r.jp.ant[DF.index.3[j]]
  p2.DF3[j]               <- p1.DF3[j]*r.jp.ci[DF.index.3[j]]/r.jp.ant[DF.index.3[j]]

  cond.p2.DF3[j]            <- p2.DF3[j]/(1-p1.DF3[j])

  y.DF.Ant[DF.index.3[j]]   ~ dbin(p1.DF3[j],R.DF[DF.index.3[j]])
  temp10[j]                 <- R.DF[DF.index.3[j]]  - y.DF.Ant[DF.index.3[j]]
  y.DF.CI[DF.index.3[j]]    ~ dbin(cond.p2.DF3[j], temp10[j])
}

#Mossdale recoveries (2 releases)
for(j in 1:n.MD.3) {
  p1.MD3[j]   <- S.md.jp[MD.index.3[j]]*r.jp.ant[MD.index.3[j]]
  p2.MD3[j]   <- p1.MD3[j]*r.jp.ci[MD.index.3[j]]/r.jp.ant[MD.index.3[j]]

  cond.p2.MD3[j]   <- p2.MD3[j]/(1-p1.MD3[j] )

  y.MD.Ant[MD.index.3[j]]  ~ dbin(p1.MD3[j], R.MD[MD.index.3[j]])
  temp11[j]                <- R.MD[MD.index.3[j]]  - y.MD.Ant[MD.index.3[j]]
  y.MD.CI[MD.index.3[j]]   ~ dbin(cond.p2.MD3[j] , temp11[j])
 fit.MD.CI.3[j] <- R.MD[MD.index.3[j]]*p1.MD3[j]
  fit.MD.Oc.3[j] <- R.MD[MD.index.3[j]]*p2.MD3[j]

}

#Dos Reis recoveries (3 releases)
for(j in 1:n.DR.3) {
  p1.DR3[j]        <- S.dr.jp[DR.index.3[j]]*r.jp.ant[DR.index.3[j]]
  cond.p2.DR3[j]   <- S.dr.jp[DR.index.3[j]]*r.jp.ci[DR.index.3[j]]/(1-p1.DR3[j])

  y.DR.Ant[DR.index.3[j]]   ~ dbin(p1.DR3[j] , R.DR[DR.index.3[j]])
  temp12[j]                 <- R.DR[DR.index.3[j]]  - y.DR.Ant[DR.index.3[j]]
  y.DR.CI[DR.index.3[j]]    ~ dbin(cond.p2.DR3[j], temp12[j])
 }

#Jersey Point recoveries (4 releases)
for(j in 1:n.JP.3) {
  cond.p2.JP3[j] <- r.jp.ci[JP.index.3[j]]/(1-r.jp.ant[JP.index.3[j]])
```

```
      y.JP.Ant[JP.index.3[j]]  ~ dbin(r.jp.ant[JP.index.3[j]] ,R.JP[JP.index.3[j]])
      temp13[j]                <- R.JP[JP.index.3[j]]  - y.JP.Ant[JP.index.3[j]]
      y.JP.CI[JP.index.3[j]]   ~ dbin(cond.p2.JP3[j], temp13[j])
    }
}
```

Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta during the Winter of 2007-2008

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Abstract

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating from natal tributaries of the Sacramento River may use a number of possible migration routes to negotiate the Sacramento–San Joaquin River Delta (hereafter, "the Delta"), each of which may influence their probability of surviving. In a previous report, we developed and applied a mark-recapture model to data from acoustically tagged juvenile late-fall Chinook salmon that migrated through the Delta during the winter of 2007. This study was repeated during the winter of 2008, and this report presents findings from our second year of research. First, population-level survival through the Delta (S_{Delta}) during 2008 was substantially lower than in 2007, and we found little difference in S_{Delta} between releases. For releases in December 2007, $\hat{S}_{\text{Delta}}$ was 0.174 ($\hat{\text{S}}$E =0.031) and for January 2008, $\hat{S}_{\text{Delta}}$ was 0.195 ($\hat{\text{S}}$E = 0.034), compared to 0.351 and 0.543 for the same release groups in 2007. In contrast to our previous study, we found that the fraction of the population entering the interior Delta was similar between releases (26.7% for December, 31.1% for January), despite the Delta Cross Channel being open during December and closed during January. However, similar to previous findings, survival of fish migrating through the interior Delta was significantly less than survival probabilities for fish remaining in the Sacramento River. The ratio of survival for fish migrating through the interior Delta relative to the Sacramento River was ≤35.2% ($\hat{\text{S}}$E ≤0.11) during both releases. Thus, migration routes through the interior Delta reduced population-level survival by a similar magnitude during both releases because differences in survival between routes remained constant, as did the fraction of fish entering the interior Delta. Reach-specific survival rates in the Sacramento River (expressed as a function of reach length) were higher than reaches within other migration routes. These findings indicated that variation in route-specific survival was driven by consistent differences among migration routes, rather than by specific reaches within a route. Our studies during 2006 and 2007 highlight the variation in survival and migration route probabilities that can be expected in future research, but nonetheless, consistent patterns in route-specific survival and migration are beginning to emerge.

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Introduction

Many stocks of Chinook salmon (*Oncorhynchus tshawytscha*) in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998). In the Central Valley of California, the winter, spring, and fall/late fall runs of Chinook salmon are federally listed as endangered, threatened, and a "species of concern," respectively (NMFS 1997). Recently, due to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a Federal Disaster and closed the 2008 salmon fishery along the West Coast (NOAA 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Brandes and McLain 2001; Baker and Morhardt 2001; Williams 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento-San Joaquin River Delta (hereafter, "the Delta"), a complex network of natural and man-made river channels linking the Sacramento River with San Francisco Bay (Nichols et al. 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the mainstem Sacramento River leading directly into San Francisco Bay (see Route A in Figure 1). However, they may also migrate through longer secondary routes such as the interior Delta, the network of channels to the south of the mainstem Sacramento River (see Routes C and D in Figure 1).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the Delta. Inflow into the Delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the Delta, water distribution is affected by two water pumping projects in the Southern Delta (the State Water Project and Central Valley Project). These projects pump water from the Delta for agricultural and municipal uses and can export up to 65% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior. In addition to these human influences on water flow through the Delta, natural processes include seasonal rainfall

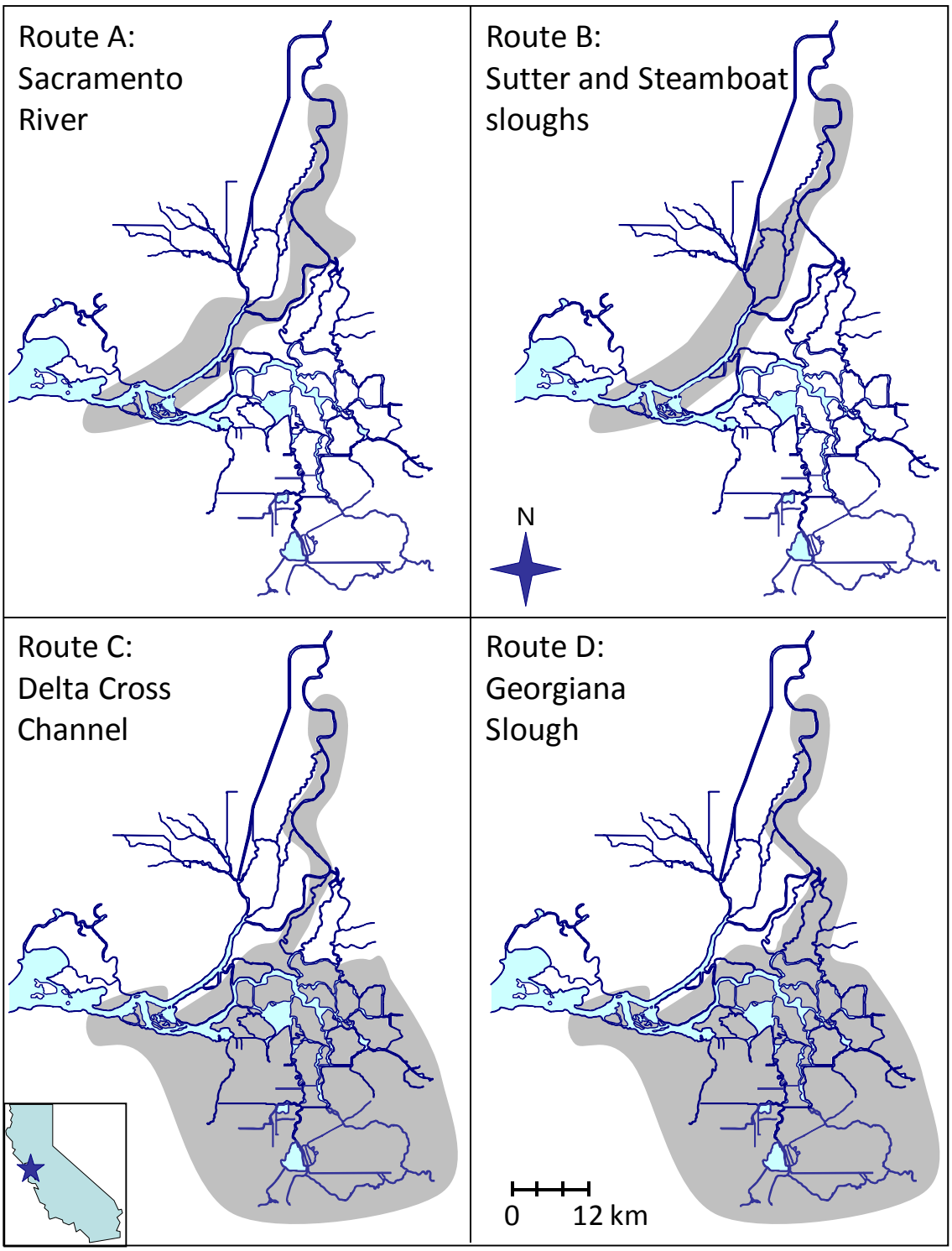

Figure 1.—Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. For routes C and D, the interior Delta is the large shaded region at in southern-most section of the migration route.

and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and bi-weekly time scales.

As juvenile salmon disperse among the complex channel network of the Delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. For example, juvenile salmon entering the interior Delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, which may decrease survival of fish using this migratory pathway (Kjelson et al.1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003; Kimmerer 2008; Newman 2008, Newman and Brandes in press). However, whether low survival through a particular route has a large effect on survival of the population will depend on the fraction of the population migrating through that route (Newman and Brandes, in press; Perry et al. 2008, in press). Thus, population-level survival rates of juvenile salmon migrating through the Delta will be driven by 1) the survival rates arising from biotic and abiotic processes unique to each migration route, and 2) the proportion of the population using each migration route.

Currently, there is limited understanding of how water management actions in the Delta affect population distribution and route-specific survival of juvenile salmon. In a previous study, we developed a mark-recapture model to estimate the route-specific components of population-level survival for acoustically tagged late-fall Chinook salmonsmolts migrating through the Delta during the winter of 2006/2007 (hereafter "2007", Perry et al. 2008, in press). Our study provided the first comprehensive estimates of route-specific survival through the Delta and the fraction of the population using each major migration route. Furthermore, we explicitly quantified the relative contribution of each migration route to population-level survival. As with other authors (Newman and Brandes in press), we found that survival through the interior Delta was lower than survival of fish using the Sacramento River. We also found that the proportion of the population entering the interior Delta differed between releases, which influenced population-level survival by shifting a fraction of the population from a low-survival migration route (the interior Delta) to a high-survival route (the Sacramento River). However, we also found that differences between releases in population-level survival were caused by changes in survival for given migration routes. Thus, variation in population-level survival was driven both by variation in movement among routes as well as survival within routes.

In this report, we estimate survival and migration route probabilities for acoustically tagged late-fall Chinook salmon migrating through the Delta during the winter of 2007/2008 (hereafter, "2008"). While design aspects of our previous study were maintained, we also incorporated a number of changes in study design based on insights from the first year of study. The most important limitation in our previous study was small total sample size, as well as small sample size for specific migration routes. For example, we found that up to 40% of fish migrated through Sutter and Steamboat Slough (Route B in Figure 1), which diverts fish around the two routes leading into the interior Delta (Routes C and D in Figure 1). This led to low sample size and poor precision of parameter estimates for routes through the interior Delta, which in turn led to low power to detect differences in survival among migration routes. Thus, we took two approaches to improve precision. First, the total sample size was tripled from 140 tagged fish in 2007 to 419 tagged fish in 2008. Second, because the interior Delta is an important migration route with many management concerns, we also released a subsample of fish directly into the interior Delta via Georgiana Slough (Route D in Figure 1).

We also added new telemetry stations which allowed us to better partition survival among specific reaches and to quantify movement among channels within major migration routes. For example, in our previous study we observed a substantial difference between releases in survival for Sutter and Steamboat sloughs. However, because this migration route encompassed numerous unmonitored river channels it was impossible to determine whether changes in route-specific survival were due to shifts in mortality within a particular reach, or occurred due to changes in survival over all reaches with this route. Therefore, we incorporated additional telemetry stations with this migration route (and others) to better partition within-route survival among specific reaches and channels.

We first report results for population-level survival through the Delta, route-specific survival through the Delta, and dispersal among migration routes, contrasting estimates from this study to those from 2007. Given more detailed information within migration routes, we then examined patterns in reach-specific survival to understand whether variation in route-specific survival through the Delta was driven by particular reaches within a route. Last, in addition to dispersal among the major migration routes shown in Figure 1, we explicitly accounted for movement among other channels within routes, and discuss the influence of these movements on population-level migration and survival dynamics.

Methods

Telemetry System

Telemetry stations were deployed to monitor movement of tagged fish among four major migration routes through the Delta (Figure 1): the mainstem Sacramento River (Route A), Steamboat and Sutter Slough (Route B), the interior Delta via the Delta Cross Channel (Route C), and the interior Delta via Georgiana Slough (Route D; Figure 1). Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 2). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco Ltd., Model VR2) that identified individual fish based on the unique pattern of acoustic pulses emitted from a transmitter. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route is denoted as A_i from the release site to the last telemetry station in the Delta at Chipps Island (A_9). Sutter and Steamboat sloughs (labeled B_i) diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_7. We deployed numerous telemetry stations within Sutter and Steamboat sloughs to better quantify survival and movement within this region, relative to our previous study in 2007 (Perry et al. 2008, in press). Specifically, Sutter Slough and Miner Slough form a northern route and stations along this route are labeled B_{11} (entrance to Sutter Slough), B_{12}, and B_{13} (Miner Slough; Figure 2). A southern route is formed by Steamboat Slough and these stations are labeled as B_{21}, B_{22}, and B_{23}. The entrance to the interior Delta via the Delta Cross Channel was labeled as C_1 where it diverges from the Sacramento River at the second river junction. Telemetry stations within Georgiana Slough and the interior Delta were labeled as D_i beginning where Georgiana Slough diverges from the mainstem Sacramento River at the second river junction (D_1) until the convergence of the interior Delta with the Sacramento River at D_7. Following this hierarchy, routes A, B, C, and D contained 8, 6, 1, and 7 telemetry stations, whereas in 2007, the same routes contained 7, 1, 2, and 3 telemetry stations. In addition, to quantify movement between the lower Sacramento River and the lower San Joaquin River, we included a telemetry station within Three Mile Slough (E_1) for a total of 23 telemetry stations within the Delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see **Model Development** section below).

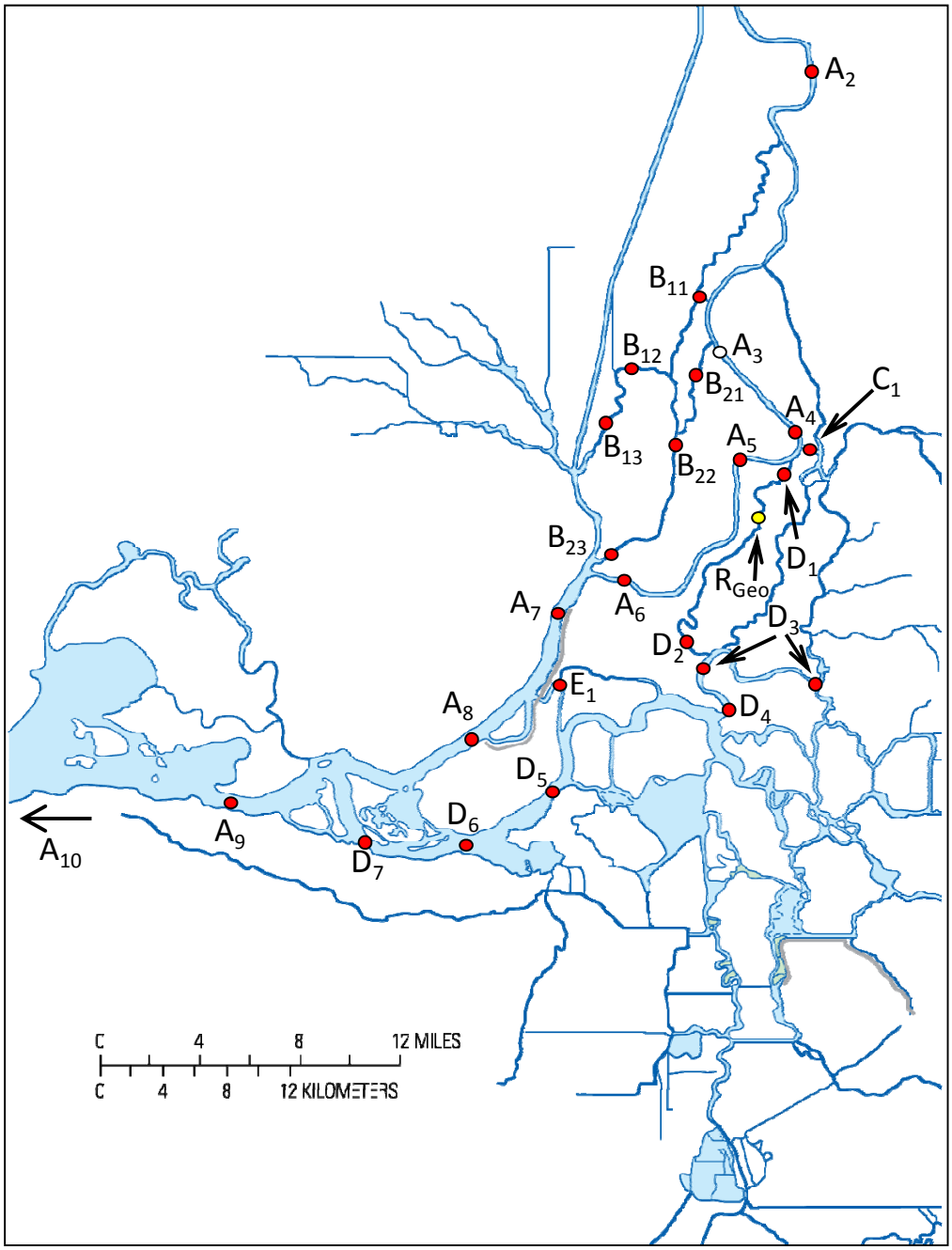

Figure 2.—Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2007/2008. Red-filled circles labeled as h_i show the location of telemetry station i with route h. The Delta extends from station A_2 at Freeport to station A_9 at Chipps Island. The first river junction occurs where Sutter Slough (B_{11}) and Steamboat Slough (B_{12}) diverge from the Sacramento River at location A_3. Location A_3 is denoted by an unfilled circle to indicate that a telemetry station was not implemented at this location during the winter of 2007/2008. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The two site labeled D_3 were treated as a single station in the mark-recapture model. The Sacramento release site was 19 river kilometers upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

With this configuration of telemetry stations, survival in the final reach (downstream of A_8 and D_7) is confounded with detection probability at the last telemetry station (Skalski et al. 2001). Therefore, to estimate survival to the terminus of the Delta and detection probability at the last station in the Delta (A_9), we formed one additional telemetry station by pooling detections from numerous stations downstream of A_9 in San Francisco Bay (Figure 2). Most of these detections occurred at telemetry stations mounted to bridges that provided nearly complete cross-sectional coverage of San Francisco Bay, but single-monitor stations at other locations were also included.

Fish Tagging and Release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (approximately 340 river kilometers upstream of the release sites near Sacramento, CA). We used a 1.6-g tag with a 70-d expected battery life (Vemco Ltd., Model V7-2L-R64K). Except for a minimum size criteria of 140-mm fork length, fish were randomly selected for tagging resulting in a mean fork length of 155.0 mm (SD = 10.2) and mean weight of 42.0 g (SD = 9.6). The tag weight represented 3.8% of the mean fish weight (range = 1.9%–5.4%). Fish were fasted for 24 h prior to surgery to ensure they were in a post-absorptive state. To surgically implant transmitters, fish were anaesthetized and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4-0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for seven days prior to release.

To release fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (20 km upstream of A_2) or Georgiana slough (about 5 km downstream from D_1; Figure 2). Fish were then transferred to perforated 19-L buckets (2 fish per bucket) and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Releases at Sacramento were conducted at roughly hourly intervals, whereas release at Georgiana Slough were conducted every other hour over a 24-h period. Each release was carried out over a 24-h period to distribute release times over the tidal and diel cycle. The total sample size for the study was 419 acoustically tagged fish, with 208 fish released in December when the

Delta Cross Channel was open and 211 fish released in January when the Delta Cross Channel was closed (Table 1). For the first release, 28% of the fish were released into Georgiana Slough, but this fraction was increased to 38% for the second release in anticipation that a lower proportion of the Sacramento release group would enter the interior Delta with the Delta Cross Channel closed (Table 1). Fish were released into Georgiana Slough two days later than the Sacramento release group to match release times in Georgiana Slough with the travel time of fish from Sacramento to Georgiana Slough (R. Perry, unpublished data).

Table 1.—Summary of release dates, locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2007/2008.

Release date	Release number	Release location	Sample size
4 December 2007	1	Sacramento	149
6 December 2007	1	Georgiana Slough	59
15 January 2008	2	Sacramento	130
17 January 2008	2	Georgiana Slough	81

Model Development

We expanded upon the model developed by Perry et al. (2008, in press) to explicitly quantify more detail in reach-specific survival of juvenile salmon through regions such as Sutter Slough, Steamboat Slough, and the interior Delta. As in our previous model, we estimate detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (ψ_{hl}). However, to capture complexity in movement of fish among different channels we also estimated joint survival-entrainment probabilities ($\phi_{hi,jk}$). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h = A, B, C, D; Figure 2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to i+1 within route h (i.e., to the next downstream telemetry station), conditional on surviving to station i (Figure 2 and 3). Route entrainment probabilities (ψ_{hl}) estimate the probability of a fish entering route h at junction l (l = 1, 2), conditional on fish migrating through junction l (Figures 2 and 3). Joint survival-entrainment probabilities ($\phi_{hi,jk}$) estimate the joint probability of surviving from site h_i to j_k and moving into route j. The $\phi_{hi,jk}$ parameters are estimated in reaches with river junctions that split into two channels, but where telemetry stations within each river channel are located some distance downstream the river junction. For example, fish passing station A_7 in the Sacramento River may enter Three Mile

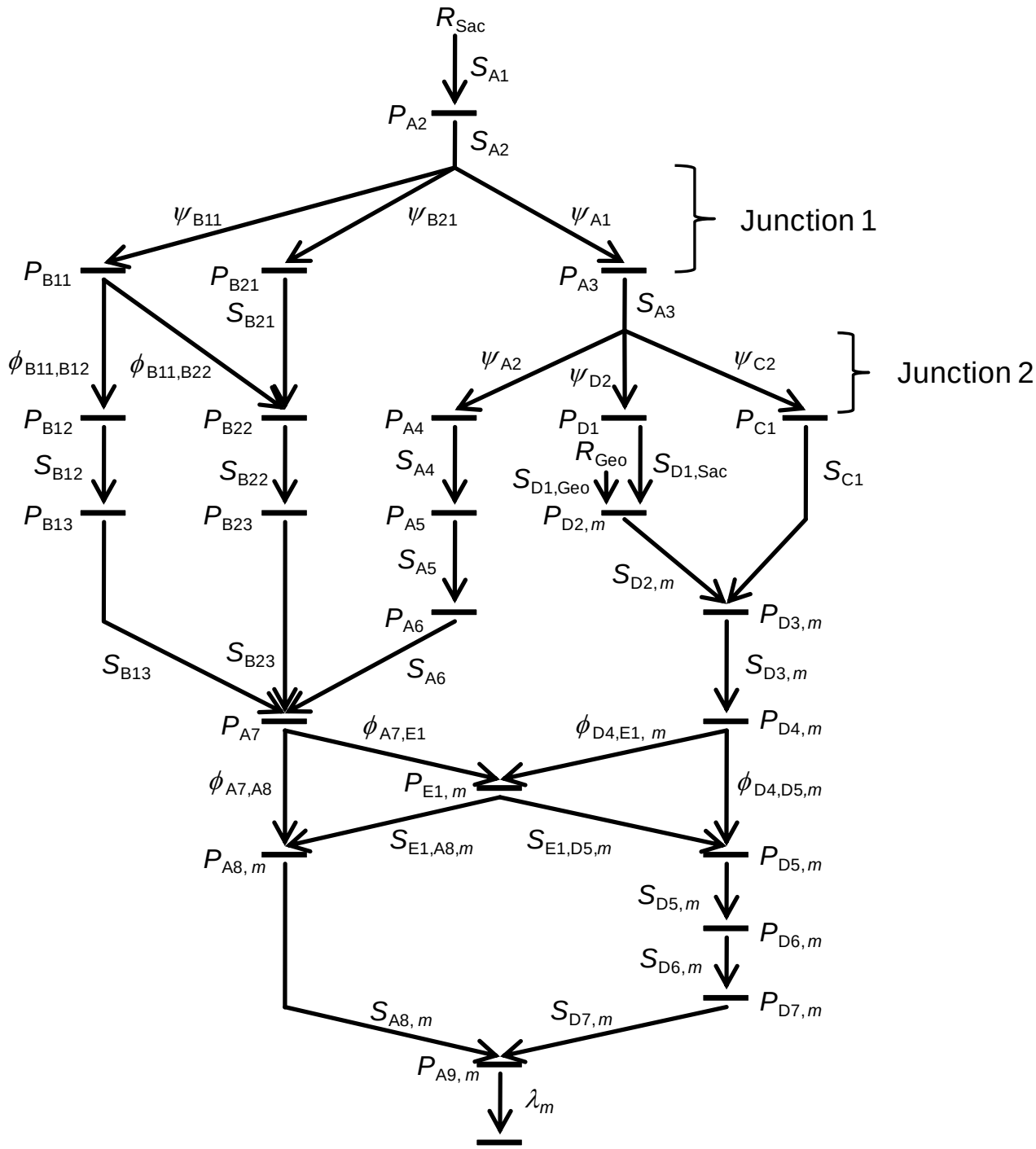

Figure 3.—Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (ψ_{hl}), and joint survival-entrainment ($\phi_{hi,\,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made December 2007 and January 2008. Release sites are denoted by R_m (m = Sac (Sacramento) and Geo (Georgiana Slough)), and parameters subscripted by m denote parameters which can be estimated separately for each release site.

Slough (E_1) or remain the Sacramento River for another 5.5 km below this junction to pass station A_8 (Figure 2). Thus $\phi_{A7,A8}$ is the joint probability of surviving from A_7 to its junction with Three Mile Slough, remaining in the Sacramento River at this junction, and then surviving from the junction to A_8.

In our 2007 study, telemetry arrays at the entrance to Sutter and Steamboat sloughs were pooled in the model to estimate a single route entrainment probability for both sloughs. For this study, however, telemetry stations within Sutter and Steamboat slough downstream of each entrance allowed us to estimate route entrainment probabilities separately for each slough (Figures 2 and 3). Thus, the parameter ψ_{B11} estimates the probability of being entrained into Sutter Slough at station B_{11} and ψ_{B21} estimates the probability of being entrained into Steamboat Slough at station B_{21}. Since route entrainment probabilities must sum to one at a given river junction, $1-\psi_{B11}-\psi_{B21}=\psi_{A1}$ is the probability of remaining in the Sacramento River at the first junction (Figures 2 and 3). As in 2007, the second junction was modeled as a three-branch junction where ψ_{A2}, ψ_{C2}, and $1-\psi_{A2}-\psi_{C2}=\psi_{D2}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2 (Figures 2 and 3).

Joint survival-entrainment probabilities were estimated for three reaches where 1) fish entering Sutter Slough (B_{11}) may subsequently continue down either Miner Slough (B_{12}) or Steamboat Slough (B_{22}), 2) fish entering the San Joaquin River at D_4 may subsequently exit this reach through either Three Mile Slough at E_1 or the San Joaquin River at B_5, and 3) fish passing A_7 in the Sacramento River may exit this reach at either E_1 or A_8 (Figures 2 and 3). Each of these reaches consist a single river channel, a junction where the channel splits, and then two separate channels through which fish migrate before being detected at telemetry stations in each channel. In these locations, interest may lie in estimating the proportion of fish entering each channel (i.e., the route entrainment probabilities, ψ_{hl}). However, when telemetry stations are located kilometers downstream of the river junction where fish enter one route or another, then estimates of ψ_{hl} may be biased if survival probabilities downstream of the junction differ between the two channels. However, the joint probability of surviving and migrating through a given channel (i.e., $\phi_{hi,jk}$) will remain unbiased in these circumstances. Although the $\phi_{hi,jk}$ parameters are difficult to interpret biologically, being the joint probability of entrainment and

survival, their sum yields the total reach survival. Thus, in the three reaches where $\phi_{hi,jk}$ parameters are estimated, $S_{\mathrm{B11}} = \phi_{\mathrm{B11,B12}} + \phi_{\mathrm{B11,B22}}$, $S_{A7} = \phi_{\mathrm{A7,E1}} + \phi_{\mathrm{A7,A8}}$, and $S_{D4} = \phi_{\mathrm{D4,E1}} + \phi_{\mathrm{D4,D5}}$ are the probabilities of surviving from each upstream telemetry station to either of the next downstream stations.

Other than the differences noted above, our model structure for this study differed in two other aspects relative to our study conducted in 2007. First, in our previous study, about 14% of fish from one release passed the Delta Cross Channel when it was both open and closed, requiring us to incorporate a parameter to estimate the probability of fish passing the Delta Cross Channel under each condition (ω_{open}, see Perry et al. 2008, in press). However, for this study, only 3 fish (4%) released when the Delta Cross Channel was open passed the Delta Cross Channel after it had closed. Therefore, we did not include ω_{open} in the model. Second, having two release sites leads to two estimates of the same parameter for reaches within the interior Delta (e.g., $S_{\mathrm{D3},m} = S_{\mathrm{D3,Sac}}$ or $S_{\mathrm{D3,Geo}}$, Figure 3). With this model structure, the full model contains 75 unique parameters; 55 parameters from the Sacramento release and 20 for the Georgiana Slough release (Figure 3);

Parameter Estimation

Prior to parameter estimation, the records of tag-detections were processed to eliminate false positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given telemetry stations, and simultaneous tag transmissions "collide" to produce a valid tag code that is not actually present at the monitor (Pincock 2008). Our first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimized the probability of accepting a false positive detection, Pincock (2008) showed that a pair of false positive detections with a time interval <30 min occurred on average once every 30 d when simulating ten tags simultaneously present at a monitor. Thus, our second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002). The detection records of about 10% of tagged fish suggested they had been

consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento and San Joaquin rivers (sites A_7–A_8 and D_5–D_7), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, a fish with the history AA0AAAAEDDDAA indicates it was released at Sacramento ("A"), detected in the Sacramento River at A_2 ("A"), and not detected in the Sacramento River at A_3 ("0"). This fish was subsequently detected at every other telemetry station as it emigrated from the Sacramento River ("AAAA") through Three Mile Slough ("E"), down the San Joaquin River ("DDD"), and finally past Chipps Island into San Francisco Bay ("AA"). Each detection history represents one cell of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, route entrainment, and joint survival-entrainment probabilities (See Perry et al. 2008 for an example). Given these cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters:

$$L_{km}\left(\underset{\sim}{\beta}\middle| R_{km}, n_{jkm}\right) \propto \prod_{j=1}^{J} \pi_{jkm}^{n_{jkm}}$$

where L_{km} is the likelihood for the kth release group (k = 1, 2) at the mth release site (m = Sacramento (Sac), Georgiana Slough (Geo)), R_{km} is the number of fish released for each release group and release site, n_{jkm} is the number of fish with the jth detection history in the kth release group at the mth release site, and π_{jkm} is the probability of the jth detection history in the kth release group at the mth release site expressed as a function of the parameters ($\underset{\sim}{\beta}$). The likelihood was numerically maximized with respect to the parameters using algorithms provided in the software programs R (R Development Core Team 2008) and USER (Lady et al. 2008). Parameters were estimated separately for each release (k) but simultaneously for both release sites by expressing the joint likelihood as the product of $L_{k,\mathrm{Sac}}$ and $L_{k,\mathrm{Geo}}$. The variance-

covariance matrix was estimated as the inverse of the Hessian matrix. We used the delta method (Seber 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\psi_{C2} = 1 - \psi_{B2} - \psi_{D2}$). Uncertainty in parameter estimates is presented both as standard errors and 95% profile likelihood confidence intervals.

Although we planned to have a telemetry station in the Sacramento River at junction 1 (A_3), this station was not implemented in 2008, so we set P_{A3} to zero. Absence of this telemetry station makes it impossible to uniquely estimate the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B12}. However, these parameters can be estimated by assuming that $S_{A2} = S_{A3}$. This assumption was supported by estimates of S_{A2} and S_{A3} in 2007 (Perry et al. 2008, in press). Nonetheless, given that three of four releases thus far (in 2007 and 2008) have occurred without a telemetry station at A_3, we undertook a sensitivity analysis to examine the magnitude of bias introduced into route entrainment probabilities due to deviation from the assumption that $S_{A2} = S_{A3}$ (see Appendix 2). Since it is impossible to apportion mortality between the reach above and below A_3, we examined bias under the extreme scenarios where all mortality occurs either upstream of the first river junction (i.e., $S_{A3} = 1$) or downstream of the first river junction (i.e., $S_{A2} = 1$).

For each release, the full model was considered as the model with the fewest parameter constraints which still allowed all parameters to be uniquely estimated. When parameter estimates occur at the boundaries of one (or zero) they cannot be estimated through iterative maximum likelihood techniques and must be set to one (or zero). In our study, many detection probabilities were set to one because all fish passing a given location were known to have been detected at that location. In some cases, survival probabilities were fixed to one because all fish detected at a given telemetry station were also detected at the next downstream location. In addition, parameters for Route C (the Delta Cross Channel) were set to zero for the second release when the Delta Cross Channel was closed. A full detailing of parameter constraints applied under the full model can be found in Appendix Table 1.2.

The purpose of including a separate release into Georgiana Slough was to improve precision within the interior Delta by boosting the sample size of fish migrating through this region. Pooling data across release sites can improve precision but assumes that the fish released into the Sacramento River and Georgiana Slough experience similar survival and detection probabilities in reaches through which both release groups migrate. Therefore, we used likelihood ratio tests (Casella and Berger, 2002) to evaluate hypotheses about equality in

detection and survival parameters between release sites. Lack of significance at $\alpha = 0.05$ indicates that the full model fits the data no better than the reduced model where parameters are set equal among releases, in which case the reduced model is selected over the full model. For each release, we first compared the full model to a reduced model where all parameters were set equal between releases. We then used parameter estimates from the selected model for estimating population-level and route-specific survival through the Delta.

Survival through the Delta

Survival through the Delta is defined as the probability of survival from the entrance to the Delta at station A_2 (Freeport) to the exit of the Delta at station A_9 (Chipps Island). Population-level survival through the Delta was estimated from the individual components as:

$$S_{\text{Delta}} = \sum_{h=\text{A}}^{\text{D}} \psi_h S_h \tag{1}$$

where S_h is the probability of surviving the Delta given the specific migration route taken through the Delta, and ψ_h is the probability of migrating through the Delta via one of four migration routes (A = Steamboat Slough, B = Sacramento River, C = Georgiana Slough, D = Delta Cross Channel). Thus, population survival through the Delta is a weighted average of the route-specific survival probabilities with weights proportional to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\psi_{\text{A}} = \psi_{\text{A1}}\psi_{\text{A2}} \tag{2}$$

$$\psi_{\text{B}} = \psi_{\text{B11}} + \psi_{\text{B21}} \tag{3}$$

$$\psi_{\text{C}} = \psi_{\text{A1}}\psi_{\text{C2}} \tag{4}$$

$$\psi_{\text{D}} = \psi_{\text{A1}}\psi_{\text{D2}} \tag{5}$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta

Cross Channel (ψ_{C}) is the product of these route entrainment probabilities, $\psi_{\mathrm{A1}}\psi_{\mathrm{C2}}$. Since route entrainment probabilities can be estimated separately for Sutter Slough and Steamboat Slough, the probability of migrating through either Sutter or Steamboat Slough (ψ_{B}) is the sum of the route-entrainment probabilities for each slough (ψ_{B11} and ψ_{B21})

When population level survival can be broken down into components of route-entrainment probabilities and reach specific survival, then survival through the Delta for a given migration route (S_h) is simply the product of the reach-specific survival probabilities that trace each migration path through the Delta between the points A_2 and A_9 (see Perry et al. 2008, in press). However, when joint survival-entrainment probabilities are included in the model, survival through a given route must take into account all possible within-route pathways that involve the $\phi_{hi,jk}$ parameters. For example, survival through the Delta for fish that remain in the Sacramento River through the first and second river junctions is expressed as:

$$S_{\mathrm{A}} = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{\mathrm{A4}}S_{\mathrm{A5}}S_{\mathrm{A6}}\left(\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}\right)$$

The bracketed term is the weighted average survival between A_7 (Rio Vista) and A_9 (Chipps Island) with the $\phi_{hi,jk}$ parameters weighting survival of fish that remain in the Sacramento River ($\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}}$) and survival of fish that finish their migration in the lower San Joaquin after passing through Three Mile Slough ($\phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}$). Thus, Delta survival for Route A (the Sacramento River) includes some mortality of fish that enter the interior Delta, and it is impossible to factor out this mortality without explicitly estimating route entrainment probabilities at the junction of the Sacramento River with Three Mile Slough. Nonetheless, the $\phi_{hi,jk}$ parameters provide information about the relative contribution of the interior Delta to survival through Route A. For example, $\phi_{\mathrm{A7,E1}} \square \phi_{\mathrm{A7,A8}}$ would suggest that movement through Three Mile Slough is a small component of the total survival for fish that migrated in the Sacramento River up to that point. Survival through the Delta for fish taking the Delta Cross Channel (Route C) and Georgiana Slough (route D) is expressed similarly, and explicitly accounts for fish that pass through Three Mile Slough and finish their migration in the lower Sacramento River:

$$S_C = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{C1}S_{D3}\left(\phi_{D4,D5}S_{D5}S_{D6}S_{D7} + \phi_{\mathrm{D4,E1}}S_{\mathrm{E1,A8}}S_{\mathrm{D8}}\right),$$

and $$S_D = S_{A2}S_{A3}S_{D1}S_{D2}S_{D3}\left(\phi_{D4,D5}S_{D5}S_{D6}S_{D7} + \phi_{D4,E1}S_{E1,A8}S_{A8}\right).$$

To facilitate comparison with findings from our first year in 2007, we pooled Sutter and Steamboat Slough into a single migration route, but survival through the Delta can be estimated separately for fish that enter Sutter Slough and fish that enter Steamboat Slough:

$$S_B = \psi_{B11}S_{B1} + \psi_{B21}S_{B2}$$

where S_B is survival through the Delta for fish that enter either Sutter or Steamboat Slough, S_{B1} and S_{B2} are survival through the Delta for fish that enter Sutter Slough and Steamboat Slough, respectively, and where S_{B1} and S_{B2} are estimated as:

$$S_{B1} = S_{A2}\left(\phi_{B11,B12}S_{B12}S_{B13} + \phi_{B11,B22}S_{B22}S_{B23}\right)\left(\phi_{A7,A8}S_{A8} + \phi_{A7,E1}S_{E1,D5}S_{D5}S_{D6}S_{D7}\right),$$

and $$S_{B2} = S_{A2}S_{B21}S_{B22}S_{B23}\left(\phi_{A7,A8}S_{A8} + \phi_{A7,E1}S_{E1,D5}S_{D5}S_{D6}S_{D7}\right).$$

For fish entering Sutter Slough, note that the first bracketed term in S_{B1} accounts for survival of fish taking either Miner Slough ($S_{B12}S_{B13}$) or Steamboat Slough ($S_{B22}S_{B23}$) weighted by the joint probability of surviving and taking each of these routes ($\phi_{B11,B12}$ and $\phi_{B11,B22}$).

We used an approach similar to Newman and Brandes (in press) to quantify survival through each migration route relative to survival of fish that migrate within the Sacramento River:

$$\theta_h = \frac{S_h}{S_A} \qquad h \neq A$$

We measured each route relative to route A because the Sacramento River is considered the primary migration route. For Georgiana Slough, θ_D is nearly analogous to θ estimated by Newman and Brandes (in press), who estimated the ratio of recovery rates of coded wire tagged fish released into Georgiana Slough and the Sacramento River near A_4. Survival through the Delta for route h is equal to Route A when $\theta_h = 1$, and survival through route h is less (greater) than Route A when θ_h is less (greater) than one. We interpreted survival through route h as significantly different than Route A at $\alpha = 0.05$ when $\theta_h = 1$ fell outside the 95% profile likelihood confidence interval of $\hat{\theta}_h$.

To aid in interpreting differences in survival through the Delta among routes and between releases, we examined variation in reach-specific survival rates. Survival probabilities estimate the proportion of fish that survive through a given reach, but direct comparison of survival

probabilities among reaches can be hampered by variation in the length of each reach. In our study, reach length varied from just a few kilometers to over 20 km. Therefore, we scaled survival probabilities relative to reach length by calculating survival rates per unit distance:

$$s_{hi} = \sqrt[x_{hi}]{S_{hi}}$$

where s_{hi} is the per-kilometer probability of surviving from telemetry station h_i to the next downstream station, x_{hi} is the distance (km) from telemetry station h_i to the next downstream telemetry station, and S_{hi} is the probability of surviving over x_{hi} kilometers. For reaches where more than one exit location is possible (reaches beginning at B_{11}, A_7, and D_4), we used the average distance to each of the exit points. The length of some reaches is ill-defined because fish may take multiple, unmonitored routes (e.g., the interior Delta between D_4 and D_5). For these reaches, reach length was calculated as the shortest distance between upstream and downstream telemetry stations (usually the main channel). If fish took longer routes which led to higher mortality, then survival probabilities (S_{hi}) scaled to the shortest possible migration route (s_{hi}) would appear low relative to other routes. Thus, this approach is of utility in identifying reaches of high mortality relative to the shortest possible pathway through a reach.

Results

River conditions and migration timing

River conditions differed for the two release groups and influenced their travel times through the Delta (Figure 4). For first release, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport was between 10,000 ft^3/s and 14,000 ft^3/s. The central 80% of this release group passed junction 2 (Stations A_4, C_1, and D_1; Figure 1) over a 5-day period between 7 December and 11 December. The Delta Cross Channel closed at 1138 hours on 14 December 2007 and remained closed for the balance of the study (Figure 4). In contrast, the second release group passed the two river junctions on the descending limb of a freshet, during which flows declined from about 19,000 ft^3/s to 14,000 ft^3/s. Under these flow conditions, the second release group passed junction 2 over a two-day period between 17 January and 19 January. Travel times from release to junction 2 were also shorter for the second release

group, with a median travel time of 2.7 d for the first release compared to 1.5 d for the second release.

During their migration through the lower regions of the Delta, most of first release group experienced relatively low and stable discharge accompanied by declining water exports, whereas migration of the second release group coincided with a second freshet during which discharge increased to about 40,000 ft^3/s and exports remained stable (Figure 4). As a consequence, 80% of the first release group passed Chipps Island over a 29-d period (12 December to 10 January), but the central 80% of the second release group passed Chipps Island over only a 16-d period (24 January to 9 February). Although the median travel time from release to Chipps Island for the first release (9.7 d) was less than for the second release (12.9 d), the 90th percentile for the first release (35.9 d) was substantially longer than for the second release (23.9 d). These findings suggest that the main effect of the freshet during the second release was to compress the tail of the travel time distribution rather than shift its central tendency. For both releases, it was difficult to compare travel time among migration routes because ≤4 fish per route were detected at Chipps Island for all routes but the Sacramento River.

Route-specific survival through the Delta

Comparison of parameters between release sites (Sacramento and Georgiana Slough) suggested no difference in survival or detection probabilities, allowing us to set parameters equal between release sites to improve precision of survival estimates. For both releases, likelihood ratio tests were not significant (for December, χ^2_9=12.4, P = 0.192; for January, χ^2_9=14.8, P = 0.097), so the reduced model was used to estimate route-specific survival and S_{Delta}. We found little difference between releases in survival through the Delta. The probability of surviving through the Delta was 0.174 for the December release and 0.195 for the January release (Table 2). For the December release, fish remaining in the Sacramento River exhibited higher survival than all other routes (S_A = 0.283), whereas fish migrating through the interior Delta via the Delta Cross Channel and Georgiana Slough exhibited the lowest survival (S_C = 0.041, S_D = 0.087, Table 2 and Figure 5). In contrast, for the January release, fish migrating through Sutter and Steamboat sloughs (S_B = 0.245) exhibited similar survival as fish migrating within the Sacramento River (S_A = 0.244), whereas survival through the interior Delta via Georgiana Slough remained lower than the other migration routes (S_D = 0.086). For both releases, separate

estimates of route-specific survival for Sutter Slough and Steamboat Slough revealed fish entering Steamboat Slough exhibited survival that was about 9 percentage points higher than for fish that entering Sutter Slough (Table 2).

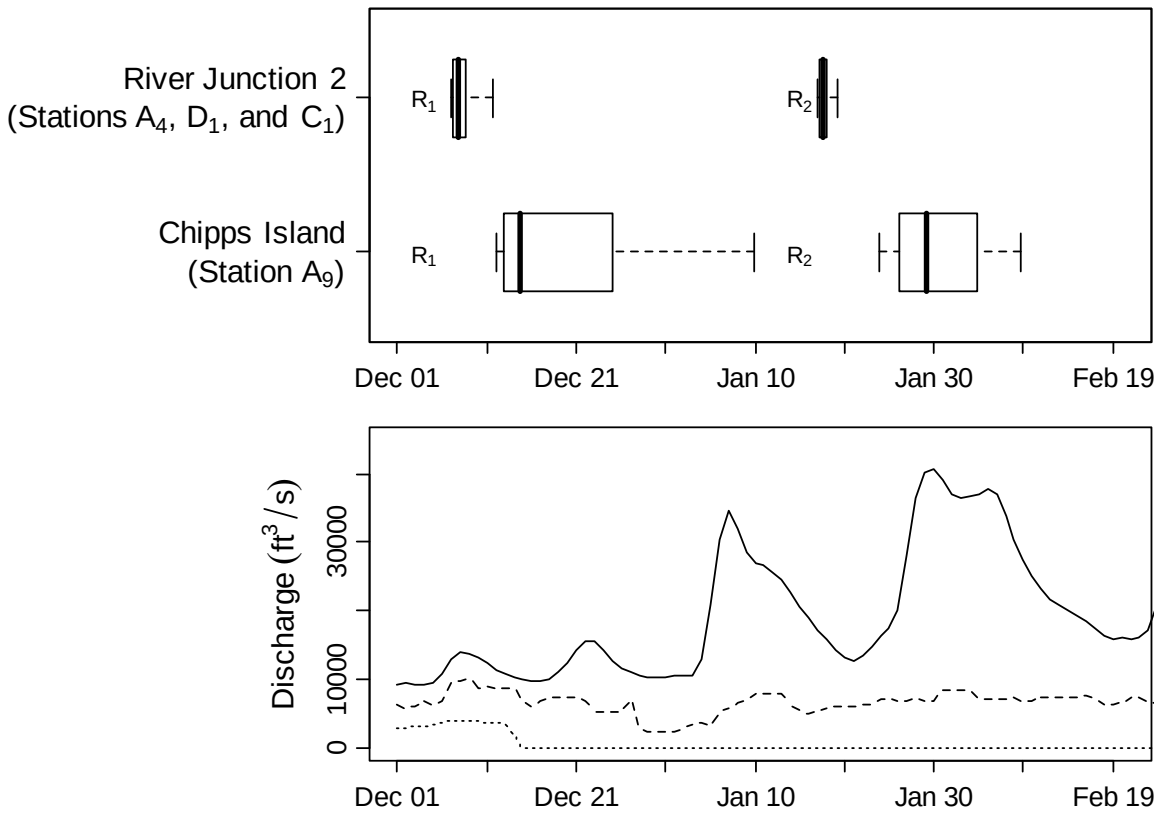

Figure 4.—River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2007/2008. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A4, C1, and D1) and at Chipps Island, the terminus of the Delta (telemetry station A9). The two release dates are shown as R_1 = 4 December 2006 for a release size of 149 tagged fish and R_2 = 15 January 2007 for a release size of 130 fish. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. River discharge (solid line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

Table 2.—Route-specific survival through the Sacramento–San Joaquin River Delta (S_h) and the probability of migrating through each route (ψ_h) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 (R_1) and January 2008 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ (SE)	95% Profile Likelihood Interval	$\hat{\psi}_h$ (SE)	95% Profile Likelihood Interval
R_1: December 2007				
A) Sacramento R.	0.283 (0.054)	0.187, 0.397	0.387 (0.044)	0.304, 0.475
B) Sutter & Steamboat S.	0.136 (0.039)	0.073, 0.225	0.345 (0.042)	0.267, 0.430
B_1) Sutter S.	0.107 (0.037)	0.050, 0.196	0.230 (0.037)	0.163, 0.308
B_2) Steamboat S.	0.193 (0.060)	0.095, 0.327	0.115 (0.028)	0.068, 0.178
C) Delta Cross Channel	0.041 (0.021)	0.013, 0.096	0.117 (0.029)	0.068, 0.182
D) Georgiana S.	0.087 (0.028)	0.043, 0.153	0.150 (0.033)	0.094, 0.221
S_{Delta} (All routes)	0.174 (0.031)	0.119, 0.242		
R_2: January 2008				
A) Sacramento R.	0.244 (0.048)	0.160, 0.346	0.490 (0.048)	0.397, 0.584
B) Sutter & Steamboat S.	0.245 (0.059)	0.143, 0.372	0.198 (0.037)	0.133, 0.278
B_1) Sutter S.	0.192 (0.070)	0.078, 0.343	0.086 (0.026)	0.044, 0.147
B_2) Steamboat S.	0.286 (0.070)	0.162, 0.430	0.112 (0.029)	0.033, 0.253
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.086 (0.023)	0.048, 0.140	0.311 (0.045)	0.229, 0.403
S_{Delta} (All routes)	0.195 (0.034)	0.135, 0.268		

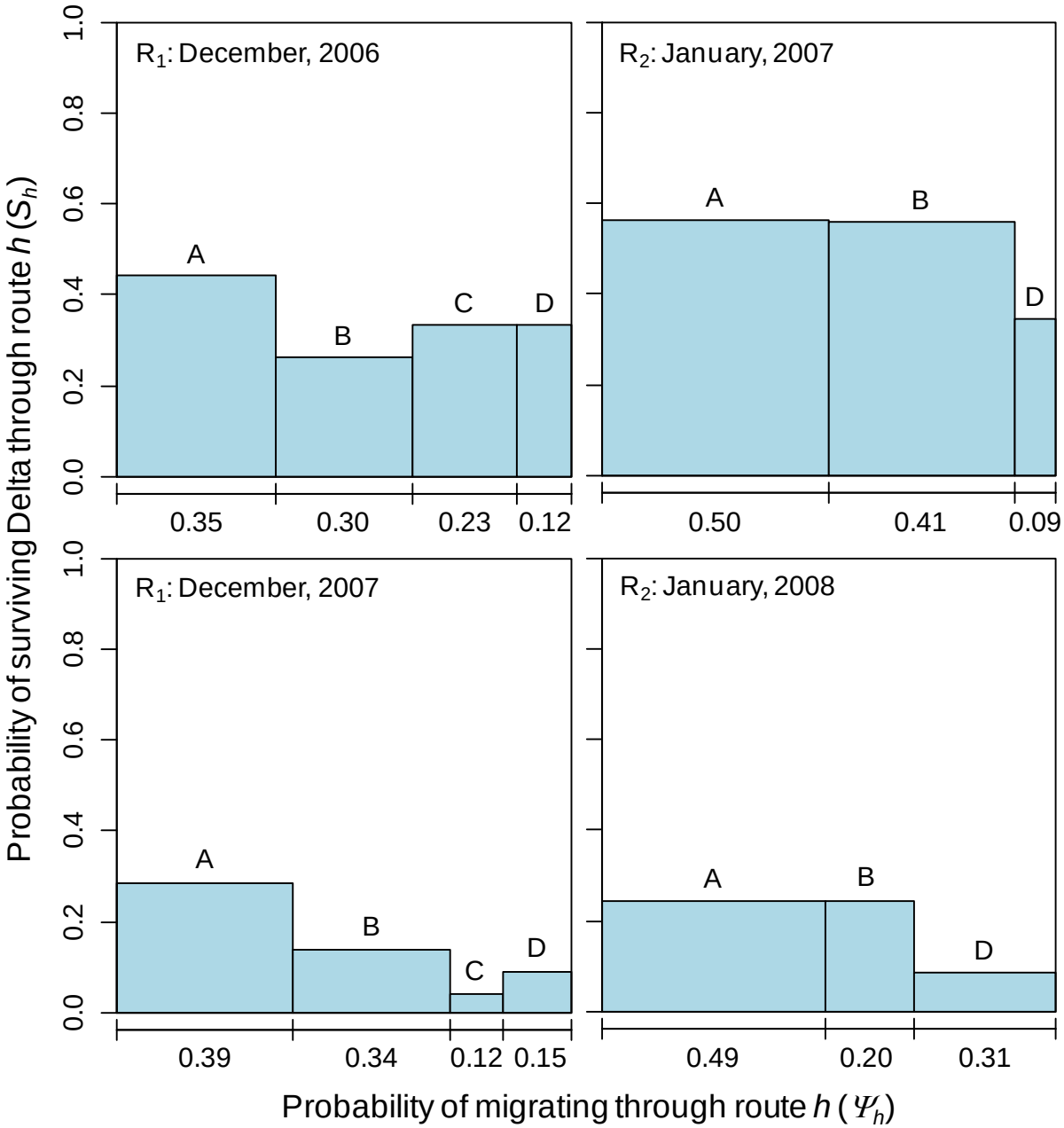

Figure 5.—Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon emigrating from the Sacramento River. The width of each bar shows the fraction of fish migrating through each route (ψ_h), and the total area under the bars yields S_{Delta}. The top panels show estimates from the winter of 2006/2007 (Perry et al. 2008, in press), and the bottom panels show estimates from this study during the winter of 2007/2008. Labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively.

We detected significant differences between survival for the Sacramento River and survival for other migration routes. For the December release, the ratio of survival for each major migration route relative to the Sacramento River (i.e., θ_h) ranged from 0.14 for the Delta Cross Channel to 0.48 for Sutter and Steamboat Slough, showing that survival through other routes was less than half that of the Sacramento River. Since $\theta_h = 1$ fell outside the 95% confidence intervals of $\hat{\theta}_h$ for all major routes, these findings support the hypothesis that all routes had significantly lower survival than the Sacramento River (Table 3). Considering Sutter Slough and Steamboat Slough separately, only the estimate of θ_{B2} for Steamboat Slough was not significantly different from one, likely due to small sample size and low precision for this secondary route. In contrast, in January, $\hat{\theta}_B = 1.005$ whereas $\hat{\theta}_D = 0.352$, showing that survival through the interior Delta (Route D) was only about one third that of other available routes. Survival for the interior Delta was significantly lower than for the Sacramento River for the January release, but survival for Sutter and Steamboat Slough (and each slough separately) was not significantly different than the Sacramento River (Table 3).

Table 3.—The ratio (θ_h) of survival through route h (S_h) to survival through the Sacramento River (S_A) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 and January 2008.

	R_1: December 2007		R_2: January 2008	
Migration route	$\hat{\theta}_h$ (SE)	95% Profile Likelihood Interval	$\hat{\theta}_h$ (SE)	95% Profile Likelihood Interval
B) Sutter & Sutter S.	0.481 (0.132)	0.265, 0.794	1.005 (0.215)	0.621, 1.480
B_1) Sutter S.	0.380 (0.127)	0.182, 0.689	0.787 (0.273)	0.330, 1.365
B_2) Steamboat S.	0.683 (0.205)	0.346, 1.153	1.172 (0.255)	0.698, 1.714
C) Delta Cross Channel	0.146 (0.077)	0.044, 0.363	NA	
D) Georgiana S.	0.307 (0.109)	0.145, 0.596	0.352 (0.110)	0.186, 0.642

Migration Routing

For some migration routes, we found that the proportion of the population migrating through a given route deviated from the fraction of mean discharge in a route. As juvenile salmon migrated past the first river junction, 34.5% of fish left the Sacramento River to migrate through Steamboat and Sutter Slough (ψ_B, Figure 5 and Table 2), about 10 percentage points higher than the fraction of total discharge entering this route (Figure 6). In contrast, for the

January release, only 19.8% of fish entered Sutter and Steamboat Slough ($\hat{\psi}_B$, Figure 5 and Table 2) despite 37% of river discharge entering this route (Figure 6). Route entrainment probabilities for each slough showed that the difference in $\hat{\psi}_B$ between releases occurred at the entrance to Sutter Slough (Table 2). In December, twice the fraction of fish entered Sutter Slough ($\hat{\psi}_{B11}$ = 0.230) as compared to Steamboat Slough ($\hat{\psi}_{B21}$ = 0.115), whereas in January, the proportion entering Sutter Slough declined to 0.086 while the fraction entering Steamboat Slough remained unchanged at 0.112 (Table 2). As a consequence, 65% of fish remained in Sacramento River at the first river junction during the December release, whereas 80% remained in the Sacramento River for the January release (see ψ_{A1} in Appendix Table 1.3). Thus, for the January release, a larger fraction of the population remained in the Sacramento River at the first junction, which increased exposure of the population to the second river junction where they could enter into the interior Delta.

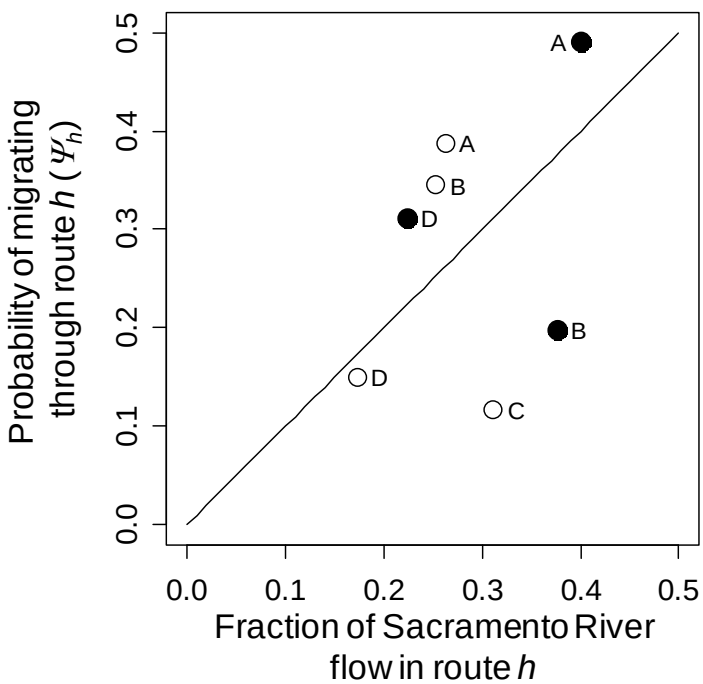

Figure 6.—The probability of migrating through route h (ψ_h) as a function of the proportion of total river flow in route h for tagged late-fall juvenile Chinook salmon released in December 2007 (open circles) and January 2008 (filled circles). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The fraction of river flow in each route was calculated as the proportion of tidally filtered daily discharge of each route relative to the total discharge of the Sacramento River at Freeport. The reference line shows where the fraction of fish migrating through each route is equal to the proportion of flow in each route (i.e., a 1:1 ratio).

For the December release, of fish that arrived at the second river junction where the Delta Cross Channel is located, 18% entered the Delta Cross Channel, 23% entered Georgiana Slough, and 59.2% remained in the Sacramento River (see ψ_{C2}, ψ_{D2}, and ψ_{A2} in Appendix Table 1.3). In contrast, for the January release when the Delta Cross Channel was closed, 38.8% of fish arriving at the second river junction entered Georgiana Slough, with the remaining 61.2% migrating through the Sacramento River. Accounting for both river junctions, migration route probabilities for the December release indicated that 38.7% of the population migrated within the Sacramento River and 26.7% of the population entered the interior Delta. However, only 11.7% entered the interior Delta through the Delta Cross Channel even though 31% of the flow entered the Delta Cross Channel (Figures 5 and 6, Table 2). During January, nearly one third of the population was entrained into the interior Delta through Georgiana Slough (Figure 5, Table 2) despite the Delta Cross Channel being closed. Consequently, the fraction of the population entering the interior Delta was similar between release dates.

Relative Contributions to S_{Delta}

Estimates of S_{Delta} were driven by 1) variation among routes in survival through the Delta ($\hat{S}_h$) and 2) the relative contribution of each route-specific survival to $\hat{S}_{Delta}$ as measured by migration route probabilities ($\hat{\psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_B$) relative to all other routes, but only 38.7% of the population migrated through this route ($\hat{\psi}_B$), representing a relatively small contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{Delta}$ and comprised 61.3% of the population ($\hat{\psi}_A + \hat{\psi}_C + \hat{\psi}_D$), thereby contributing substantially to $\hat{S}_{Delta}$ for the December release (Figure 5, Table 2). For the January release, 68.8% of the population ($\hat{\psi}_A + \hat{\psi}_B$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{Delta}$ for the January release (Figure 5, Table 2). In comparison, survival for the interior Delta via Georgiana Slough ($\hat{S}_C$) was lower than the other routes for the January release and accounted for 31.2% ($\hat{\psi}_C$) of the contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). Because the fraction

of the population entering the interior Delta was similar for both releases, lower survival through the interior Delta reduced population-level survival by a similar magnitude for both releases.

Comparisons between 2007 and 2008

Some patterns in survival and migration route probabilities during 2008 differed considerably from 2007, whereas other patterns remained consistent. First, $\hat{S}_{\text{Delta}}$ for both releases in 2008 (Table 2) was lower than in 2007; $\hat{S}_{\text{Delta}}$ in 2007 was estimated at 0.351 and 0.543 for the December and January release groups (Perry et al. 2008, in press). Although $\hat{S}_{\text{Delta}}$ was lower in 2008 relative to 2007, the pattern of survival probabilities among routes was similar between releases and years (Figure 5). In both years, all routes exhibited lower survival than the Sacramento River during the December release, but only fish entering the interior Delta exhibited lower survival than the Sacramento River for the January release (Figure 5). Larger sample size and the additional release site in Georgiana Slough during 2008 improved precision of route-specific survival compared to our 2007 study, allowing us to detect differences in survival among routes. We also found notable differences between years in route entrainment probabilities at the two primary river junctions. In 2007, migration route probabilities were similar to the fraction of flow in each route, but migration route probabilities deviated from this pattern in 2008. Consequently, in 2008 we found little difference between releases in the fraction of fish entering the interior Delta, whereas in 2007, the fraction of fish was lower during the January release when the Delta Cross Channel was closed (Perry et al. 2008, in press).

Reach-specific patterns of survival and movement

We found high variation in survival rates among reaches, ranging from as low as 0.867 km^{-1} to 1.0 km^{-1} for a few reaches where all fish survived. To put the magnitude of these survival rates in perspective, only 24% of fish will survive a 10-km reach at a survival rate 0.867 km^{-1} (i.e., $= 0.867^{10} = 0.247$) and only 6% will remain after 20 km. In contrast, at a survival rate of 0.99 km^{-1}, 90% of fish will survive 10 km and 82% will still be alive after 20 km. Reaches with the lowest survival rates occurred downstream of telemetry stations B_{13}, B_{23}, and A_6 (i.e., the Cache Slough to Rio Vista region, Figure 7). Two out of three of these reaches were among the four lowest survival rates observed in each release, highlighting a region of high local

mortality relative to the length of these reaches. In contrast, other than survival probabilities that were fixed to one (Appendix Table 1.3), the highest survival rates in both releases occurred in the first two reaches of the Sacramento River (downstream of A_2 and the Sacramento release site, A_1). These reaches were relatively long (~20 km each) and survival probabilities were >0.91 (see S_{A1} and S_{A2} in Appendix Table 1.3), leading to high survival rates relative to reach length. Reach-specific survival rates were consistent with differences among routes in survival through the Delta. For the December release, 8 of the 11 reaches with the highest survival rates were comprised of all 8 reaches in the Sacramento River (Route A, Figure 7). These reaches exhibited survival rates ≥0.96 km^{-1}. The remaining 11 reaches with the lowest survival rates were comprised solely of the other three routes, with no particular route exhibiting consistently lower reach-specific survival rates. All of these reaches exhibited survival rates <0.96 km^{-1}. For the January release, the highest-ranking survival rates were still dominated by reaches within the Sacramento River (6 of the 11 lowest mortality rates), but two reaches of the Sacramento River ranked in highest 50 percent of mortality rates (reaches beginning at A_6 and A_8).

Between releases, most reach-specific survival rates within the Sacramento River (Route A) and interior Delta (Route D) changed by less than 0.03 km^{-1} (Figure 8), and this finding agrees with the similarity in route-specific survival between releases (Figure 5). Furthermore, variation in survival rates between releases was low relative to the large variation in survival rates among reaches, especially for the Sacramento River (Figure 8). However, survival rates for all but one reach within Sutter and Steamboat sloughs increased substantially from December to January (Figure 8), which is consistent with the observed increase in survival through the Delta for this route. Thus, the observed difference in route-specific survival for Sutter and Steamboat sloughs was driven by coincident changes in survival rates for most reaches within this route and not by changes in survival within a particular reach.

One reach of particular management interest occurs downstream of D_4 in the interior Delta (see Figure 2). Although only about 17 km long by way of the San Joaquin River, this reach encompasses a large network of channels and includes the pumping stations and fish salvage facilities in the southern Delta. This reach exhibited the lowest probability of survival of

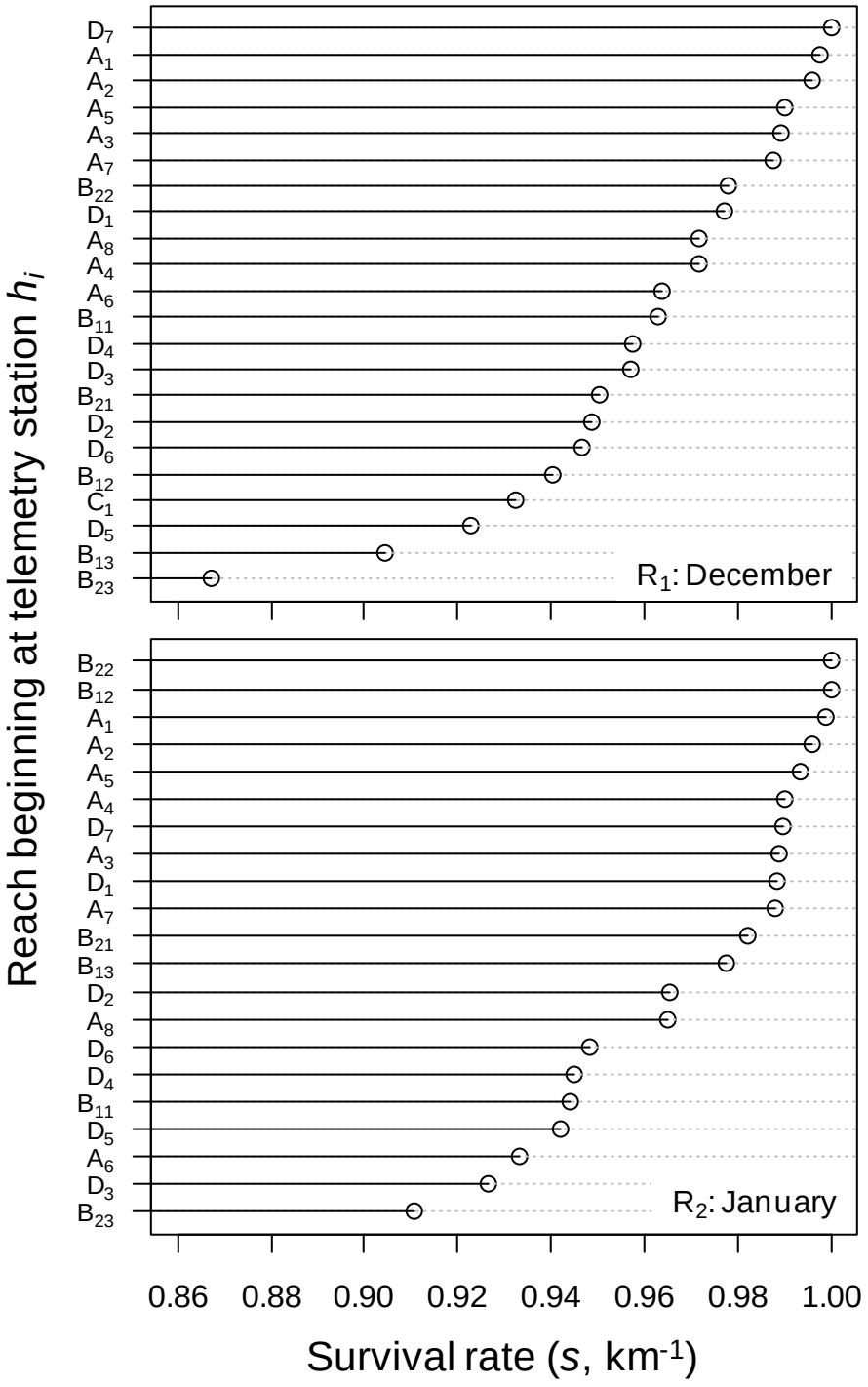

Figure 7.—Reach-specific survival rates plotted in ascending order for tagged late fall Chinook salmon released in December 2007 (top) and January 2008 (bottom). Survival rates scale survival probabilities (S_{hi}, Appendix Table 1.3) to the length of each reach from telemetry station h_i to the next downstream telemetry station.

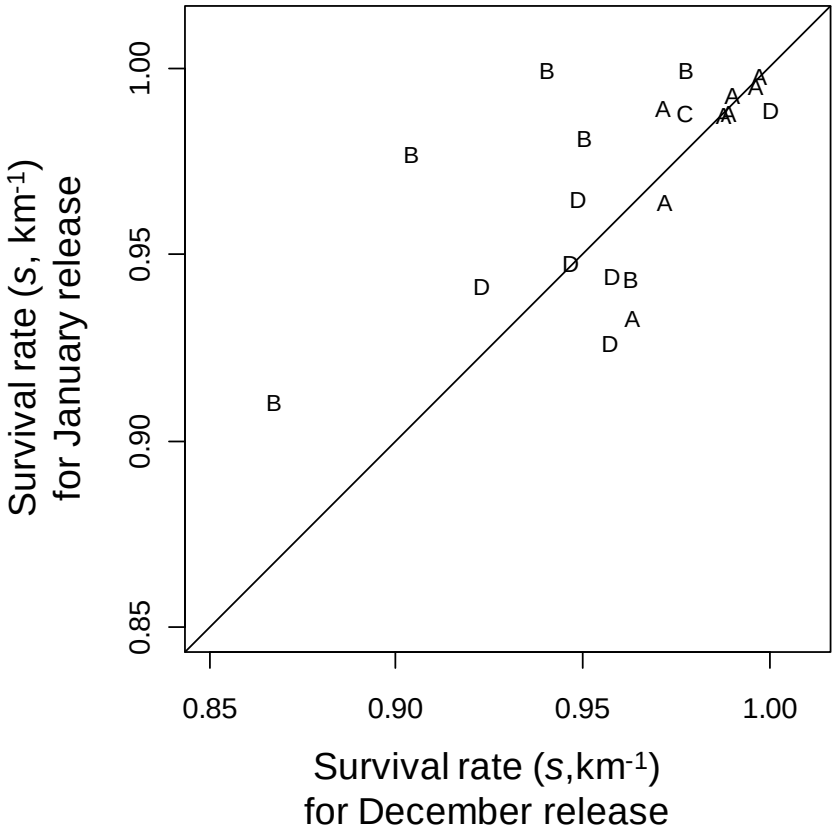

Figure 8.—Reach-specific survival rates for the December 2007 release compared to the January 2008 release for acoustically tagged late fall Chinook salmon migrating through the Sacramento-San Joaquin River Delta. The reference line shows where survival rates are equal between releases. Letters correspond to reaches within A = Sacramento River, B = Sutter and Steamboat sloughs, and D = the interior Delta via Georgiana Slough.

all reaches within the interior Delta, having observed survival probabilities of less than 50% (for R_1: $\hat{S}_{D4} = 0.484$, $\hat{SE} = 0.071$; for R_2: $\hat{S}_{D4} = 0.395$, $\hat{SE} = 0.080$; Appendix Table 1.3). However, when expressed as a function of reach length, other reaches within the interior Delta (Routes C and D) exhibited similar or lower survival rates than the reach downstream of D_4 (Figure 7). Direct mortality at the pumping stations appeared to contribute little to the estimate of S_{D4}. Both the State Water Project and Clifton Court Forebay were monitored by telemetry stations, but these stations could not be incorporated into the survival model because too few fish were detected at these locations to warrant parameter estimation. However, of the 76 fish passing D_4 that were never detected at or downstream of D_5 or E_1 (indicating probable mortality in this

reach), only one fish was detected at the salvage facilities. Overall, six tagged fish were detected at the salvage facilities, and five of these were next detected at or downstream of D_5 or E_1 suggesting they had been salvaged at the fish facilities and transported to the lower Delta. Thus, mortality rates appear high in many reaches of the interior Delta relative the Sacramento River, not just the reach that includes a primary point source of known mortality (i.e., pumping stations and salvage facilities).

Although we could not estimate route entrainment probabilities at other junctions in the Delta, we explicitly accounted for observed movement among routes by estimating joint survival-entrainment probabilities. At the junction of Sutter Slough with Miner and Steamboat Slough (the reach downstream of B_{11}; Figure 2), $\hat{\phi}_{B11,B22}$ was about twice that of $\hat{\phi}_{B11,B12}$ during both releases (Appendix Table 1.3). If survival was similar for the two reaches downstream of the junction, then these findings suggest that about two-thirds of fish entering Sutter Slough migrated down Steamboat Slough and one-third traveled through Miner Slough.

For both releases we observed fish passing in both directions through Three Mile Slough (E_1 in Figure 2). However, Three Mile slough appears to play a relatively minor role in movement dynamics through the Delta relative to contribution of the major migration routes. In the Sacramento River, fish moving from A_7 to A_8 contributed a substantially larger fraction of the total survival through this reach (for R_1: $\hat{\phi}_{A7,A8} = 0.837$, $\hat{SE} = 0.074$; for R_2: $\hat{\phi}_{A7,A8} = 0.781$, $\hat{SE} = 0.070$) compared to fish moving from A_7 to E_1 (for R_1: $\hat{\phi}_{A7,E1} = 0.049$, $\hat{SE} = 0.034$; for R_2: $\hat{\phi}_{A7,E1} = 0.109$, $\hat{SE} = 0.046$). In the San Joaquin River, fish moving from D_4 to E_1 contributed more to the total reach survival for the first release compared to the second release. For the first release, $\hat{\phi}_{D4,E1} = 0.140$ ($\hat{SE} = 0.049$) and $\hat{\phi}_{D4,D5} = 0.351$ ($\hat{SE} = 0.070$), whereas for the second release $\hat{\phi}_{D4,E1} = 0.041$ ($\hat{SE} = 0.023$) and $\hat{\phi}_{D4,D5} = 0.354$ ($\hat{SE} = 0.079$). Whether a higher fraction of fish in the San Joaquin River passed through Three Mile Slough (E_1) during the first release is difficult to ascertain because lower survival in the San Joaquin River downstream of its junction with Three-Mile Slough may also account for the observed difference.

Discussion

In our previous study, $\hat{S}_{\text{Delta}}$ differed by nearly 20 percentage points between releases, and we attributed this observed difference to both a change in the proportion of fish entering the interior Delta and a change in survival within given migration routes (Perry et al. 2008, in press). In contrast, for this study, we attribute lack of an observed difference in $\hat{S}_{\text{Delta}}$ between releases to 1) less variation between releases in survival for given migration routes, relative to 2007, 2) lower-than-expected entrainment into the Delta Cross Channel, 3) a decline in the proportion of fish entering Sutter and Steamboat sloughs in January, and 4) little difference in the proportion of fish entering the interior Delta between releases. In 2007, survival through the Delta for both the Sacramento River and Sutter and Steamboat Slough increased substantially between December and January, partly driving the large observed difference in $\hat{S}_{\text{Delta}}$ between releases (Perry et al. 2008, in press). However, during 2008 only Sutter and Steamboat sloughs exhibited a sizeable increase in survival from December to January. However, although survival increased, the proportion of fish entering Sutter and Steamboat sloughs declined from 0.34 to 0.20 from December to January. Had the proportion of fish entering Sutter and Steamboat sloughs remained unchanged, population-level survival would have received a larger boost from the increase in survival observed for this route. Given that survival for routes through the interior Delta were significantly lower than the Sacramento River during both releases, the fraction of fish entering the interior Delta dictated the magnitude of decrease in population-level survival due to fish using this migration route. Thus, the magnitude of decrease in population-level survival attributed to the interior Delta remained unchanged between releases because similar fractions of the population entered the interior Delta during both releases. However, because maximum survival for any given route during both releases was <0.30, population-level survival would remain low regardless of the fraction of fish entrained in the interior Delta.

That estimates of population-level survival were ≤0.20 for an 80-km section of river begs the question of whether the untagged population also experienced such low survival. To put the magnitude of these estimates in perspective, survival of hatchery-reared juvenile Chinook salmon over 600 km and through eight dams of the Snake and Columbia rivers ranged from

31%-59% (Williams et al. 2001). Thus, the absolute magnitude of survival relative to the distance traveled is clearly low compared to a similarly developed river system. However, factors such as source of the study fish and the effects of the transmitter could have reduced survival probabilities relative to untagged fish. Fish in this study were obtained directly from Coleman National Fish Hatchery, tagged, and then released about 40 km upstream of the first channel junction in the Delta. Initial "culling" of unfit hatchery fish obtained directly from a hatchery, a process suggested by Muir et al. (2001) and Newman (2003), could have lead to lower absolute survival compared to a population that had migrated in-river from natal tributaries or hatcheries to the Delta. If this process were pronounced in our study, we might have expected 1) low survival in the first reach following release, and 2) fish released at Sacramento to have higher survival probabilities through the interior Delta relative to fish that were released directly into the interior Delta at Georgiana Slough. In contrast, survival probabilities for the first reach of the Sacramento River were higher than all other reaches within this route (see S_{A1}, Appendix Table 1.3). Furthermore, the model with equal survival probabilities between release sites was selected over the full model with different survival probabilities for each release, providing little evidence of a "culling" effect. As for the effect of the transmitter, Hockersmith et al. (2003) found no difference in survival between radio tagged and PIT-tagged juvenile Chinook salmon over a similar distance as that studied here. Thus, we found little evidence to suggest that the low population-level survival through the Delta was a function of the source of fish or tagging methodology used for the study.

The strength of inferences from our data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Although we found no evidence that survival probabilities were lower than expected due to fish source or tagging method, we also have little basis with which to compare survival estimates from our study population to actively migrating populations of wild or hatchery origin in the Delta. However, regardless of the absolute magnitude of survival, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, while it is uncertain whether untagged fish migrating concurrently with tagged fish also exhibited population-level survival of less than 20%, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival through the Delta relative to fish migrating within the Sacramento River. Therefore, the relative difference in survival

among routes from our data should provide stronger inference to untagged populations than will inferences about the absolute magnitude of survival probabilities. From this perspective, although survival was low for all migration routes during 2008, survival for routes through the interior Delta was at most 35% that of survival for fish remaining in the Sacramento River (see θ_C and θ_D inTable 3). Future studies that include fish obtained from Coleman National Fish Hatchery paired with releases of in-river, actively migrating hatchery or wild fish would help to interpret the absolute magnitude of survival probabilities from this study in the context of other populations of interest.

The primary working hypothesis of management actions related to the operation of the Delta Cross Channel is that closing the Delta Cross Channel will increase population-level survival by reducing the fraction of the population entering the interior Delta where survival is lower than alternative migration routes. Implicit in this hypothesis is that the fraction of fish entering the interior Delta is proportional to the fraction of flow entering the interior Delta. However, in contrast to our previous findings, we found that the proportion of fish entering each migration route did not necessarily agree with the proportion of mean discharge entering a route. Furthermore, deviations from this "expected" relationship acted to decrease the proportion of fish entering the interior Delta during the December release, but increase it during the January release. Based on distribution of mean discharge, closing the Delta Cross Channel reduced the total fraction of flow entering the interior Delta from 48.4% during the December release to 22.5% during the January release. However, for the December release, the proportion of fish entering the Delta Cross Channel was only about one-third the proportion of flow entering this route, whereas the proportion of fish entering Georgiana Slough was similar to the proportion of flow (Figure 6). Thus, the proportion of fish entering the interior Delta was less than might otherwise be expected based only on the distribution of river flow during the December release. During the January release, only about 20% of fish entered Sutter and Steamboat Slough even though 37% of Sacramento River flow entered this route (Figure 6). Therefore, a higher fraction of fish remained in the Sacramento River relative to that expected based on the proportion of flow in this route, which in turn exposed a higher fraction of the population to entrainment into the interior Delta via Georgiana Slough. These findings show how variation in route entrainment probabilities at both major river junctions interacted to produce little observed difference

between releases in the fraction of the population entering the Interior Delta, despite the Delta Cross Channel being open for the first release and closed for the second.

While dispersal of the population throughout the channel network of the Delta is likely driven in part by the distribution in mean river discharge among channels, our findings provide the first evidence that the distribution of fish entering each channel can deviate considerably from the distribution of flow entering each channel. Such deviation was expected by Burau et al. (2007), who identified a number of mechanisms likely to contribute to variation in route entrainment probabilities. First, flow distribution among the river channels at each junction varies with the tides on hourly time scales (Blake and Horn 2003). Thus, diel patterns in migration behavior (Wilder and Ingram 2006; Burau et al. 2007; Chapman et al. 2007) interacting with tidal fluctuations could produce route entrainment probabilities that deviate from that expected based on mean discharge. In addition, secondary circulation at river bends (Dinehart and Burau 2005) combined with swimming behavior of juvenile salmon could concentrate the lateral distribution of migrating fish along the outside of river bends where they become more (or less) likely to be entrained into a given channel at a river junction (Burau et al. 2007). These fine-scale processes are an active area of research in the Delta (Burau et al. 2007) and should provide new insights into the mechanisms driving variability in route entrainment probabilities at river junctions.

While some aspects of migration and survival dynamics differed greatly between years, other patterns remained consistent. Although population-level survival in 2008 was lower than in 2007, the pattern of survival among routes was similar. During both releases, survival of fish migrating through the interior Delta was significantly less than for fish that remained in Sacramento River, which is consistent our findings in 2007 (Perry et al. 2008, in press) and with the findings of previous studies (Brandes and McLain 2001; Newman and Rice 2002; Newman 2008, Brandes and Newman in press). This weight of evidence suggests that management actions that shift the distribution of the population from the interior Delta to the Sacramento River will improve population-level survival through the Delta. Similar to 2007, we also found that survival through the Delta for fish migrating in Sutter and Steamboat Sloughs was significantly lower than the Sacramento River during the December release, but was comparable to the Sacramento River during the January release. Higher total river discharge (Figure 4) in January combined with a higher fraction of that discharge entering Sutter and Steamboat sloughs

(Figure 6) could have improved migration conditions and reduced predation rates during the January release. Reach-specific survival rates increased for nearly all reaches of Sutter and Steamboat Slough (Figure 8), which is consistent with an increase in discharge through these reaches.

Quantifying survival rates per unit distance allowed us to identify patterns in reach-specific survival that generally followed the pattern of route-specific survival probabilities. Most reaches within the Sacramento River exhibited the highest survival rates during both releases, while most reaches within the interior Delta exhibited survival rates lower than the Sacramento River (Figure 7). These findings suggest that particular reaches within a route did not drive the observed differences in survival among migration routes. For instance, the lowest survival probabilities for the interior Delta were observed for the longest reach and included the most complex channel network with the pumping stations (see S_{D4} in Appendix Table 1.3). Yet survival rates for this reach were comparable to other reaches within this route when expressed as a function of reach length. In addition, we observed locally high mortality in the Cache Slough region downstream of stations B_{13}, B_{23}, and A_6 for both releases. Last, survival rates in Sutter and Steamboat sloughs increased in January for nearly all reaches within this route. These patterns of variation among reaches suggest that factors influencing survival are operating at a spatial scale larger than an individual reach.

Reach-specific survival rates expressed with respect to distance traveled changed little between releases relative to the variability observed among reaches, especially for the Sacramento River (Figure 9). These findings suggest that factors other than migration distance (e.g., travel time) may also influence mortality rates. In contrast, in the Columbia River, survival rates of juvenile Chinook salmon have been significantly related to migration distance, but only weakly correlated to travel time (Muir et al. 2001, Anderson et al. 2005). Anderson et al. (2005) offered a hypothesis explaining this apparently contradictory finding. When prey migrate through a "gauntlet" of predators, predator-prey encounter rates will be such that each prey encounters a predator at most once. Under these circumstances, predator-prey theory predicts that survival will be driven by distance traveled, but not by travel time. In contrast, when prey migration speeds are slow relative to predator swimming speeds such that multiple encounters are possible, then the situation reverses: the probability of survival becomes dependent on travel time. This hypothesis could partially explain the wide range in mortality rates among reaches

within the Sacramento River, but low variability between releases (Figure 8). Within our study area the Sacramento River transitions from river-driven discharge in the uppermost reaches to tidally driven discharge in the lower reaches. Coincident with this transition, fish movement patterns shift from downstream-only movements to both upstream and downstream movements in the lower reaches of the Delta. Thus, in lower reaches of the Delta fish may pass through a given reach more than once, which could increase predator encounter rates relative to the length of each reach.

This research continues to provide critical information to understand factors influencing migration and survival dynamics of juvenile Chinook salmon migration through the Delta. Improved precision of parameter estimates allowed us detect statistically significant differences in survival among migration routes. While some findings were similar to our previous study, such as low survival through the Interior Delta relative to the Sacramento River, other findings deviated considerably between years. Survival through the Delta was less than 20% during 2008 (compared to 35%-54% in 2007), route-entrainment probabilities deviated from the fraction of mean river discharge entering each channel, and the proportion of the population entering the interior Delta was similar between releases despite closure of the Delta Cross Channel. Given the substantial variation in survival, route entrainment, and migration route probabilities observed among four releases and two years, we suspect that we are just beginning to unmask the temporal and spatial variability in migration and survival dynamics in the Delta. Nonetheless, even with such variability, patterns in survival and movement dynamics are beginning to emerge. With the addition of migration data collected during the winter of 2008/2009, we plan to formally model hypotheses about reach- and route-specific factors that influence survival and migration route probabilities. Such information should provide insights into management actions that will improve survival of juvenile salmon populations migrating through the Sacramento-San Joaquin River Delta.

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Appendix 1

Appendix Table 1.1.—Counts of detection histories for the model shown in Figure 3 for a release of R_1 = 208 fish on 4 December 2007 and R_2 = 211 fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A "0" indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with "0 0 0 D" indicate fish released in Georgiana Slough whereas those beginning with "A" are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0 0 0 0	11	0 0 0 D 0 0 0 0 0 0 0 0 0	5
0 0 0 D D 0 0 0 0 0 0 0 0	5	0 0 0 D D 0 0 0 0 0 0 0 0	4
0 0 0 D D D 0 0 0 0 0 0 0	7	0 0 0 D D D 0 0 0 0 0 0 0	21
0 0 0 D D D D 0 0 0 0 0 0	20	0 0 0 D D D D 0 0 0 0 0 0	32
0 0 0 D D D D D 0 0 0 0 0	6	0 0 0 D D D D D 0 0 0 0 0	4
0 0 0 D D D D E 0 0 0 0 0	3	0 0 0 D D D D E 0 0 0 0 0	1
0 0 0 D D D D D 0 D 0 0 0	2	0 0 0 D D D D 0 0 D 0 0 0	1
0 0 0 D D D D D 0 D D A 0	1	0 0 0 D D D D D 0 D 0 0 0	2
0 0 0 D D D D E A 0 0 A A	2	0 0 0 D D D D 0 0 D D 0 0	1
0 0 0 D D D D D 0 0 D A A	1	0 0 0 D D D D 0 0 0 0 A 0	1
0 0 0 D D D D D 0 D D A A	1	0 0 0 D D D D E A 0 0 0 A	1
A 0 0 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D D 0 D D 0 A	1
A A 0 0 0 0 0 0 0 0 0 0 0	18	0 0 0 D D D D 0 0 0 0 A A	1
A 0 B1 0 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D D 0 0 0 A A	1
A A B1 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D E A 0 0 A A	1
A A B2 0 0 0 0 0 0 0 0 0 0	3	0 0 0 D D D D D 0 D 0 A A	2
A A 0 A 0 0 0 0 0 0 0 0 0	7	0 0 0 D D D 0 D 0 0 D A A	1
A A B1 B1 0 0 0 0 0 0 0 0 0	4	0 0 0 D D D D D 0 0 D A A	1
A A B1 B2 0 0 0 0 0 0 0 0 0	1	A 0 0 0 0 0 0 0 0 0 0 0 0	6
A 0 B2 B2 0 0 0 0 0 0 0 0 0	1	A A 0 0 0 0 0 0 0 0 0 0 0	16
A A B2 B2 0 0 0 0 0 0 0 0 0	2	A A B1 0 0 0 0 0 0 0 0 0 0	4
A 0 0 C 0 0 0 0 0 0 0 0 0	1	A A B2 0 0 0 0 0 0 0 0 0 0	1
A A 0 C 0 0 0 0 0 0 0 0 0	9	A A 0 A 0 0 0 0 0 0 0 0 0	3
A A 0 D 0 0 0 0 0 0 0 0 0	6	A 0 0 D 0 0 0 0 0 0 0 0 0	2
A 0 0 A A 0 0 0 0 0 0 0 0	1	A A 0 D 0 0 0 0 0 0 0 0 0	4
A A 0 A A 0 0 0 0 0 0 0 0	5	A 0 0 A A 0 0 0 0 0 0 0 0	1
A A B1 B1 B1 0 0 0 0 0 0 0 0	7	A A 0 A A 0 0 0 0 0 0 0 0	6
A A B1 B2 B2 0 0 0 0 0 0 0 0	4	A 0 B1 B1 B1 0 0 0 0 0 0 0 0	1
A A B2 B2 B2 0 0 0 0 0 0 0 0	2	A 0 B2 B2 B2 0 0 0 0 0 0 0 0	1
A A 0 D D 0 0 0 0 0 0 0 0	1	A A B2 B2 B2 0 0 0 0 0 0 0 0	3
A A 0 0 A A 0 0 0 0 0 0 0	1	A A 0 D D 0 0 0 0 0 0 0 0	3
A A 0 A A A 0 0 0 0 0 0 0	4	A A 0 A A A 0 0 0 0 0 0 0	10
A A 0 D D D 0 0 0 0 0 0 0	1	A 0 0 D D D 0 0 0 0 0 0 0	1

Appendix Table 1.1.—Continued.

A A 0 A A 0 A 0 0 0 0 0 0	1	A A 0 D D D 0 0 0 0 0 0 0	2
A A B1 B2 B2 0 A 0 0 0 0 0 0	1	A A B1 B2 B2 0 A 0 0 0 0 0 0	1
A A B2 B2 B2 0 A 0 0 0 0 0 0	1	A A B2 B2 B2 0 A 0 0 0 0 0 0	1
A A 0 A A A A 0 0 0 0 0 0	2	A 0 0 A A A A 0 0 0 0 0 0	1
A A 0 C 0 D D 0 0 0 0 0 0	3	A A 0 A A A A 0 0 0 0 0 0	2
A A 0 D D D D 0 0 0 0 0 0	3	A 0 0 D D D D 0 0 0 0 0 0	4
A A B2 B2 B2 0 0 A 0 0 0 0 0	1	A A 0 D D D D 0 0 0 0 0 0	12
A A 0 A A 0 A A 0 0 0 0 0	1	A A B1 B1 B1 0 0 A 0 0 0 0 0	1
A A B1 B1 B1 0 A A 0 0 0 0 0	1	A 0 B1 B2 B2 0 0 A 0 0 0 0 0	1
A A B2 B2 B2 0 A A 0 0 0 0 0	1	A A B2 B2 B2 0 0 A 0 0 0 0 0	1
A 0 0 A A A A A 0 0 0 0 0	1	A A 0 A A A 0 A 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 0 0	9	A A 0 A A 0 A A 0 0 0 0 0	1
A A 0 D D D D D 0 0 0 0 0	1	A A B1 B1 B1 0 A A 0 0 0 0 0	2
A A 0 D D D D E 0 0 0 0 0	1	A A B2 B2 B2 0 A A 0 0 0 0 0	3
A A 0 D D D D 0 0 D 0 0 0	1	A 0 0 A A A A A 0 0 0 0 0	1
A A 0 A A 0 0 A 0 0 0 A 0	1	A A 0 A A A A A 0 0 0 0 0	5
A A B1 B2 B2 0 A A 0 0 0 A 0	1	A A 0 D D D D D 0 0 0 0 0	2
A A B2 B2 B2 0 A A 0 0 0 A 0	1	A A 0 A A A A E 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 A 0	2	A A 0 A A 0 A E 0 D 0 0 0	1
A A B1 0 B1 0 0 E D D D A 0	1	A A 0 A A A A 0 0 0 0 A 0	1
A A 0 0 A 0 A 0 0 0 0 0 A	1	A A 0 A A A A A 0 0 0 A 0	3
A A 0 D D D D D 0 D D 0 A	2	A A 0 A A A A E 0 D 0 A 0	1
A A 0 A A A A E D D D 0 A	1	A A 0 D D D D D 0 D D A 0	1
A A 0 A A A A 0 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 0 A	1
A A B2 B2 B2 0 0 A 0 0 0 A A	1	A 0 0 A A 0 A E 0 D 0 0 A	1
A A 0 A A A 0 A 0 0 0 A A	2	A A 0 D D D D 0 0 0 0 A A	1
A A 0 A A 0 A A 0 0 0 A A	1	A A 0 A A A 0 A 0 0 0 A A	1
A A B1 B1 B1 0 A A 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 A A	3
A A B2 B2 B2 0 A A 0 0 0 A A	2	A 0 B2 B2 B2 0 A A 0 0 0 A A	1
A A 0 A A A A A 0 0 0 A A	5	A A B2 B2 B2 0 A A 0 0 0 A A	2
A A 0 C 0 D D E A 0 0 A A	1	A 0 0 A A A A A 0 0 0 A A	1
A A 0 D D D D D 0 0 D A A	1	A A 0 A A A A A 0 0 0 A A	5
A A 0 D D D D D 0 D D A A	1	A A 0 D D D D D 0 0 0 D A A	1
Total released (R_k)	208		211

Appendix Table 1.2.—Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
S_{A3}	$= S_{A2}$	ψ_{C2}	$= 0$
$S_{D7,\ Sac}$	$= 1$	$\phi_{D4,E1,Sac}$	$= 0$
$S_{E1,D5}$	$= 1$	S_{A3}	$= S_{A2}$
P_{A3}	$= 0$	S_{B12}	$= 1$
P_{A5}	$= 1$	S_{B22}	$= 1$
$P_{E1,Sac}$	$= 1$	S_{C1}	$= 0$
P_{B11}	$= 1$	$S_{D7,Sac}$	$= 1$
P_{B21}	$= 1$	$S_{E1,D5}$	$= \phi_{D4,D5,Geo}$
P_{B22}	$= 1$	$S_{E1,A8,Sac}$	$= 0$
P_{B13}	$= 1$	P_{A3}	$= 0$
P_{B23}	$= 1$	P_{A4}	$= 1$
P_{C1}	$= 1$	P_{A5}	$= 1$
P_{D1}	$= 1$	P_{B11}	$= 1$
$P_{D2,Sac}$	$= 1$	P_{B12}	$= 1$
$P_{D3,Sac}$	$= 1$	P_{B13}	$= 1$
$P_{D4,Sac}$	$= 1$	P_{B21}	$= 1$
$P_{D7,Sac}$	$= 1$	P_{B22}	$= 1$
$S_{D7,Geo}$	$= 1$	P_{B23}	$= 1$
$P_{D2,Geo}$	$= 1$	P_{C1}	$= 0$
$P_{D3,Geo}$	$= 1$	P_{D1}	$= 1$
$P_{D4,Geo}$	$= 1$	$P_{D2,Sac}$	$= 1$
$P_{D5,Geo}$	$= 1$	$P_{D3,Sac}$	$= 1$
$P_{D7,Geo}$	$= 1$	$P_{D4,Sac}$	$= 1$
$P_{A8,Geo}$	$= 1$	$P_{E1,Sac}$	$= 1$
$P_{A9,Geo}$	$= 1$	$P_{D2,Geo}$	$= 1$
$P_{E1,Geo}$	$= 1$	$P_{D3,Geo}$	$= 1$
$S_{A8,Geo}$	$= 1$	$P_{A8,Geo}$	$= 1$
		$P_{E1,Geo}$	$= 1$
		$S_{A8,Geo}$	$= 1$

Appendix Table 1.3.—Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2007 (R_1) and January, 2008 (R_2). Parameters not estimated are indicated by an "NA" in the estimate column, and parameters fixed at a constant value are noted by an "NA" in the profile likelihood column.

	R_1: December 2007		R_2: January 2008	
Parameter	Estimate (SE)	95% Profile likelihood interval	Estimate (SE)	95% Profile likelihood interval
S_{A1}	0.951 (0.019)	0.907, 0.981	0.975 (0.020)	0.927, 1.000
S_{A2}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A3}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A4}	0.841 (0.055)	0.715, 0.928	0.942 (0.032)	0.857, 0.985
S_{A5}	0.874 (0.062)	0.734, 0.984	0.914 (0.061)	0.785, 1.000
S_{A6}	0.843 (0.075)	0.671, 0.963	0.728 (0.078)	0.563, 0.864
S_{A7}	0.886 (0.068)	0.733, 1.000	0.890 (0.058)	0.758, 1.000
S_{A8}	0.618 (0.090)	0.441, 0.789	0.548 (0.087)	0.380, 0.716
S_{B11}	0.715 (0.087)	0.534, 0.876	0.600 (0.155)	0.299, 0.855
S_{B12}	0.692 (0.128)	0.423, 0.893	1.000	NA
S_{B13}	0.308 (0.149)	0.087, 0.623	0.765 (0.221)	0.282, 1.000
S_{B21}	0.800 (0.103)	0.560, 0.946	0.923 (0.074)	0.702, 0.995
S_{B22}	0.790 (0.094)	0.576, 0.929	1.000	NA
S_{B23}	0.616 (0.130)	0.360, 0.841	0.728 (0.123)	0.464, 0.921
S_{C1}	0.286 (0.121)	0.099, 0.545	NA	
$S_{D1,Sac}$	0.667 (0.111)	0.437, 0.852	0.818 (0.067)	0.665, 0.923
$S_{D1,Geo}$	0.814 (0.051)	0.702, 0.898	0.938 (0.027)	0.872, 0.977
S_{D2}	0.900 (0.039)	0.808, 0.959	0.932 (0.025)	0.873, 0.970
S_{D3}	0.862 (0.045)	0.758, 0.934	0.772 (0.051)	0.672, 0.885
S_{D4}	0.491 (0.073)	0.352, 0.635	0.395 (0.080)	0.262, 0.604
S_{D5}	0.658 (0.129)	0.411, 0.946	0.733 (0.180)	0.415, 1.000
S_{D6}	0.700 (0.145)	0.393, 0.915	0.709 (0.181)	0.155, 1.000
S_{D7}	1.000	NA	0.866 (0.159)	0.463, 1.000
$S_{E1,D5}$	1.000	NA	0.750 (0.288)	0.245, 1.000
$S_{E1,A8}$	0.433 (0.189)	0.130, 0.780	0.683 (0.279)	0.165, 1.000
ψ_{A1}	0.655 (0.042)	0.570, 0.733	0.802 (0.037)	0.722, 0.868
ψ_{B11}	0.230 (0.037)	0.163, 0.308	0.086 (0.026)	0.044, 0.147
ψ_{B21}	0.115 (0.028)	0.068, 0.178	0.112 (0.029)	0.063, 0.178
ψ_{A2}	0.592 (0.056)	0.481, 0.696	0.612 (0.053)	0.506, 0.711
ψ_{C2}	0.179 (0.043)	0.105, 0.273	0.000	NA
ψ_{D2}	0.230 (0.048)	0.146, 0.331	0.388 (0.053)	0.289, 0.494

Appendix Table 1.3.—Continued.

$\phi_{B11,B12}$	0.482 (0.096)	0.305, 0.674	0.400 (0.155)	0.146, 0.700
$\phi_{B11,B22}$	0.233 (0.077)	0.108, 0.403	0.200 (0.127)	0.036, 0.499
$\phi_{A7,A8}$	0.837 (0.074)	0.679, 0.978	0.781 (0.07)	0.634, 0.914
$\phi_{A7,E1}$	0.049 (0.034)	0.008, 0.143	0.109 (0.046)	0.040, 0.220
$\phi_{D4,D5}$	0.351 (0.070)	0.225, 0.497	0.354 (0.079)	0.225, 0.564
$\phi_{D4,E1}$	0.140 (0.049)	0.063, 0.253	0.041 (0.023)	0.010, 0.102
P_{A2}	0.959 (0.018)	0.915, 0.985	0.852 (0.034)	0.777, 0.910
P_{A3}	0	NA	0.000	NA
P_{A4}	0.949 (0.035)	0.850, 0.991	1.000	NA
P_{A5}	1.000	NA	1.000	NA
P_{A6}	0.821 (0.072)	0.655, 0.932	0.781 (0.073)	0.620, 0.899
P_{A7}	0.829 (0.064)	0.683, 0.928	0.850 (0.057)	0.719, 0.937
$P_{A8,Sac}$	0.905 (0.064)	0.734, 0.983	0.950 (0.049)	0.798, 0.997
$P_{A8,Geo}$	1.000	NA	0.950 (0.049)	0.798, 0.997
$P_{A9,Sac}$	0.812 (0.084)	0.618, 0.937	0.846 (0.071)	0.678, 0.949
$P_{A9,Geo}$	1.000	NA	0.846 (0.071)	0.678, 0.949
P_{B11}	1.000	NA	1.000	NA
P_{B12}	0.900 (0.095)	0.628, 0.994	1.000	NA
P_{B21}	1.000	NA	1.000	NA
P_{B22}	1.000	NA	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	1.000	NA	1.000	NA
P_{C1}	1.000	NA	NA	
P_{D1}	1.000	NA	1.000	NA
P_{D2}	1.000	NA	1.000	NA
P_{D3}	1.000	NA	1.000	NA
P_{D4}	1.000	NA	0.958 (0.041)	0.829, 0.998
P_{D5}	0.922 (0.075)	0.699, 0.995	0.500 (0.118)	0.133, 0.872
P_{D6}	0.778 (0.139)	0.458, 0.959	0.500 (0.134)	0.255, 0.745
P_{D7}	1.000	NA	0.385 (0.135)	0.046, 0.848
P_{E1}	1.000	NA	1.000	NA
λ	0.748 (0.082)	0.570, 0.883	0.759 (0.080)	0.585, 0.888

Appendix 2

Evaluation of bias in survival and route entrainment probabilities

Since a telemetry station at location A_3 was not implemented during 2008, the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B21} could not be uniquely estimated without imposing constraints on the parameters. Therefore, we estimated these parameters under the constraint that $S_{A2} = S_{A3}$. Although estimates from one release in 2007 showed little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press), station A_3 has not been monitored for three of the four releases thus far. If S_{A2} is not equal to S_{A3}, then associated estimates of route entrainment and survival probabilities will be biased. Here we evaluate the magnitude of bias introduced by assuming $S_{A2} = S_{A3}$, when in fact S_{A2} differs from S_{A3}.

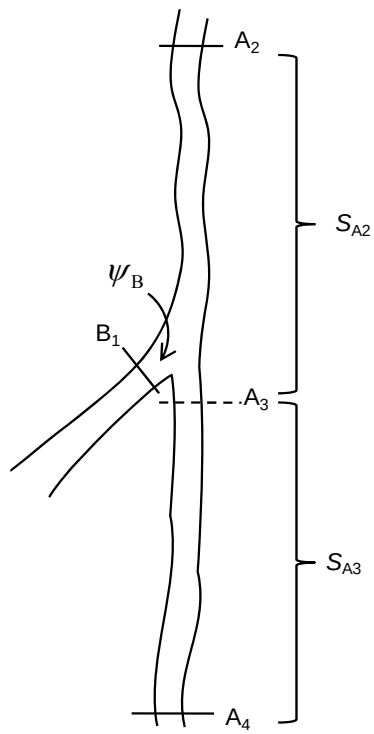
To illustrate the potential bias that might be incurred, we first simplified the problem by assuming a two-branch junction (Appendix Figure 2.1). We were interested not only in bias in ψ_B, but also in bias that might occur in the product $S_{A2}S_{A3}$. This product appears in equations for route specific survival through the Delta for Routes A, C, and D (i.e., S_h). Thus, bias in this product is more relevant than bias in each of the reach-specific survival probabilities. Appendix Figure 2.1 shows a schematic of the problem with the underlying survival and route entrainment parameters. Without a telemetry station at location A_3, only two parameters can be estimated from information provided by telemetry stations at B_1 and A_4. The two estimable parameters are the joint probabilities of the underlying parameters between stations A_2 and B_1, and between A_2 and A_4:

$$\phi_{\text{A2, B1}} = S_{\text{A2}}\psi_{\text{B}} \tag{A1}$$

$$\phi_{\text{A2, A4}} = S_{\text{A2}}S_{\text{A3}}\left(1-\psi_{\text{B}}\right) \tag{A2}$$

Where $\phi_{\text{A2, B1}}$ is the joint probability of surviving the first reach and entering channel B, and $\phi_{\text{A2, A4}}$ is the joint probability of surviving the first reach, remaining in channel A, and surviving the second reach. These two parameters can always be estimated without bias from the data, as can the total survival from A_2 to either of the downstream exit points:

$$S_{\text{total}} = \phi_{\text{A2, B1}} + \phi_{\text{A2, A4}} \tag{A3}$$



Appendix Figure 2.1.—Schematic of a two-branch river junction showing location of telemetry stations at A_2, B_2, and A_4. The dashed line notes lack of a telemetry station at A_3. Brackets show the probability of surviving between A_2 and A_3 and between A_3 and A_4. The probability of entering Channel B is Ψ_B, and the probability of remaining in Channel A is 1-Ψ_B.

To quantify bias, we substituted Eqns. A1 and A2 into Eqn. A3, set $S_{A3} = S_{A2}$, and then solved Eqn. A3 for S_{A2} and Eqn. A1 for ψ_B:

$$\tilde{S}_{A2} = \frac{\psi_B - \sqrt{\psi_B{}^2 - 4S_{total}\left(\psi_B - 1\right)}}{2\left(\psi_B - 1\right)} \tag{A4}$$

and $$\tilde{\psi}_B = \frac{\phi_{A2,\,B1}}{\tilde{S}_{A2}} \tag{A5}$$

Here, $\tilde{S}_{A2}$ and $\tilde{\psi}_B$ will be the biased estimates that result when assuming $S_{A2} = S_{A3}$ when in fact $S_{A2} \neq S_{A3}$; and S_{total} and $\phi_{A2,\,B1}$ are calculated based on the true values of S_{A2}, S_{A3}, and ψ_B.

Estimates of S_{total} from our data will be unbiased regardless of bias that might be present in estimates of S_{A2}, S_{A3}, or ψ_B, and we used this fact to establish the maximum possible bias that could arise by assuming $S_{A2} = S_{A3}$. For example, for the first release in December 2008, we

estimated $\hat{\psi}_B = 0.345$ and $\hat{S}_{A2} = \hat{S}_{A3} = 0.919$ (Appendix Table 1.3), resulting in $\hat{S}_{total} = 0.87$. Now suppose $\hat{\psi}_B = \tilde{\psi}_B = 0.345$ is the biased estimate of ψ_B: What true values of ψ_B , S_{A2}, and S_{A3} could have produced the observed estimate, $\tilde{\psi}_B$? First, the true parameter values ψ_B , S_{A2}, and S_{A3} are constrained such that $\hat{S}_{total} = 0.87$ (according to Eqn. A3) and $\tilde{\psi}_B = 0.345$ (according to Eqn. A5). Also, given that $\hat{S}_{total} = 0.87$, S_{A2} and S_{A3} are further constrained such that all of the observed mortality could have occurred in either the first reach (i.e., $S_{A3} = 1$) or the second reach (i.e., $S_{A2} = 1$). Clearly, mortality will occur in both reaches, but we used these two scenarios to bound the extremes of bias that could possibly occur given that $\hat{S}_{total} = 0.87$ and $\tilde{\psi}_B = 0.345$. Thus, maximum bias is calculated by setting $S_{A2} = 1$ (or $S_{A3} = 1$), and then finding the true values of S_{A3} (or S_{A2}) and ψ_B that satisfy $S_{total} = 0.87$ and $\tilde{\psi}_B = 0.345$. Should the maximum possible bias be low under these extreme scenarios, then we can infer that the realized bias would be even less.

Under these extreme scenarios, we found that maximum possible bias was quite low. For the December release, maximum absolute bias in ψ_B was less than 0.028, and bias in $S_{A2}S_{A3}$ was less than 0.035 (Appendix Table 2.1). Maximum possible bias for the January release was even less (Appendix Table 2.1). These findings suggest that the realized bias in these parameters will be much less than the maximum possible bias, given that we know mortality occurs in both reaches, and that past evidence suggests little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press). Our estimates are robust to deviations from $S_{A2} = S_{A3}$ partly due to the relatively high total survival (S_{total}) observed in this reach. Since S_{total} constrains the range of possible true values of S_{A2} and S_{A3}, as S_{total} decreases S_{A2} and S_{A3} may take on a wider range of values between 0 and 1. Thus, as S_{total} decreases, the possible maximum bias will increase under the extreme scenarios of all mortality occurring in either one reach or another.

Although this sensitivity analysis shows that bias was likely minimal, the appropriate course of action is to ensure a telemetry station is implemented at A_3 in future years. Given the influence of Sutter and Steamboat sloughs on migration dynamics through the entire Delta, this river junction is too important to rest future research on such assumptions.

Appendix Table 2.1.—Maximum possible bias induced by assuming $S_{A2} = S_{A3}$, when in fact, all mortality occurs in either the upstream reach or the downstream reach.

	True values				Estimates when assuming $S_{A2} = S_{A3}$		Bias	
Release	S_{A2}	S_{A3}	ψ_B	S_{total}	$\tilde{S}_{A2}$	$\tilde{\psi}_B$	$\psi_B - \tilde{\psi}_B$	$S_{A2}S_{A3} - \tilde{S}_{A2}^2$
R_1: December	0.870	1.000	0.364	0.870	0.918	0.345	-0.019	-0.025
	1.000	0.810	0.318	0.870	0.920	0.345	0.028	0.035
R_2: January	0.852	1.000	0.213	0.852	0.914	0.198	-0.014	-0.016
	1.000	0.819	0.182	0.852	0.915	0.198	0.017	0.017

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Sensitivity of survival to migration routes used by juvenile Chinook salmon to negotiate the Sacramento-San Joaquin River Delta

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Abstract Populations of juvenile salmon emigrating from natal rivers to the ocean must often traverse different migratory pathways that may influence survival. In regulated rivers, migration routes may consist of a network of channels such as in the Sacramento-San Joaquin River Delta, or of different passage structures at hydroelectric dams (e.g., turbines or spillways). To increase overall survival, management actions in such systems often focus on altering the migration routing of fish to divert them away from low-survival routes and towards high-survival routes. Here, we use a 3-year data set of route-specific survival and movement of juvenile Chinook salmon in the Sacramento-San Joaquin Delta to quantify the sensitivity of survival to changes in migration routing at two major river junctions in the Sacramento River. Our analysis revealed that changes in overall survival in response to migration routing at one river junction depended not only differences in survival among alternative routes, but also on migration routing at the other river junction. Diverting fish away from a low-survival route at the downstream river junction increased population survival by less than expected, given the difference in survival among routes, because part of the population used an alternative migration route at the upstream river junction. We also show that management actions that influence only migration routing will likely increase survival by less than actions that alter both migration routing and route-specific survival. Our analysis provides an analytical framework to help fisheries managers quantify the suite of management actions likely to maximize increases in population level survival.

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Introduction

Population dynamics of migrating fish depend on how they use space over time. Populations may traverse different migratory pathways en route to their final destination. For example, variation in ocean currents may affect migration pathways of adult salmon returning to their natal rivers (Bracis 2010). In regulated rivers, migrating juvenile salmon may negotiate dams via alternative pathways such as spillways or turbines (Skalski et al. 2002, 2009). In estuaries and river deltas, complex channel networks offer an array of possible migration routes (Perry et al. 2010). In each of these examples, survival rates may vary among migration routes due to differences in migration timing, food resources, environmental conditions, or predator abundance. Thus, understanding variation in survival among migration routes can provide important insights about population dynamics.

The Sacramento-San Joaquin River Delta (hereafter, the Delta) is a complex network of natural and man-made channels through which juvenile salmon must navigate on their journey to the ocean (Fig. 1). As juvenile salmon enter the Delta from natal streams, they disperse among the Delta's complex channel network. This dispersal process is driven by the relative quantities of discharge entering each channel, the horizontal distribution of fish in the water column as they pass a channel junction (a main channel splitting into two or more channels), and by tidal cycles that alter flow patterns at river junctions. Once fish enter a given channel, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. Eventually, alternative migration routes converge at the exit of the Delta and the population once again comes together to migrate through San Francisco Bay.

Movement of juvenile salmon among migration pathways in the Delta is influenced by water management actions that route water from the Sacramento and San Joaquin Rivers into pumping stations in the southern Delta. In this paper, we focus on the influence of water management actions on juvenile salmon emigrating from the Sacramento River. Specifically, the Delta Cross Channel is a man-made gated channel that diverts water from the Sacramento River into the interior Delta, where it then flows towards the pumping stations to be exported for agricultural and domestic uses (Fig. 1). Juvenile salmon entering the interior Delta exhibit lower survival probabilities than other migration routes, presumably due to longer migration times, entrainment at the pumping stations, and exposure to predators (Brandes and McLain 2001; Newman and Brandes 2010; Perry 2010). Furthermore, overall survival through the Delta (the fraction surviving through all routes) has averaged less than 33% for migration years 2007–2009 (Perry 2010).

Recovering endangered salmon populations in the Central Valley requires actions that mitigate the effects of water management on juvenile salmon. Increasing juvenile salmon survival in the Delta may consist of actions aimed at either reducing mortality within migration routes or directing the population away from low-survival migration routes such as the interior Delta. Quantifying potential benefits of implementing recovery actions can help fisheries managers weigh the costs of a given action against benefits measured in terms of increasing overall survival. In this study, we examine how altering migration routing can influence the overall survival of juvenile salmon.

In the Delta, migration routing of juvenile salmon can be altered in at least three ways. First, physical barriers, such as closure of the Delta Cross Channel gates, keep fish from entering a given migration route. However, physical barriers also alter the distribution of water flow, which can have unforeseen consequences on both fisheries and water resources. For example, closure of the Delta Cross Channel gates significantly alters the flows of many channels both upstream and downstream of the Delta Cross Channel, which in turn may affect entrainment and survival rates of multiple migration pathways. Closing the cross-channel gates can also increase the rate of salinity intrusion into the central Delta, ultimately reducing water exports in order to comply with mandated salinity standards. As this example shows, simply closing off a channel in the Delta is nontrivial, which has spurred investigation of alternative approaches for altering migration routing of salmon. For instance, non-physical behavioral barriers such as bubble curtains and strobe lights can elicit an avoidance response from juvenile salmon (Coutant 2001) while allowing water to flow unrestricted into a given channel.

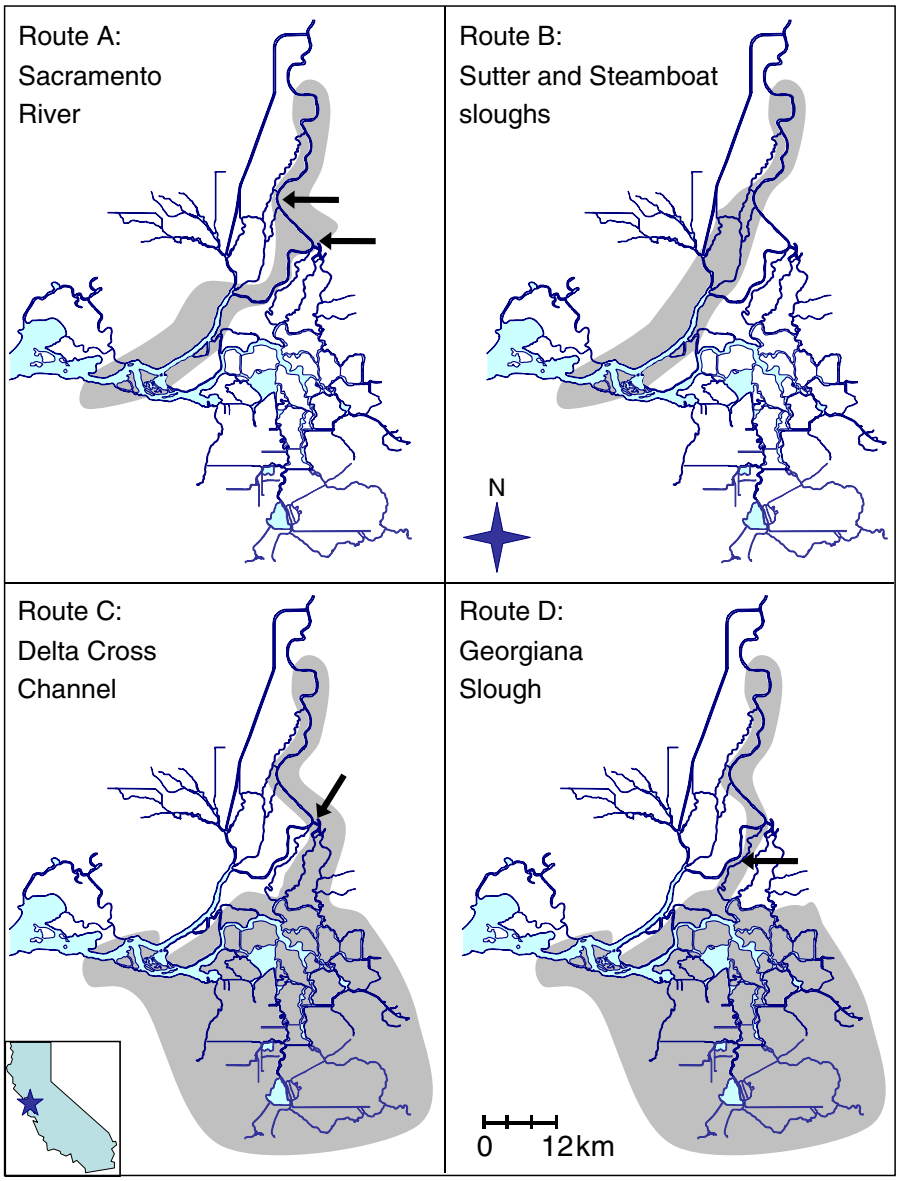

Fig. 1 Maps of the Sacramento–San Joaquin River Delta with shaded areas showing regions comprising survival through the Delta for four different migration routes. For each route, survival was estimated from Freeport on the Sacramento River (the northern most extent of the shaded area) to Chipps Island at the exit of the Delta (the western-most extent of the shaded area). In Route A, *arrows* show the two river junctions where migration routes diverge from the Sacramento River. For routes C and D, the interior Delta is the large shaded region to the south of the Sacramento River. The location of the Delta Cross Channel is indicated by the arrow in Route C. The Sacramento River release site (off the map) is 19 river kilometers upstream of Freeport, and the Georgiana Slough release site is shown by the arrow in Route D

Finally, behavioral responses to the hydrodynamics at junctions may play a role in the entrainment rates at a given river junction. Thus, structural changes in channel geometry at a river junction may provide a means of altering migration routing without changing the distribution of water flow. Currently, both physical and non-physical behavioral barriers are being investigated in the Delta in attempt to guide fish away from low-survival migration routes.

To quantify the influence of migration routing on overall survival, we used estimates of movement and reach-specific survival obtained from acoustically tagged juvenile salmon collected over 3 years. Biotelemetry techniques combined with mark-recapture statistical models provide a powerful tool to simultaneously quantify dispersal and survival of juvenile salmon migrating through the Delta. Uniquely identifiable transmitters provided detailed information about the temporal and spatial movements of individuals migrating through a series of monitoring stations in the Delta. This information was then synthesized using a multistate mark-recapture model that quantified dispersal of the population among migration routes and survival within these routes (Perry et al. 2010). Simultaneously estimating these quantities allowed overall survival to be derived from each of

these components. For this exercise, we examined the sensitivity of overall survival to migration routing by altering the distribution of fish at critical river junctions and then used the observed route-specific survival estimates to quantify how such actions would affect overall survival in the Delta.

Methods

To examine how migration routing influences overall survival of juvenile Chinook salmon in the Delta (S_{Delta}), we used estimates of survival and routing probabilities provided by Perry et al. (2010) for the 2007 migration year and Perry (2010) for the 2008 and 2009 migration years. Route-specific survival, the fraction of fish migrating through each route, and overall survival were estimated from acoustic-tagged juvenile salmon using a multistate mark-recapture model applied to detection data from a system of telemetry stations situated throughout the Delta.

Telemetry system

Telemetry stations monitored movement of tagged fish among four primary migration routes through the Delta (Fig. 1): the mainstem Sacramento River (Route A); Sutter and Steamboat sloughs (Route B); the interior Delta via the Delta Cross Channel (Route C); and the interior Delta via Georgiana Slough (Route D). Each telemetry station consisted of single or multiple monitors (Vemco Ltd., Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. The number of telemetry stations varied among years (14, 23, and 20 stations in 2007, 2008, and 2009, respectively), but stations needed to estimate migration routing and survival to the terminus of the Delta remained constant among years. Detailed maps of the each year's telemetry system can be found in Perry (2010).

Fish tagging and release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery in Anderson, California. For the first release in December 2006, a 1.44-g tag (Vemco Ltd., Model V7-1L-R64K, 40-d expected battery life) was used. For all other releases, we used a 1.6-g tag (Vemco Ltd., Model V7-2L-R64K, 70-d expected battery life). Fish above 140 mm fork length were randomly selected for tagging. Transmitters were surgically implanted into fish using methods described by Perry et al. (2010).

To release tagged fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (all years) or Georgiana Slough (2008 and 2009; Fig. 1). The Georgiana Slough release site was added for 2008 and 2009 to increase the number of fish entering the interior Delta. In 2007 and 2008, fish were transferred to net pens (3-m square holding nets supported by pontoons) at the release site and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. For 2009, fish were transferred to perforated 121-L containers (2 fish per bucket) and held for 24 h in-river prior to release. Each release was carried out over a 24-h period to distribute tagged fish over the tidal and diel cycle. Two releases were performed in each migration year; one in December and another in January. For example, in migration year 2007, fish were released in December, 2006 when the Delta Cross Channel was open, and again in January, 2007 when the Delta Cross Channel was closed.

Linking migration routing to overall survival

The mark-recapture model described by Perry et al. (2010) estimates three sets of parameters: detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (Ψ_{hl}; Perry 2010; Perry et al. 2010). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h=A, B, C, D). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to i+1 within route h, conditional on surviving to station i. Route entrainment probabilities (Ψ_{hl}) estimate the probability of a fish entering route h at junction l (l=1, 2), conditional on fish surviving to junction l. Estimates of these parameters can be found in Perry (2010).

The first river junction was modeled as a two-branch junction where the entrance to Sutter and Steamboat Slough was pooled to estimate a single route entrainment probability. The parameter Ψ_{B1} estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Fig. 2). Conversely, $1 - \Psi_{\mathrm{B1}} = \Psi_{\mathrm{A1}}$ is the probability

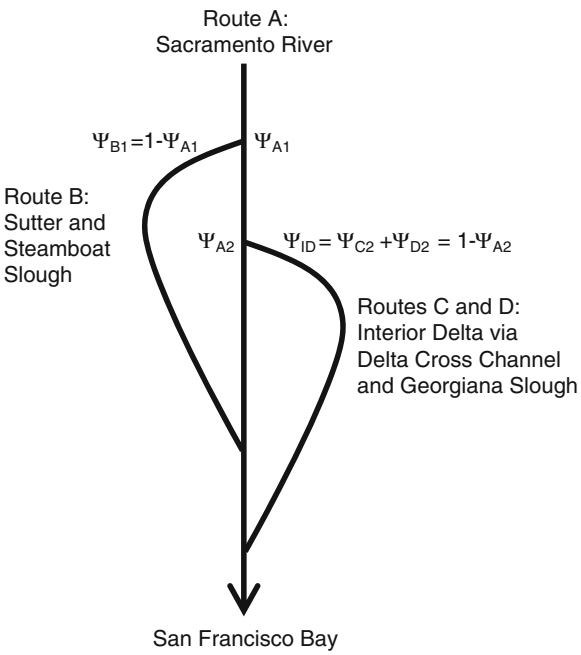

Fig. 2 Schematic showing the simplified routing structure and route entrainment probabilities (Ψ_{hl}) at each river junction

of remaining in the Sacramento River at the first junction. The second junction was modeled as a three-branch junction where Ψ_{A2}, Ψ_{C2}, and $1 - \Psi_{A2} - \Psi_{C2} = \Psi_{D2}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2.

The mark-recapture model estimates the individual components that comprise survival of the population migrating through the Delta, defined as survival of tagged fish from the entrance to the Delta at Freeport (rkm 73) to the exit of the Delta at station Chipps Island (rkm -9), a distance of 82 km by way of the Sacramento River. Overall survival through the Delta was estimated from the individual components as:

$$S_{\text{Delta}} = \sum_{h=\text{A}}^{\text{D}} \Psi_h S_h \tag{1}$$

where S_h is the probability of surviving the Delta given the specific migration route used to negotiate the Delta, and Ψ_h is the probability of migrating through the Delta via one of four migration routes (A=Sacramento River, B=Sutter and Steamboat sloughs, C=Delta Cross Channel, D=Georgiana Slough). Overall survival through the Delta is a weighted average of the route-specific survival probabilities with weights equal to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\Psi_{\text{A}} = \Psi_{\text{A1}}\Psi_{\text{A2}} \tag{2}$$

$$\Psi_{\text{B}} = \Psi_{\text{B1}} \tag{3}$$

$$\Psi_{\text{C}} = \Psi_{\text{A1}}\Psi_{\text{C2}} \tag{4}$$

$$\Psi_{\text{D}} = \Psi_{\text{A1}}\Psi_{\text{D2}} \tag{5}$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability Ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability Ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (Ψ_C) is the product of these route entrainment probabilities, $\Psi_{A1}\Psi_{C2}$.

Survival through the Delta for a given migration route (S_h) is the product of the reach-specific survival probabilities (S_{hi}) that trace each migration path between the entrance to the Delta and its terminus at Chipps Island. Thus, S_h is comparable among years even though annual differences in the telemetry system resulted in different reaches over which S_{hi} was estimated. Furthermore, S_h is directly comparable among routes because it estimates survival between the same starting and ending locations, but for fish migrating through different routes.

For our analysis, we focused on the probability of entering the interior Delta (Ψ_{ID}), which is the sum of the route entrainment probabilities for the Delta Cross Channel (Ψ_{C2}) and Georgiana Slough (Ψ_{D2}, Fig. 2). Survival through the interior Delta was estimated as the average survival of fish entering Routes C and D, weighted by the entrainment probabilities for each route. We aggregated Routes C and D for this analysis because survival estimates for fish entering the interior Delta were consistently lower than other routes (Fig. 3) regardless of whether fish entered the interior Delta via the Delta Cross Channel or Georgiana Slough. Thus, the specific

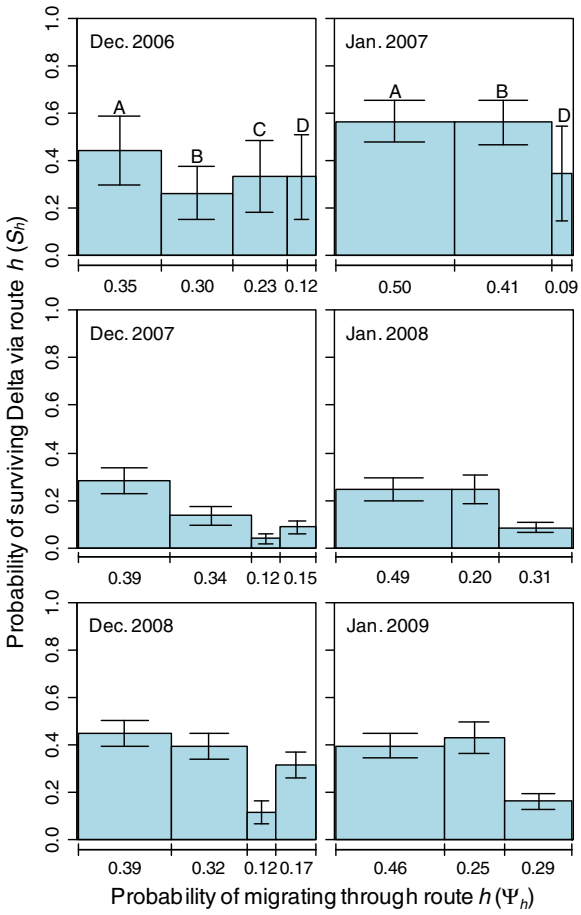

Fig. 3 Route-specific survival and the fraction of the population migrating through each migration route in the Sacramento – San Joaquin River Delta (from Perry et al. 2010; Perry 2010). Migration routes are labeled as follows: A=Sacramento River, B=Sutter and Steamboat sloughs, C=Delta Cross Channel, D=Georgiana Slough. Error bars show ±1 standard error

route used to enter the interior Delta is immaterial with respect to the sensitivity of overall survival to Ψ_{ID}.

Influence of migration routing on S_{Delta}

To quantify the influence of migration routing on S_{Delta}, we examined the change in S_{Delta} caused by varying route entrainment probabilities while holding constant the route-specific survival probabilities. Specifically, we examined the change in S_{Delta} when varying 1) the probability of fish entering Sutter and Steamboat sloughs (Ψ_{B1}), and 2) the conditional probability of entering the interior Delta (Ψ_{ID}), given fish that remained in the Sacramento River at its junction with Sutter and Steamboat Slough (Fig. 2). For each release group, we varied entrainment probabilities between zero and one at each river junction, and then recalculated S_{Delta}. We then quantified the predicted change in S_{Delta} relative to the observed estimate of S_{Delta} as both the absolute (i.e., additive) and relative (i.e., proportional) difference. This approach provides an understanding of how S_{Delta} might have changed had survival probabilities been the same but migration routing different for each release group.

To understand the response of S_{Delta} to changes in Ψ_{hl}, we also used demographic analysis techniques for matrix population models, which can be generalized to any transition matrix. For a Leslie matrix, sensitivity and elasticity measure the additive and proportional change in λ, the finite rate of population change, with respect to each demographic parameter in the model (Caswell 2001). In our case, S_{Delta} is analogous to λ in that it measures the rate of population change between the beginning and ending points of the Delta. Applying these techniques to our model, sensitivity is calculated as

$$s_{\Psi_{hl}} = \frac{\partial S_{Delta}}{\partial \Psi_{hl}} \tag{6}$$

and elasticity as

$$e_{\Psi_{hl}} = \frac{\Psi_{hl}}{S_{Delta}} \frac{\partial S_{Delta}}{\partial \Psi_{hl}}, \tag{7}$$

where $s_{\Psi_{hl}}$ and $e_{\Psi_{hl}}$ are sensitivity and elasticity with respect to a given route entrainment probability, Ψ_{hl}.

Sensitivity and elasticity can be interpreted in a number of ways to provide insights into how route entrainment probabilities affect S_{Delta}. First, sensitivity measures the slope of the relationship between absolute changes in S_{Delta} and Ψ_{hl}, while elasticity measures the slope of proportional changes in S_{Delta}. The steeper the slope, the larger will be the effect on S_{Delta} from a given change in Ψ_{hl}. Positive estimates indicate that increasing Ψ_{hl} will increase S_{Delta}, whereas negative values indicate that increasing Ψ_{hl} will reduce S_{Delta}. Second, sensitivity and elasticity can be interpreted as the additive and proportional change in S_{Delta}, respectively, when increasing Ψ_{hl} from zero to one. For example, if $s_{\Psi_{ID}} = -0.20$ then increasing Ψ_{ID} from zero to one will reduce S_{Delta} by 20 percentage points (e.g., from 0.50 to 0.30). In contrast, $e_{\Psi_{ID}} = -0.20$ indicates a 20% change in S_{Delta} (e.g., from 0.50 to 0.40). Last, applying Eq. 6 to S_{Delta} Eq. 1

yields a formula for the slope as a function of the route survival and entrainment parameters, elucidating which parameters affect the sensitivity of S_{Delta} to route entrainment probabilities. Although differences in survival among routes will certainly influence sensitivity of S_{Delta} to migration routing, sensitivity will also be a function of routing at both river junctions.

Last, we predicted S_{Delta} by varying both Ψ_{B1} and Ψ_{ID} simultaneously to quantify the range in overall survival that could be obtained by altering entrainment at both river junctions. Such insights will help fisheries managers better understand how to target management actions aimed at altering route entrainment probabilities in order to maximize overall survival in the Delta.

Results

Interannual patterns in route-specific survival and migration probabilities

We observed substantial variation in the magnitude of within-route survival among years, yet stable patterns of survival across routes over all years (Perry 2010; Perry et al. 2010). Among migration years, 2008 stands out as having the lowest survival at both the route scale and the Delta scale (Fig. 3). Survival through the Delta was <0.20 for 2008, but >0.33 for all other years and releases (Table 1). Over all years, estimates of S_{Delta} exceeded 0.40 for only one release group (Jan. 2007), and only during migration year 2007 did observed estimates of S_{Delta} differ considerably between releases (Table 1). For all releases, detection probabilities (P_{hi}) were high at most sites (median=1.0, mean=0.915, minimum=0.385), leading to favorable precision of survival probabilities relative to releases sample sizes (Table 1, Fig. 3).

Although rankings of route-specific survival vary somewhat across release groups, one pattern remained consistent: survival probabilities for the Sacramento River were always greater than survival for migration routes through the interior Delta (via Georgiana Slough and the Delta Cross Channel; Fig. 3). In addition, Sutter and Steamboat sloughs exhibited either similar survival to the Sacramento River (typically for January releases) or lower survival than the Sacramento River (typically for December releases; Fig. 1). Except for the Dec. 2007 release group, observed survival estimates for Sutter and Steamboat Sloughs were greater than for routes leading to the interior Delta.

Sensitivity of S_{Delta} to route entrainment probabilities

The effect of varying route entrainment probabilities on overall survival differed among river junctions. At the first river junction, sensitivity of S_{Delta} to entrainment into Sutter and Steamboat Slough (Ψ_{B1}) followed no consistent trend among releases. Increasing Ψ_{B1} decreased S_{Delta} for two of the releases, increased it for two releases, and resulted in a slight positive change in S_{Delta} for two releases (Table 1; Fig. 4a, b). In addition, the standard errors for sensitivity and elasticity of Ψ_{B1} indicate that the 95% confidence intervals overlap

Table 1 Sensitivity of S_{Delta} to route entrainment probabilities for Sutter and Steamboat sloughs and the interior Delta. Also shown is sample size and estimates of S_{Delta} for each release group (from Perry et al. 2010, Perry 2010). Standard errors are given in parentheses and were based on variances estimated using the Delta method

Release group	Number released	S_{Delta}	Sutter and Steamboat Slough, Ψ_{B1}		Interior Delta, $\Psi_{ID} = \Psi_{C2}+\Psi_{D2}$	
			Sensitivity	Elasticity	Sensitivity	Elasticity
Dec. 2006	64	0.351 (0.101)	−0.125 (0.116)	−0.105 (0.098)	−0.078 (0.123)	−0.111 (0.175)
Jan. 2007	80	0.543 (0.070)	0.030 (0.101)	0.023 (0.077)	−0.129 (0.126)	−0.036 (0.038)
Dec. 2007	208	0.174 (0.031)	−0.059 (0.042)	−0.117 (0.085)	−0.142 (0.038)	−0.331 (0.085)
Jan. 2008	211	0.195 (0.034)	0.062 (0.051)	0.063 (0.052)	−0.127 (0.041)	−0.252 (0.073)
Dec. 2008	292	0.368 (0.037)	0.038 (0.058)	0.033 (0.050)	−0.148 (0.045)	−0.170 (0.053)
Jan. 2009	292	0.339 (0.035)	0.125 (0.071)	0.093 (0.054)	−0.176 (0.044)	−0.200 (0.054)

zero for all release groups (95% confidence interval=estimate ± 1.96*SE). In contrast, at the second river junction, increasing entrainment into the interior Delta (Ψ_{B1}) decreased S_{Delta} for every release group, and the confidence intervals for four of the six releases exclude zero (Table 1; Fig. 4c, d).

Changes in S_{Delta} in response to migration routing at a given junction are driven partly by differences in survival among migration routes and partly by entrainment probabilities at other river junctions. For example, for the two releases where S_{Delta} declined when increasing Ψ_{B1} (Dec. 2006 and Dec. 2007; Fig. 4a, b), the negative slope was driven by lower survival in Sutter and Steamboat Sloughs than in the Sacramento River (Fig. 3). For all other releases, survival was similar between the Sutter and Steamboat Sloughs (Route B) and the Sacramento River (Route A, Fig. 3), yet S_{Delta} responded positively to increasing the proportion of fish entering Sutter and Steamboat Slough (Table 1; Fig. 4a, 4a). Examining the equation for sensitivity of S_{Delta} with respect to Ψ_{B1} reveals why this pattern emerges:

$$s_{\Psi_{B1}} = (S_B - S_A) + \Psi_{ID}(S_A - S_{ID}).$$

The first term shows that sensitivity is partly a function of the difference in survival between the Sacramento River and Sutter and Steamboat sloughs (S_B-S_A). However, the second term in the equation shows

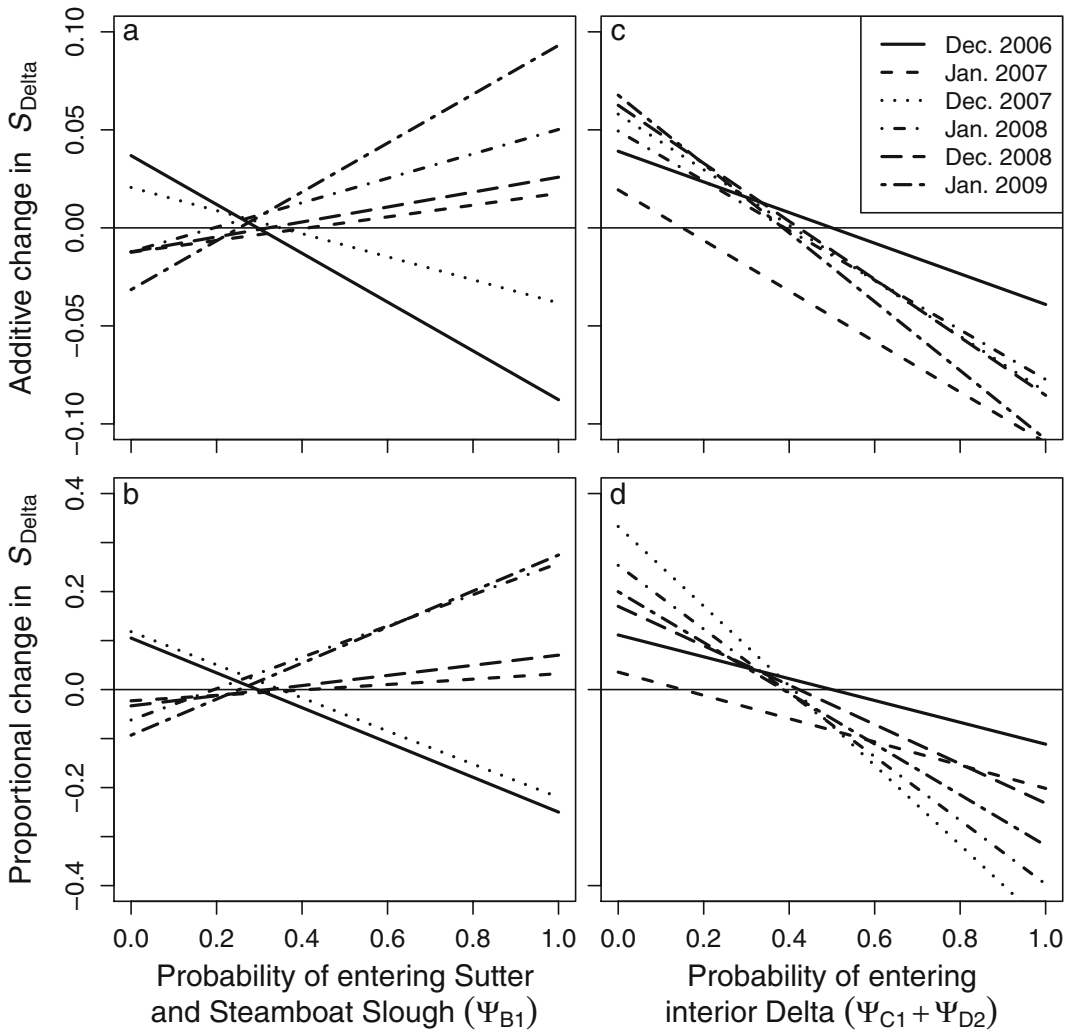

Fig. 4 Predicted change in estimates of S_{Delta} for each release group in response to varying route entrainment probabilities between zero and one

that sensitivity is also driven by 1) the probability of entrainment into the interior Delta (Ψ_{ID}), and 2) the difference in survival between the Sacramento River and interior Delta (S_A-S_{ID}). Consequently, when survival for Sutter and Steamboat sloughs is on par with the Sacramento River (S_B - $S_A \approx 0$), increasing Ψ_{B1} increases S_{Delta} by routing fish away from the interior Delta where survival was lower than the Sacramento River.

At the second river junction, increasing entrainment into the interior Delta always reduced S_{Delta} because survival for the interior Delta (Routes C and D) was lower than the Sacramento River (Route A) for all release groups (Fig. 3). However, the magnitude of change in S_{Delta} depends on not only differences in survival between these routes, but also on the fraction of the population remaining in the Sacramento River at the first river junction:

$$s_{\Psi_{ID}} = \Psi_{A1}(S_{ID} - S_A).$$

Although the difference in survival between these routes determines the direction of change in S_{Delta}, Ψ_{A1} scales the magnitude of change. For example, for the Jan. 2009 release group, survival of fish entering the interior Delta was 0.235 less than the Sacramento River (i.e., $S_{ID} - S_A$=0.163–0.398). But because 25% of the tagged population entered Sutter and Steamboat Slough at the first river junction (Fig. 3), the maximum possible change in S_{Delta} is only 0.175 when changing Ψ_{ID} from one to zero (Table 1). These findings illustrate how the magnitude of change in S_{Delta} from altering entrainment at one river junction depends not only on differences in survival between alternative routes, but also on the fraction of the population passing the river junction.

Eliminating entrainment into the interior Delta is expected to result in a 2–7 percentage point increase in overall survival (Fig. 4c). As discussed above, the magnitude of this change is, in part, due to only a fraction of the tagged population passing by this river junction. However, the small absolute increase in survival is also due to low survival probabilities observed in all routes. Route-specific survival for all routes was <0.5 for most release groups (Fig. 3). Thus, while shifting the distribution of fish among routes influences overall survival, the magnitude of absolute change in S_{Delta} is constrained by maximum survival observed in any given route. Further increases in S_{Delta} would require management actions that affect not only migration routing, but also survival within migration routes.

In contrast, proportional changes in S_{Delta} provide insight into the relative change in survival in response to altering route entrainment probabilities. S_{Delta} varied considerably among years (Table 1) even though relative differences in survival between the Sacramento River and interior Delta remained consistent among years (Fig. 3). Therefore, given interannual variation in overall survival, proportional changes in S_{Delta} allow comparison among release groups on a common relative scale. From this perspective, the relative change in S_{Delta} is considerably larger than the absolute change, increasing by 10–35% for five of the six releases in response to eliminating entrainment into the interior Delta. This analysis shows how understanding changes in S_{Delta} on both absolute and relative scales is important, particularly when overall survival is low and varies through time.

Altering entrainment at both river junctions simultaneously revealed that 1) overall survival could vary considerably in response to migration routing, 2) the optimal strategy for maximizing survival varied among releases, and 3) sensitivity of overall survival to entrainment at one junction depended the value of entrainment at the other river junction. Depending on release group, maximum S_{Delta} was 1.5 to 2.4 times the minimum survival (Fig. 5). Although survival can be maximized simply by directing fish to the highest-survival route, the set of entrainment probabilities that maximize survival varied among release groups. For December releases, since the Sacramento River (Route A) exhibited higher survival than other routes, overall survival is maximized when all fish remain in the Sacramento River (i.e., when Ψ_{B1}=0 and Ψ_{ID}=0; Fig. 5). However, for January release groups, overall survival is maximized by minimizing entrainment into the interior Delta but maximizing entrainment in Sutter and Steamboat Slough. Because survival in the Sacramento River was similar to Sutter and Steamboat Slough during January releases, diverting fish into Sutter and Steamboat Slough maximizes overall survival by routing fish away from the second river junction where they become exposed to entering the interior Delta.

Simultaneously altering entrainment probabilities at both river junctions illustrated how sensitivity of S_{Delta} to entrainment at one junction depends on the value of entrainment at the other river junction (Fig. 5). Vertical

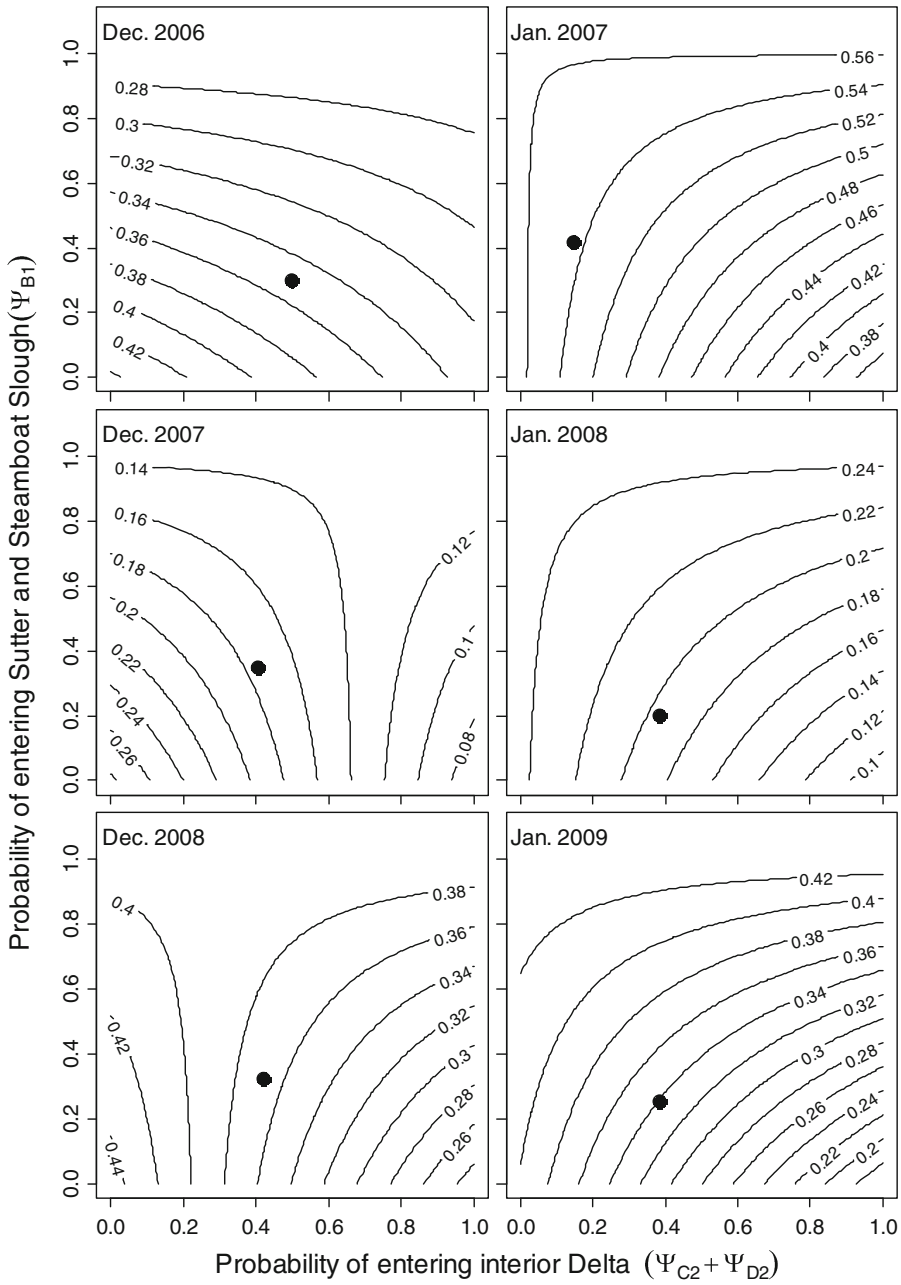

Fig. 5 Contour plot showing overall survival through the Sacramento – San Joaquin River Delta (S_{Delta}) predicted as a function of entrainment probabilities into the interior Delta and Sutter and Steamboat Slough. *Filled circles* show the observed overall survival and route entrainment probabilities for each release group

contour lines in Fig. 5 indicate regions where S_{Delta} is insensitive to Ψ_{B1}, horizontal contour lines reveal insensitivity to Ψ_{ID}, and closely-spaced contour lines reveal regions of high sensitivity. For example, as entrainment into Sutter and Steamboat Slough increases, S_{Delta} becomes less sensitive to changes in Ψ_{ID} because most of the population is diverted away from the second river junction. For January releases, S_{Delta} is insensitive to Ψ_{B1} when Ψ_{ID} is low, as is indicated by the wide range of Ψ_{B1} that yields similar overall survival. These relationships help to understand how survival through Delta varies in response to migration routing.

Discussion

Our analysis reveals the magnitude of change in overall survival that might be expected from management

actions that alter migration routing through the Delta. Given the substantial difference in survival between the interior Delta and the Sacramento River, we might have expected a larger boost in survival from eliminating entrainment into the interior Delta. In a simpler system with only one branching junction (e.g., a dam), change in overall survival with respect to migration routing is directly proportional to the difference in survival among migration routes. However, due to the channel complexity of the Delta, altering migration routing at one river junction yields changes in S_{Delta} that are less than proportional to the difference in survival between alternative migration routes. We showed that changes in S_{Delta} with respect to migration routing at one river junction depends also on migration routing at other river junctions. Therefore, by considering how management actions at multiple river junctions affect S_{Delta}, managers may be able to optimize the suite of actions required to maximize the expected increase in S_{Delta}. These are important insights about the magnitude of increase in S_{Delta} expected from management actions to alter migration routing.

The strength of inferences from acoustic tag data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Potential tag effects on survival (Adams et al. 1998) or differences in survival between hatchery and wild fish (Reisenbichler and McIntyre 1977; Kostow 2004) could result in lower absolute survival of tagged fish relative to untagged fish. In our study, although it is unknown whether tagged fish of hatchery origin exhibit lower survival than untagged fish of wild origin, absolute changes in survival should be interpreted with caution (i.e., Fig. 4a, c). Regardless of the absolute magnitude of survival, however, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival relative to fish migrating within the Sacramento River. Therefore, relative changes in survival in response to altering migration routing (i.e., Fig. 4c, d) should provide stronger inferences to untagged populations than will absolute change in survival probabilities.

We focused our analysis on river junctions where management actions are likely to have the largest influence on population survival. For example, we showed that Steamboat and Sutter Slough is an important migration route because fish using this route avoid entering the interior Delta where survival is lower than other routes. The Delta's channel geometry is hierarchical in nature such that secondary (and finer level) migration routes are nested within primary routes. At each secondary and tertiary river junction, the population divides into a smaller and smaller fraction of the whole. Therefore, management actions focused at secondary junctions will have less population-level influence than at primary river junctions simply because a small fraction of the population will be influenced. In contrast, management actions have the potential for influencing much of the population at the two primary river junctions examined in our analysis.

Sensitivity and elasticity measure changes in S_{Delta} with respect to migration routing at a junction while holding all other parameters constant. Thus, our analysis assumes that management actions alter only migration routing but not route-specific survival probabilities. This assumption may be violated in two ways. First, changing migration routing will alter the abundance of juvenile salmon in each route, which could cause a density dependent predator response. At very low prey densities, increasing smolt abundance within a route could increase predation rates via the predator's numerical or functional response to prey. In contrast, increasing smolt abundance to high levels within a route could reduce predation rates through predator swamping. Second, management actions that affect water routing at a particular junction (e.g., physical barriers) could influence route-specific survival or entrainment at other junctions by changing discharge and hydrodynamics within a migration route. For example, physical barriers alter discharge entering each channel, and juvenile salmon survival has been positively correlated with discharge in the Delta (Newman and Rice 2002; Perry 2010). Such simultaneous changes in migration routing and route-specific survival are not captured by our analysis.

In terms of the magnitude of change in population survival, managers must consider both the expected change in migration routing and the expected change in route-specific survival caused by implementation of physical and non-physical barriers. With respect to migration routing, physical barriers are 100% effective whereas non-physical barriers typically divert less than 100% of fish. Therefore, under the assumption of constant route-specific survival, non-physical barriers would realize only a fraction of the maximum possible increase in population survival. With respect to route-specific survival, physical barriers may yield

a larger change in survival than non-physical barriers because physical barriers alter discharge and hydrodynamics of each migration route. However, the direction and magnitude of change in route-specific survival in response to physical and non-physical barriers is poorly understood. This uncertainty highlights the importance of quantifying simultaneous changes in both migration routing and route-specific survival in field studies evaluating physical and non-physical barriers in the Delta.

Our sensitivity analysis has application to other regulated river systems where managers must balance the costs of water management actions against benefits to fish populations. On the Columbia River, for example, millions of dollars are spent annually to evaluate survival of juvenile salmon migrating past dams. Management actions such as spilling water over dams results in foregone power generation but improves population survival of juvenile salmon by diverting them away from turbines. Our analytical approach could be used to quantify expected changes in population survival by implementing such actions, helping managers to better design dam operations to achieve recovery targets at minimum cost. More importantly, in the Delta and other regulated river systems, our analytical approach can be used to help design recovery actions before such actions are implemented. Given scarce resources with which to recover endangered salmon populations, such analyses can help direct resources towards actions most likely to yield the largest improvement in survival.

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Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary

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Abstract. We examined trends in abundance of four pelagic fish species (delta smelt, longfin smelt, striped bass, and threadfin shad) in the upper San Francisco Estuary, California, USA, over 40 years using Bayesian change point models. Change point models identify times of abrupt or unusual changes in absolute abundance (step changes) or in rates of change in abundance (trend changes). We coupled Bayesian model selection with linear regression splines to identify biotic or abiotic covariates with the strongest associations with abundances of each species. We then refitted change point models conditional on the selected covariates to explore whether those covariates could explain statistical trends or change points in species abundances. We also fitted a multispecies change point model that identified change points common to all species. All models included hierarchical structures to model data uncertainties, including observation errors and missing covariate values. There were step declines in abundances of all four species in the early 2000s, with a likely common decline in 2002. Abiotic variables, including water clarity, position of the 2‰ isohaline (X2), and the volume of freshwater exported from the estuary, explained some variation in species' abundances over the time series, but no selected covariates could explain statistically the post-2000 change points for any species.

Key words: change point; delta smelt; hierarchical Bayes; longfin smelt; Sacramento–San Joaquin Delta, California, USA; striped bass; threadfin shad; upper San Francisco Estuary, California, USA.

Introduction

Declines in ecological condition across large areas are increasingly common around the world (e.g., Sala et al. 2000, Palmer et al. 2008, Cunningham et al. 2009), reflecting the increase in scope and intensity of human land use during the past century. The condition of estuaries has declined as a result of changing levels of terrestrial, freshwater, and marine stressors, including toxicants, nutrient enrichment, reduction of freshwater inputs, commercial and recreational harvest, dredging, and invasions of nonnative species (Lotze et al. 2006). The San Francisco Estuary, California, USA, experiences all of these stressors, and populations of many aquatic species have declined since intensive human activities began in the mid-1800s (Bennett and Moyle 1996, Brown and Moyle 2005).

The San Francisco Estuary is the largest estuary on the Pacific coast of North America and consists of four major regions: San Francisco Bay, the most seaward region; San Pablo Bay and Suisun Bay, two intermediate brackish regions; and the generally freshwater Sacramento–San Joaquin Delta (Fig. 1). The Delta is at the core of a massive system of dams and canals that store and divert water from the estuary for agricultural, industrial, and domestic use in central and southern California (Nichols et al. 1986). The water diversion facilities export ~30% of the freshwater flow into the Delta on average, although that percentage has exceeded 60% during many recent summers (Kimmerer 2004).

The social, economic, and ecological effects of freshwater flows and diversions throughout the San Francisco Estuary have received tremendous attention. About 25 million Californians and 12 000 km^2 of agricultural land rely on water diversions from the Delta. Annual agricultural revenue from California's Central Valley, which accounts for about half of the

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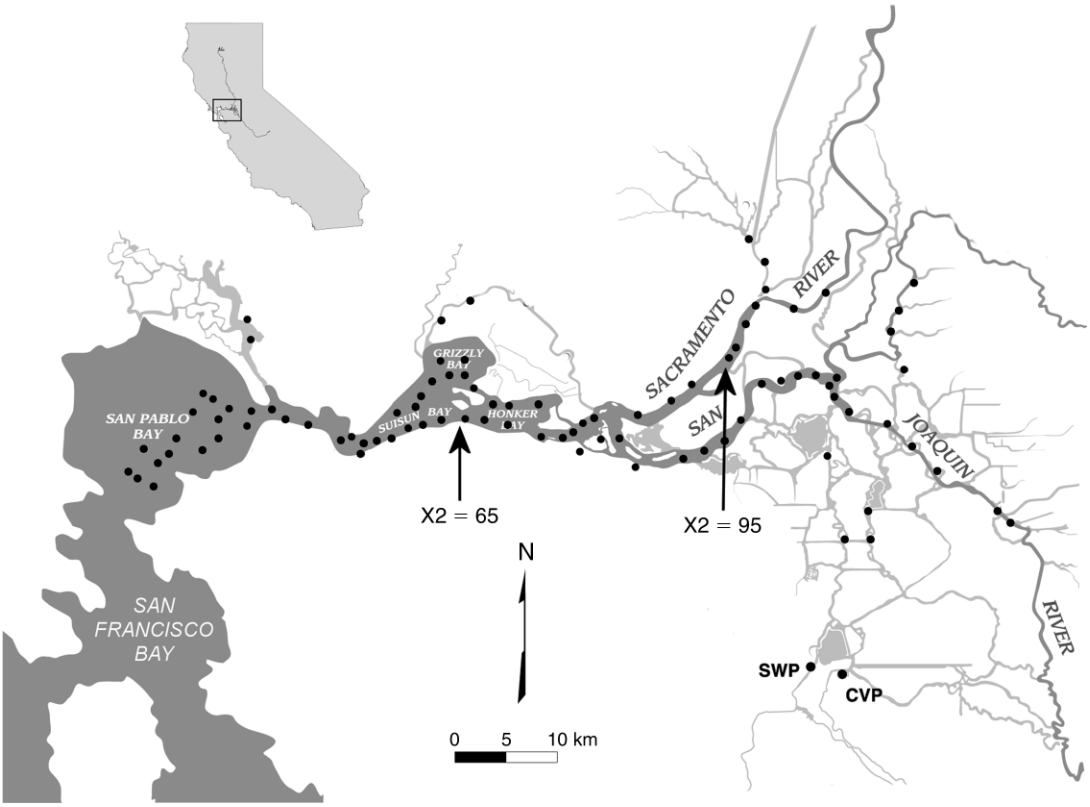

FIG. 1. Location and physiography of the upper San Francisco Estuary, California, USA. Solid circles denote sampling locations of the autumn midwater trawl surveys; arrows indicate two representative positions of the 2‰ isohaline (X2); SWP (State Water Project) and CVP (Central Valley Project) are locations of water exports from the estuary.

production of fruits and vegetables in the United States, frequently approaches US$15 billion. Regulations on water diversions, including standards for the position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow; Jassby et al. 1995), locally termed X2, have become increasingly stringent.

Conflicts over water management in the Delta have intensified because of the apparently precipitous decline in abundance of four species of pelagic fish (delta smelt [*Hypomesus transpacificus*], longfin smelt [*Spirinchus thaleichthys*], striped bass [*Morone saxatilis*], and threadfin shad [*Dorosoma petenense*]) since ca. 2000 (Sommer et al. 2007). Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993 and the listing was revised to endangered under the California act in 2009. Recent litigation to protect the species resulted in court orders to halt water diversions temporarily (Wanger 2007*a*, *b*). Longfin smelt was listed as threatened under the California Endangered Species Act in 2009 and was proposed but declined for federal listing.

Analyses of existing data and new field investigations have identified various factors that may help to explain the declines, but the relative importance of these factors, particularly water diversions, is unclear (Sommer et al. 2007). Identification of the processes causing declines and their relative effects is critical because the solutions under consideration include major investments in infrastructure, changes in water management, and rehabilitation of species' habitats that collectively will cost billions of dollars. Although an experimental evaluation of potential drivers is impossible for a system of this size, multi-decadal sets of data exist on abundances of pelagic fishes and biotic and abiotic characteristics of their environment, allowing for a robust correlative analysis.

There is interest in determining whether the recent declines in species' abundances are the continuation of longer term trends or more abrupt changes in population dynamics, which we refer to as ecological "change points" (Beckage et al. 2007). If the latter, identifying when these changes occurred and if and when similar changes have occurred previously is an important step toward understanding their causes and possible mitigation. We define a change point as a point in time when an abrupt change occurred in the functional relationship between the mean abundance of a species and time. A change point may be either a step change, which is an abrupt change in abundance; a trend change, which is an abrupt change in the temporal trend in abundance; or both. Manly and Chotkowski (2006) used a bootstrap approach to explore the timing of one or more change

points in the abundance of delta smelt. But no method has been applied to detect objectively multiple change points for all four species, whether individually or as a group. Neither has there been a rigorous examination of factors that might explain statistically specific change points.

Here, we characterize abundance trends of delta smelt, longfin smelt, striped bass, and threadfin shad over the period of record (1967–2007), identify change points for species individually and collectively, and examine whether biotic and abiotic covariates are related to those trends or change points. To identify statistically the number, timing, and magnitude of any changes in abundance trajectories and to integrate uncertainties into parameter estimates and inference, we constructed models based on Bayesian change point techniques (Beckage et al. 2007). We used hierarchical model structures to separate explicitly observation error from natural process variation, to handle missing data, and to fit a multispecies change point model. Hierarchical Bayesian models are ideally suited to the complexity of analyzing ecological time series (Webb and King 2009) because they can integrate multiple sources of information and uncertainty to provide more robust inferences about parameters and processes of interest (Cressie et al. 2009).

Biological background

Delta smelt are endemic to the San Francisco Estuary. They reach 60–70 mm standard length (SL), feeding throughout their life on mesozooplankton (Bennett 2005). Delta smelt are weakly anadromous. Upstream migration begins in mid-December and spawning occurs from March through May in freshwater. Most delta smelt spawn 12–15 months after birth. A small percentage live two years, possibly spawning in one or both years (Bennett 2005). Young delta smelt move downstream in early summer and remain in the low-salinity zone (0.5–10 on the practical salinity scale) until they migrate for spawning.

Longfin smelt also are native to the San Francisco Estuary. Longfin smelt reach 90–110 mm SL with a maximum size of 120–150 mm SL (Moyle 2002, Rosenfield and Baxter 2007). Longfin smelt are anadromous. They spawn at age-2 in freshwater in the Delta from approximately December to April. Young longfin smelt occur from the low-salinity zone seaward throughout the estuary and into the coastal ocean. Longfin smelt feed on copepods as larvae and primarily on mysids as juveniles and adults.

Striped bass were deliberately introduced to the Delta from the east coast of the United States in 1879 and now support a popular sport fishery (Moyle 2002). The striped bass is a large (>1 m), long-lived (>10 years) anadromous species. Females begin to spawn at age-4 in the Sacramento River and to a lesser extent in the San Joaquin River from April through June. Their semi-buoyant eggs hatch as they drift with the current. The larvae drift into the low-salinity zone where they grow, later dispersing throughout the estuary. Adults occur throughout the estuary to the coastal ocean, except during spawning migrations. Age-0 striped bass feed mainly on copepods, later switching to macroinvertebrates and then to fish.

Threadfin shad was introduced into California reservoirs as a forage fish in 1954 and eventually spread to the Delta (Moyle 2002). Adult threadfin shad are typically <100 mm total length and primarily inhabit freshwater. They switch between filter feeding and particle feeding, consuming phytoplankton, zooplankton, and detritus. Most threadfin shad spawn in their second summer of life, although some may spawn at the end of their first year. Spawning occurs mainly in June and July. Threadfin shad is the most abundant pelagic fish in the upper San Francisco Estuary and is important as prey for piscivorous species.

Statistical analyses

We used a Bayesian framework to fit a series of log-linear models to explore temporal patterns in species abundances and relationships with biotic and abiotic covariates. First, we used piecewise regression models (Denison et al. 1998, Fearnhead 2006) to characterize temporal trends in abundance of each species and to identify change points in either the absolute abundance (step changes) or in the rate of change in abundance (trend changes). Next, we used Bayesian model selection (Green 1995) to identify covariates with the strongest associations with abundances of each species. We then fitted change point models conditional on the selected variables to explore whether those covariates could account statistically for changes detected by the trend model or lead to detection of other change points. We also fitted a multispecies change point model to determine whether there were years in which all species collectively experienced abrupt changes in abundance not explained by the selected covariates.

Hierarchical log-linear trend models

For each species, we fitted a log-linear trend model using piecewise linear splines (Denison et al. 1998) that allow for changes in the intercept or slope parameters at particular times (i.e., change points). We used a hierarchical model to account explicitly for sampling error. For each species, the observations (y_t) were the mean number of individuals captured during autumn trawl surveys conducted each year from 1967 to 2007 (Stevens and Miller 1983). The mean for each year was based on monthly (September, October, November, December) samples from 100 different locations; thus, the yearly average was based on ~400 observations (data and station details *available online*)[10]. We assumed that the observations were unbiased estimates of the true

[10] ⟨http://knb.ecoinformatics.org/knb/metacat/nceas.958.8/nceas/⟩

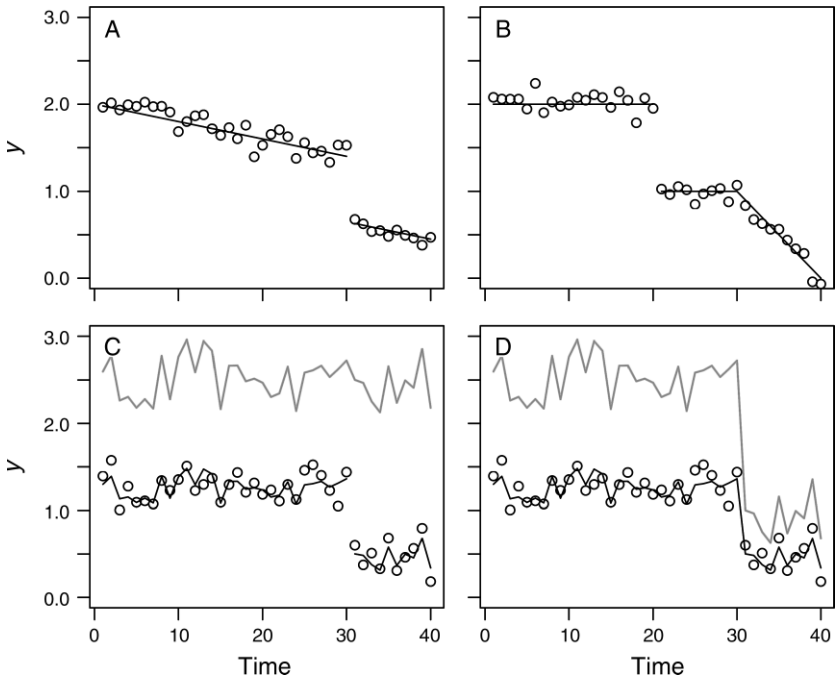

FIG. 2. Examples of change point models. All examples show a hypothetical time series y (circles) and corresponding piecewise linear models (dark lines): (A) a step change at time 31, modeled by $y_t = 2 - 0.75I(t \geq 31) - 0.02t + \varepsilon_t$; (B) a step change at time 21 and trend change at time 31, modeled by $y_t = 2 - 1I(t \geq 21) - 0.03(t - 31)I(t \geq 31) + \varepsilon_t$; (C) a covariate model with step change at time 31, modeled by $y_t = 0 - 0.75I(t \geq 31) + 0.5x_t + \varepsilon_t$; (D) a covariate model with no change points (change point at time 31 in panel C is predicted by covariate), modeled by $y_t = 0 + 0.5x_t + \varepsilon_t$. In panels (C) and (D), gray lines show the time series of the covariate x. For all models, ε_t is the residual error, and all other parameters are as defined in Eqs. 1–3.

mean abundance (n_t) in a standard trawl sample over the four-month period in year t and that the 100 sampling stations are an adequate spatial representation of the estuary. The resulting hierarchical model for observations and true abundances was

$$y_t \sim \text{Normal}\left(n_t, \sigma^2_{\text{O}t}\right) \tag{1}$$

$$n_t \sim \text{Lognormal}\left(\alpha_t + f_t(t), \sigma^2_{\text{p}}\right). \tag{2}$$

Simultaneously estimating observation noise, $\sigma_{\text{O}t}$, and process variation, σ_{p}, is difficult for such hierarchical models (e.g., Dennis et al. 2006). Therefore, we substituted the observed standard errors of trawl samples as estimates of $\sigma_{\text{O}t}$ in the fitting procedure.

The parameters of the state process model, α_t and $f_t(t)$ in Eq. 2, allowed for abrupt changes in the (log) abundances and changes in the relationship between abundance and time, respectively. The following submodel accounted for abrupt changes to the intercept, or step changes:

$$\alpha_t = \alpha_1 + \sum_{j=1}^{k_\alpha} \chi_j I(t \geq \delta_j). \tag{3}$$

In this submodel, α_1 is the initial log abundance of a given species, k_α is the number of step changes in abundance, δ_j is the timing of the jth step change, and χ_j is the value of the change. $I(t \geq \delta_j)$ is an indicator function that equals 1 when $t \geq \delta_j$ and is 0 otherwise. To illustrate, we present an example of the state process model (Eq. 2) fitted to abundance data with a single step change and constant linear trend (Fig. 2A).

We modeled the temporal trend, $f_t(t)$, as a piecewise linear regression with an unknown number k_β of changes in slope (trend changes) and a corresponding set of times θ_j of trend changes, or "knots" (Harrell 2001):

$$f_t(t) = \beta_1 t + \sum_{j=1}^{k_\beta} \beta_{[j+1]}(t - \theta_j)_+. \tag{4}$$

The term $(t - \theta_j)_+$ equals $I(t \geq \theta_j)(t - \theta_j)$. Given a particular intercept, the term $f_t(t)$ is a piecewise linear and continuous function of time, but when the intercept α_t varies, the combination $\alpha_t + f_1(t)$ is a discontinuous piecewise linear model (Fig. 2B).

Given uncertainty about when or if step or trend changes occurred, we treated the numbers, k_α and k_β, and timing, δ_j and θ_j, of change points as unknown parameters to be estimated as part of the model. We used a Bayesian framework with reversible jump Markov chain Monte Carlo sampling (MCMC; Lunn et al. 2006, 2008) to evaluate the posterior model probabilities (i.e., evidence) for all possible models, or

combinations of change points. The range of models considered possible is specified in the prior distributions, which are detailed here. The resulting posterior distributions allow for probabilistic inferences about the occurrence of change points in particular years, accounting for uncertainties in both data and other model parameters (including magnitudes and timing of other change points). The posterior probability that a change point occurred in year y is the summed posterior probabilities of all models that include a change point in year y (e.g., of all values of δ that include y as an element).

Prior distributions for parameters

In Bayesian analysis, prior distributions must be specified for the unknown parameters (Gelman et al. 2004). Our prior distributions limited the number of step and trend changes to a maximum of four each and included the possibility of zero change points: $k \sim$ Binomial(4, 0.5). This prior reflects our expectation that, in a system subjected to increasing anthropogenic influence over the period of record, there may have been multiple changes in abundance trends. The prior explicitly limits the number of change points so the larger and more abrupt changes are highlighted (see the Appendix for further discussion of priors). The priors were uninformative with respect to the timing of change points, with equal prior probability [$p_0 = (0.5 \times 4)/39 = 0.05$] of change points in each year (Appendix). With this prior, a posterior probability $p_1 > 0.14$ for a change point in year y corresponds to an odds ratio of 3, which is a threefold increase from the prior odds [$p_0/(1 - p_0)$] to the posterior odds [$p_1/(1 - p_1)$]. Odds ratios are measures of the evidence in the data in favor of one hypothesis (change point in year y) over an alternative (no change point in year y), and values >3 are generally considered to indicate "substantial" evidence (Jeffreys 1961).

We specified normal prior distributions with zero mean and standard deviations equal to [$\ln(y_{\max}) - \ln(y_{\min})$]/1.96 and $0.25 \times [\ln(y_{\max}) - \ln(y_{\min})]/1.96$ for the magnitude of step (χ) and rate (β) changes, respectively. These priors imply that step changes greater than the observed data range are unlikely (prior probability < 0.05) and that the greatest change in slope in one year is unlikely to be greater than one-quarter of the range of log values of the observed data. We used several uninformative prior distributions for the unknown parameters (numbers and magnitudes of change points) to assess sensitivity to the choice of priors (Appendix). Although absolute values of model posterior probabilities sometimes were sensitive to choice of priors, the relative probabilities, and hence inferences about change point times, were consistent.

Covariate effects

We undertook a series of steps to identify biotic or abiotic variables that may explain temporal patterns in species' abundances and to determine how those variables affected inferences about change points. First, a set of Q (12–15) candidate covariates was selected for each species on the basis of previously published work and unpublished analyses (Table 1). Next, we used Bayesian model selection to identify which of the Q candidate variables had the strongest associations with variation in the (log) abundances of each species (see *Variable selection model*, below). We then fitted change point models conditioned on the selected variables by replacing the trend component $f_t(t)$ in Eq. 2 with covariate effects $f_x(X)$. These covariate-conditioned change point models identify abrupt changes in abundance that would not be expected given the covariate values and estimated species–covariate relationships. Changes in species' abundance that are identified as change points in covariate-conditioned models are unlikely to be related to the included covariates. But if the inclusion of a covariate reduces the evidence for a previously identified change point (i.e., one identified in a trend model or model conditioned on other covariates), then a causal relationship between that covariate and the change point is plausible.

Variable selection model

The variable selection model allowed nonlinear covariate effects and temporal autocorrelation. Covariates were standardized (mean 0, SD 1) prior to model fitting and missing values were assigned normal prior distributions, which were not updated during model fitting, with mean 0 and SD 1. The model was

$$n_t \sim \text{Lognormal}\Big(\alpha + \sum_{j=1}^{Q}\sum_{m=1}^{k_j} \beta_{jm}(x_{jt} - \phi_{jm})_+ + \rho \log n_{t-1}, \sigma_{\text{p}}^2\Big). \quad (5)$$

This model has up to Q covariates with effects fitted as piecewise linear splines with k_j slope parameters $\boldsymbol{\beta}_j$ and free knots $\boldsymbol{\phi}_j$. If $k_j = 0$, variable j has zero effect; if $k_j = 1$, variable j is included as a linear effect (for $x_j > \phi_{j1}$); and if $k_j > 1$, variable j is included as a nonlinear effect. We used a categorical prior for k_j such that the prior probabilities of values 0, 1, 2, and 3 were 0.5, 0.3, 0.1, and 0.1, respectively. Thus, the prior probability that variable j was included in the model, $\Pr(k_j > 0)$, was 0.5, and linear effects were more probable a priori than were nonlinear effects. The knots were assigned uniform discrete priors with 10 possible positions evenly spaced along the range of x_j.

The relative importance of each of the covariates in model 5 was measured by the posterior probability of inclusion for each variable, $\Pr(k_j > 0)$, which is the sum of the posterior model probabilities of all models that include a particular variable. We considered $\Pr(k_j > 0) > 0.75$, corresponding to an odds ratio of 3 [(0.75/0.25)/(0.5/0.5)], to be sufficient evidence to include variables

TABLE 1. Definitions of variables used in change point models, years for which data were available, and ranges of values for variables.

Variable	Years (missing)	Range
Response variables		
Delta smelt (*Hypomesus transpacificus*) 1	1967–2007 (3)	0.06–4.02
Longfin smelt (*Spirinchus thaleichthys*) 2	1967–2007 (3)	0.03–113.16
Striped bass (*Morone saxatilis*) 3	1967–2007 (3)	0.12–59.38
Threadfin shad (*Dorosoma petenense*) 4	1967–2007 (3)	1.36–31.21
Covariates		
Calanoid copepods, spring (cal.sp)	1972–2007 (1)	0.98–43.87
Calanoid copepods, summer (cal.s)	1972–2007 (1)	2.93–27.62
Mysids (mysid)	1972–2007 (0)	0.42–35.05
Northern anchovy (*Engraulis mordax*) (Ancho.)	1980–2006 (1)	0.22–490.42
"Other zooplankton," spring (zoop)	1972–2006 (0)	3.79–56.86
Spring chlorophyll *a* in low-salinity zone (chlo.sp)	1975–2006 (0)	1.12–21.32
Cyclopoid copepod *Limnoithona tetraspina* (Limno.)	1972–2006 (0)	0–7.78
Inland silverside (*Menidia beryllina*) (silver.)	1994–2006 (0)	19.88–116.54
Largemouth bass (*Micropterus salmoides*) (lm.bass)	1994–2006 (0)	0.02–8.00
Spring X2 (X2.sp)	1967–2006 (0)	48.53–91.74
Autumn X2 (X2.aut)	1967–2006 (0)	60.24–93.18
Water clarity (clarity)	1967–2006 (0)	0.44–11.00
Winter exports (expt.w)	1967–2006 (0)	0.13–12.00
Spring exports (expt.s)	1967–2006 (0)	0.37–13.00
Duration of spawning window for delta smelt (15-20C)	1975–2007 (0)	24–85
Mean summer water temperature (temp)	1967–2006 (0)	20.45–23.65
Winter Pacific Decadal Oscillation (PDO.w)	1967–2007 (0)	−1.90–1.89
Summer Pacific Decadal Oscillation (PDO.s)	1967–2007 (0)	−1.11–2.52
Striped bass egg supply (eggs)	1970–2006 (0)	0.02–0.40

Notes: "Candidate" indicates the species (by number; see numbers following species) for which each covariate was included as a candidate predictor in variable selection models. Abbreviated names for covariates used in Figs. 3C, 4C, 5C, and 6C are shown in parentheses. Biomass was measured as mg C/m^3. The low-salinity zone was determined to be at 0.5–10‰. The X2 position was measured in km upstream from the Golden Gate Bridge. The data, along with further details and explanations, are *available online* (see footnote 10). See also Mac Nally et al. (2010: Table 2).

in subsequent covariate-conditioned change point models.

With all models (combinations of variables) equally probable a priori (prior $\Pr(k_j > 0) = 0.5$), posterior model probabilities reflect differences in marginal likelihoods, which intrinsically penalize model complexity (Kass and Raftery 1995, Beal et al. 2005). The amount of penalty depends on the prior distributions for model parameters (more diffuse priors favor fewer model parameters; George and Foster 2000), so posterior model probabilities, hence $\Pr(k_j > 0)$, can be sensitive to the choice of priors. We used a half-Cauchy prior (Gelman 2006) for the standard deviation σ_β of nonzero covariate effects, scaled so that ~90% of the resulting prior probability mass of each linear coefficient β_{jm} was in the interval (−1, 1) and 95% was in the interval (−2, 2). This prior placed most weight on more plausible coefficients (a linear coefficient of 1 equates to a 2.7-fold change in abundance for 1 SD change in the predictor) while still allowing larger effects ($e^2 = 7.4$-fold change in abundance per 1 SD change in predictor). We also fitted models with a range of alternative prior specifications and generally obtained similar results (Appendix). Any variables for which $\Pr(k_j > 0)$ values were sensitive to priors are identified in *Results*.

We fitted the variable selection model (Eq. 5) with and without the autocorrelation term ρn_{t-1} and with a conditional prior on $\rho[\rho \mid k_{Q+1} = 1 \sim \text{Normal}(0, \sigma_\beta^2); k_{Q+1} \sim \text{Bernoulli}(0.5)]$ testing for the importance of the autocorrelation term (i.e., treating n_{t-1} as a candidate predictor). $\Pr(k_j > 0)$ values for covariates were largely unaffected by the treatment of ρ, so we present results only for the models that treated n_{t-1} as a candidate predictor.

Covariate-conditioned change point model

We fitted change point models that accounted for the effects of covariates identified as probable predictors (those with $\Pr(k_j > 0) > 0.75$) to examine whether those covariates could account for changes detected by the trend model or detect other change points. The

TABLE 1. Extended.

Candidate	Definition
	autumn (Sep–Dec) midwater trawl, mean total catch (no. individuals) per trawl
	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
	autumn (Sep–Dec) midwater trawl, mean age-0 catch per trawl
	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
all	mean biomass of calanoid copepodites and adults during spring (Mar–May) in low-salinity zone
all	mean biomass of calanoid copepodites and adults during summer (Jun–Sep) in low-salinity zone
2, 3	mean biomass of mysid shrimp during Jun–Sep in low-salinity zone
1, 2, 3	mean catch per trawl of northern anchovy in the Bay Study midwater trawl (Jun–Sep) in low-salinity zone
4	mean biomass of other zooplankton (not including crab and barnacle larvae, cumaceans) during spring (Mar–May) in the freshwater zone (<0.5‰)
all	mean chl *a* (mg/m^3) during spring (Mar–May) in low-salinity zone
1, 2, 4	mean biomass of *Limnoithona* copepodites and adults during summer (Jun–Sep) in the low-salinity zone
all	mean catch per seine haul of inland silverside in the USFWS survey during Jul–Sep (for stations within the delta)
all	mean catch per seine haul of largemouth bass in the USFWS survey during Jul–Sep (for stations within the delta)
1, 2, 3	mean Mar–May position of the 2‰ isohaline (X2)
4	mean during Sep–Dec position of the 2‰ isohaline (X2)
all	mean Secchi depth (m) for the autumn midwater trawl survey
1, 2, 4	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Dec–Feb
all	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Mar–May
1	no. days for which mean temperature was between 15° and 20°C (range of water temperatures that best induce spawning by delta smelt [15°C] and limit larval survivorship [20°C]), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta
all	mean water temperature (°C), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta during Jun–Sep
2, 3	Dec–Feb
1, 2, 3	Jun–Sep
3	estimated striped bass egg supply, calculated as the sum of age-specific fecundity based on the population estimates generated by the California Department of Fish and Game (Kimmerer et al. 2000)

covariate-conditioned change point model with $q < Q$ covariates was

$$n_t \sim \text{Lognormal}\left(\alpha_t + \sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt} - \phi_{jm})_+ + \rho\log(n_{t-1}), \sigma_p^2\right). \quad (6)$$

In this model, k_j had minimum value = 1 and a prior distribution given by $k_j = 1 + \kappa_j$, where $\kappa_j \sim$ Binomial(3, 0.3), the first knot ϕ_{j1} was fixed at min(x_j), and remaining knots had continuous uniform priors. The autocorrelation term was included only if results of the variable selection model indicated that ρ probably was nonzero (i.e., when $\Pr(k_{Q+1} = 1) > 0.75$) (n.b., we confirmed that including ρ when $\Pr(k_{Q+1} = 1) < 0.75$ had no effect on other parameters in Eq. 6).

In Eq. 6, the covariate effects,

$$\sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt} - \phi_{jm})$$

replace the trend component $f_t(t)$ in Eq. 2. Including step change(s) in the intercept allowed for abrupt changes in abundance conditional on the covariates, that is, changes that would not be expected given the covariate values and estimated species–covariate relationships (Fig. 2C). If a step change in n_t was explained by a step change in the covariate, then the model intercept would remain constant (i.e., no change point; Fig. 2D).

Multispecies model

We searched for common change points among species by fitting covariate-conditioned change point models (Eq. 6) for all species simultaneously, with an additional step change submodel that was common to all species. In the multispecies model, the time-dependent intercept for species s, α_{st}, was modeled as

$$\alpha_{st} = \alpha_{s1} + \sum_{j=1}^{k_{s\alpha}}\chi_{sj}I(t \geq \delta_{sj}) + \sum_{l=1}^{k_{C\alpha}}\psi_l I(t \geq \zeta_l). \quad (7)$$

Here, $k_{C\alpha}$ is the number of step changes common to all four species, with magnitude and timing given by vectors $\boldsymbol{\psi}$ and $\boldsymbol{\zeta}$, respectively. The other parameters in Eq. 7 define species-specific change points as in Eq. 3, with subscript s in Eq. 7 denoting species-specific parameters. The full model for each species was identical in all other respects to Eq. 6.

The multispecies model identified any year(s) in which abundances of all species changed unexpectedly given the values of relevant covariates. We fitted the model once with prior distributions that allowed only common change points ($k_{s\alpha} = 0$, $k_{C\alpha} \sim$ Binomial(4, 0.5)) and once with prior distributions that allowed both common and species-specific change points ($k_{s\alpha} \sim$ Binomial(2, 0.5), $k_{C\alpha} \sim$ Binomial(2, 0.5)). We also examined combinations of fewer species to determine whether results of the four-species models were overly influenced by one species.

Implementation

All models were estimated using the reversible jump MCMC add-on (Lunn et al. 2006, 2008) for WinBUGS version 1.4 (Lunn et al. 2000) with three chains of 200 000 iterations each after 50 000 iteration burn-in periods. The MCMC mixing and convergence were established by inspection of chain histories, autocorrelation plots, and Brooks-Gelman-Rubin statistics. We used the cut() function in WinBUGS (Lunn et al. 2000) to prevent updating the prior distributions for missing values, which otherwise may be tuned to fit the model, leading to selection of covariates with many missing values as predictors. This treatment of missing values allowed all available data to be used in the analysis, rather than omitting years in which any covariate values were missing (Carrigan et al. 2007). We did not use imputation methods to estimate missing values because these methods assume values are missing at random, which generally was not the case (e.g., values for the first six years of surveys were missing for some variables).

WinBUGS code for all models is available in the Supplement.

Results

Overview of results relevant to recent declines

The trend models identified probable step or trend changes in the early 2000s for delta smelt (trend change 2000–2002; Fig. 3A), striped bass (step decline 2002; Fig. 4A), and threadfin shad (step decline 2002; Fig. 5A). Longfin smelt abundances also declined after 2000, but this decline was modeled as a continuation of a long-term declining trend that was interrupted by sudden increases in the late 1970s and mid-1990s (Fig. 6A).

The species-specific, covariate-conditioned change point models indicated step declines in abundances (i.e., abrupt declines that could not be modeled by the included covariates) of delta smelt and longfin smelt in 2004 (Figs. 3B and 6B) and of striped bass (Fig. 4B) and threadfin shad (Fig. 5B) in 2002.

In the multispecies change point models, there was strong evidence of a common change point in 2002, regardless of whether species-specific change points were allowed (Fig. 7). Evidence for step declines in abundance of delta smelt and longfin smelt in 2004 remained in the multispecies model that allowed species-specific change points (Fig. 7). Similar results were obtained from multispecies models fitted with any combination of three species, so the high probability of a common change point in 2002 is not driven by any single species.

To ensure that our variable selection criterion ($\Pr(k_j > 0) > 0.75$) had not excluded variables that could explain the post-2000 declines, we refitted covariate-conditioned change point models including all variables with $\Pr(k_j > 0) > 0.5$ (i.e., variables with some evidence of effects). We also fitted models with variables that had strong effects in a multivariate autoregressive (MAR) analysis of an expert-elicited model of this system (up to six variables per species; see Mac Nally et al. 2010 for details). With one possible exception (detailed in *Species-specific results: Striped bass* below), inclusion of additional variables had no substantive effects on posterior probabilities of post-2000 change points in single- or in multispecies models.

Water clarity emerged as a likely predictor of the abundance of delta smelt, longfin smelt, and striped bass, but the other variables with $\Pr(k_j > 0) > 0.75$ were unique to each species (Table 2). No species had more than two variables with $\Pr(k_j > 0) > 0.75$. All of the covariates with $\Pr(k_j > 0) > 0.75$ had monotonic effects, and most were modeled adequately by a single linear coefficient ($k_j = 1$).

The autocorrelation coefficient, ρ, had low probability of inclusion (low $\Pr(k_{Q+1} = 1)$), and was close to zero when included, for all species except striped bass (Figs. 3C, 4C, 5C, and 6C and Table 2). Low values of ρ may indicate that the mean abundance from September through December is poorly correlated with abundance of spawning adults in a given year.

Species-specific results

Delta smelt.—In the variable-selection model for delta smelt, water clarity and winter exports had high probability of inclusion ($\Pr(k_j > 0) > 0.75$; Fig. 3C). Both variables had negative effects (Table 2). The effect of winter exports was approximately linear, but marginal effects of water clarity were greatest at high values. The probability of inclusion for winter exports was sensitive to the prior distribution specified for linear coefficients. Priors that weighted large effect sizes (e.g., absolute linear coefficients > 0.5) more heavily yielded low $\Pr(k_j > 0)$ values for winter exports. This sensitivity indicates that the data support relatively small effects of winter exports ($|\beta| < 0.5$), but models with larger export coefficients fitted the data poorly. The estimated mean linear coefficient in the step change model ($\beta = -0.25$; Table 2) implies that an increase of one standard deviation in volume of winter exports ($= 0.62$ km^3) would be associated with a 22% decline (95% posterior interval = −45% to +9%) in abundance of delta smelt, assuming other factors were constant.

Evidence for change points in the periods 1981–1983 and 2000–2002 was weaker in the covariate-conditioned

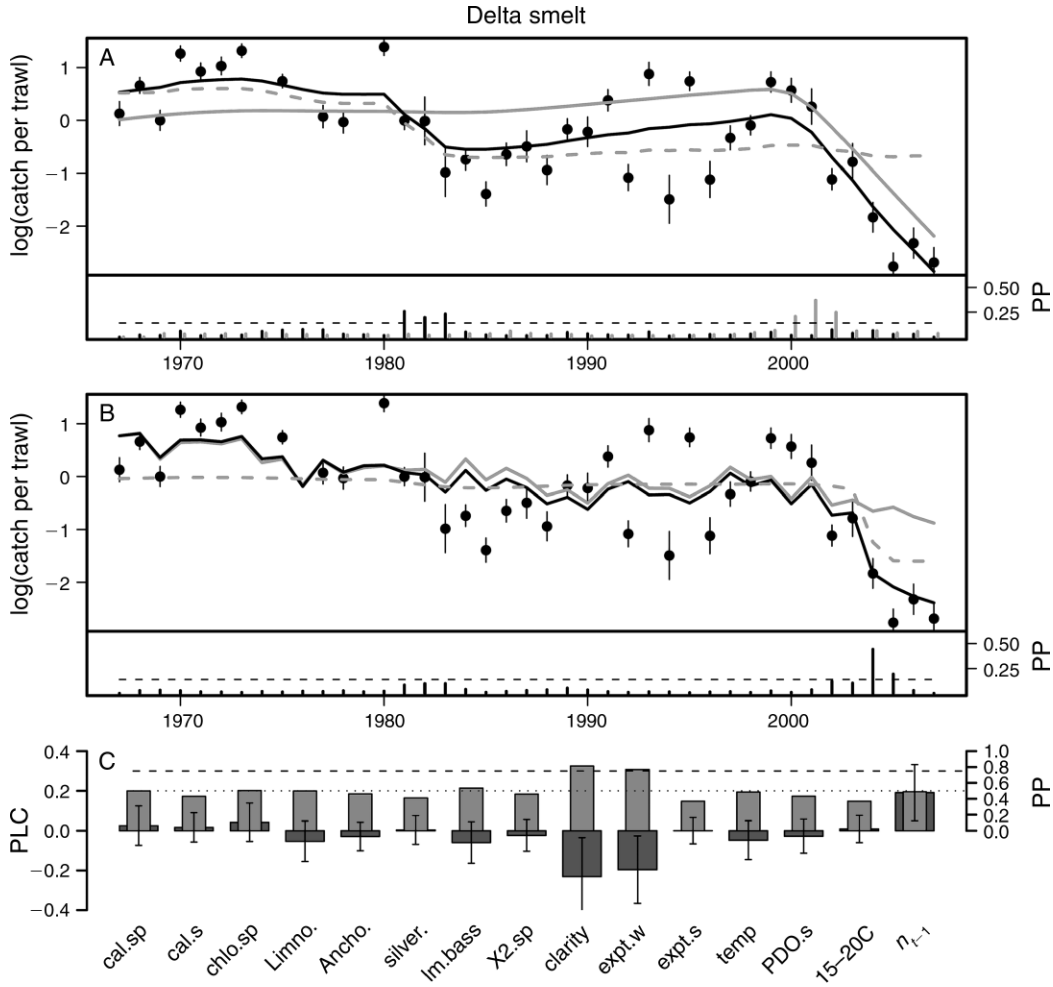

FIG. 3. (A) Results of the trend model (Eq. 2) for delta smelt. The fitted trend is shown as a black line, and observed values [log(catch per autumn trawl), mean ± SE] are shown as data points. Intercept (α_t) values are shown as dashed gray lines, and the trend component [$f_t(t)$] is shown as a solid gray line. The lower panel shows posterior probabilities (PP) of step changes (black) or trend changes (gray) in each year for the trend model (Eq. 2). (B) Results of the covariate-conditioned change point model (Eq. 6) for delta smelt. Fitted values are shown as a black line, the intercept (α_t) as a dashed gray line, and the covariate component [f(water clarity) + f(winter exports), where $f(\,)$ is a linear spline] as a solid gray line. The posterior probabilities of step changes (abrupt changes unexplained by covariates) for each year are shown in the lower panel. (C) Results of the covariate selection model (Eq. 5) for delta smelt. Posterior probabilities of variable inclusion (light gray bars, right axis) and posterior mean (±SE) linear coefficients (PLC; dark gray bars, left axis) are shown for each candidate predictor. The variable n_{t-1} is the previous year's abundance; see Table 1 for explanations of other covariate abbreviations. Mean linear coefficients were calculated as the mean slope of the fitted linear-spline model over the data range. In all panels, the horizontal dashed lines show posterior probabilities corresponding to odds ratios of 3 (0.14 for change points, 0.75 for variable inclusion), which we consider substantial evidence for a change point occurring in a year (panels A and B) or for a variable having an effect on abundance (panel C). In panel (C) the prior probability of inclusion (0.5) is shown as a dotted line.

model (Fig. 3B) than in the trend model (Fig. 3A), suggesting that those declines in abundance may have been associated with combined effects of increasing water clarity and high winter exports (Fig. 8). However, there was evidence of an unexplained decline in 2004 in the single-species model (Fig. 3B) and of unexplained declines in 2002 and 2004 in the multispecies model (Fig. 7). The mean effect of winter exports was slightly less negative in the multispecies model than in the single-species model (Table 2) because the multispecies model assigned more weight to an unexplained step decline in 2002, reducing the estimated effect of high winter exports in that year.

Longfin smelt.—In the variable-selection model for longfin smelt, water clarity and spring X2 had high probability of inclusion ($\Pr(k_j > 0) > 0.75$). Both variables had negative effects that were approximately linear (Fig. 6C, Table 2).

The change point model conditioned on spring X2 and water clarity indicated unexpected declines in

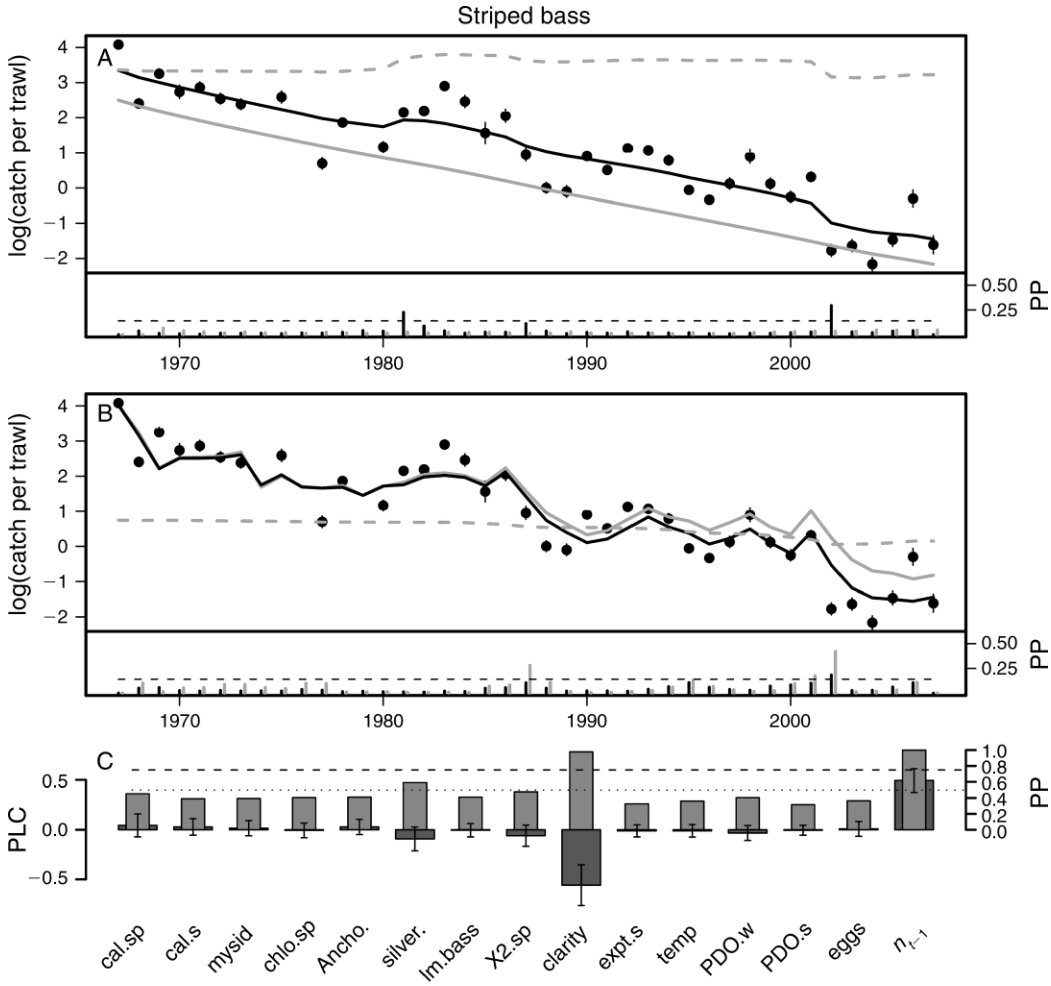

FIG. 4. Results of the models for striped bass. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(water clarity) + $\rho \log(n_{t-1})$. The gray bars in panel (B) show the posterior probabilities of change points in each year if $\rho = 0$; $\rho \log(n_{t-1})$ is the temporal autocorrelation term in Eq. 6 (see *Statistical analyses: Covariate-conditioned change point model*).

abundance from 1989 to 1991 and in 2004 (Fig. 6B). The sharp increases in longfin smelt abundance in 1978 and 1995, identified as step increases in the trend model, were modeled as responses to sharp declines in X2 (increases in outflow; Fig. 8) in the covariate-conditioned change point model. The estimated relationship between water clarity and longfin smelt abundance was weaker in the single-species change point model than in the multispecies change point model (Table 2). This disparity relates mainly to differences in the way the models explained abundance from 1988 through 1992. A sharp decline in longfin abundance in that period was largely modeled as an unexplained step decline in the single-species model, but, when species-specific change points were given lower prior probability in the multispecies model, that decline was partially attributed to increasing water clarity (Fig. 8). If change points were omitted, as in the variable-selection model, the water clarity effect was very strong. These results suggest that the relationship between longfin smelt abundance and water clarity, after accounting for a strong effect of spring X2, generally was weak throughout the time series and that the strong relationship identified in the variable-selection model was driven largely by data for the period 1988–1992.

Striped bass (age-0).—In the variable-selection model for striped bass, water clarity and the autocorrelation term had $\Pr(k_j > 0) > 0.75$. Water clarity had an approximately linear negative effect (Table 2).

Evidence for a step decline in striped bass abundance in 2002 was lower in the covariate-conditioned change point model (Fig. 4B) than in the trend model (Fig. 4A) and was lower still (odds ratio < 3) in a model that included the biomass of inland silverside (*Menidia beryllina*; $\Pr(k_j > 0) = 0.59$; Fig. 4C). These results suggest that high water clarity (Fig. 8) or biomass of inland silverside could have contributed to the 2002 step decline in striped bass abundance. However, the

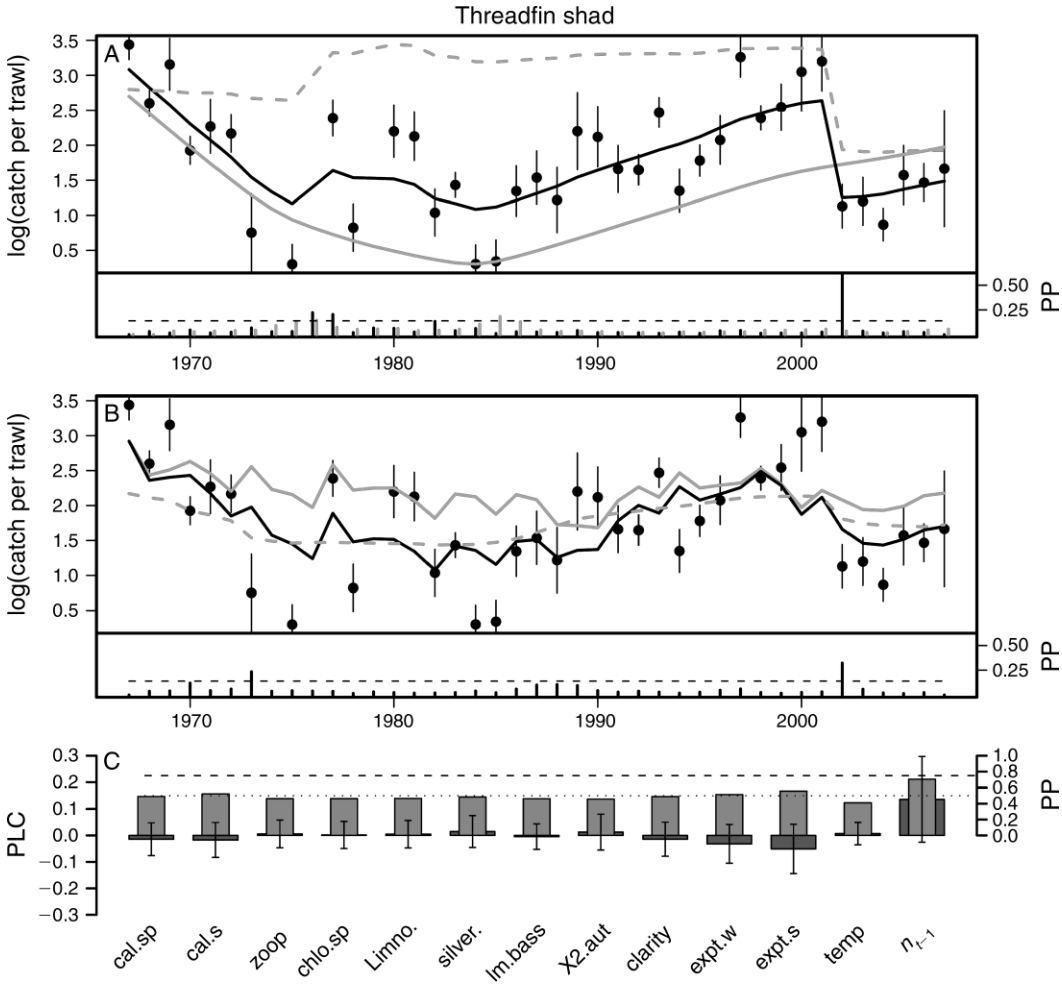

FIG. 5. Results of the models for threadfin shad. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(winter exports) + f(spring exports), and the dashed gray line represents the time-dependent intercept α_t plus a nonlinear trend $f(t)$.

presence of partial autocorrelation ($0 < \rho < 1$) complicated change point detection in these log-linear models because the interpretation of α, and hence appropriate prior distributions for change points, depends on ρ (see Appendix). When autocorrelation was omitted from covariate-conditioned, change point models for striped bass, regardless of the inclusion of inland silverside biomass, the posterior probability of a step change in 2002 was >0.4 (Fig. 4B).

In all covariate-conditioned models for striped bass, relatively low water clarity in 1981 accounted for the apparent step increase in abundance in that year (Fig. 4A vs. Figs. 4B and 7).

Threadfin shad.—No variables had high probability of inclusion in the threadfin shad variable selection model. The highest-ranked variables, other than the autocorrelation term, were biomass of summer calanoids in the low-salinity zone and winter and spring export volumes, which each had posterior probability of inclusion marginally higher than the prior probability (Fig. 5C), indicating only weak evidence of effects. However, probabilities of inclusion for winter and spring exports were sensitive to the prior distribution for the linear coefficients, and priors that put more weight on smaller coefficients yielded $\Pr(k_j > 0) > 0.75$ for both variables; no other variables showed this level of sensitivity to priors. Therefore, we included winter and spring exports in covariate-conditioned change point models for threadfin shad. We also included time as a covariate in the single-species model for threadfin shad because the model with export volumes alone fit too poorly ($R^2 = 0.33$) to make meaningful inferences about change points (i.e., unusual departures from "expected" abundance given covariate values).

The estimated relationship between log(abundance) of threadfin shad and spring exports was similar in form and magnitude to the relationship between log(abundance) of delta smelt and winter exports (Table 2) and was consistent among single- and multispecies models with and without time included as a covariate. An

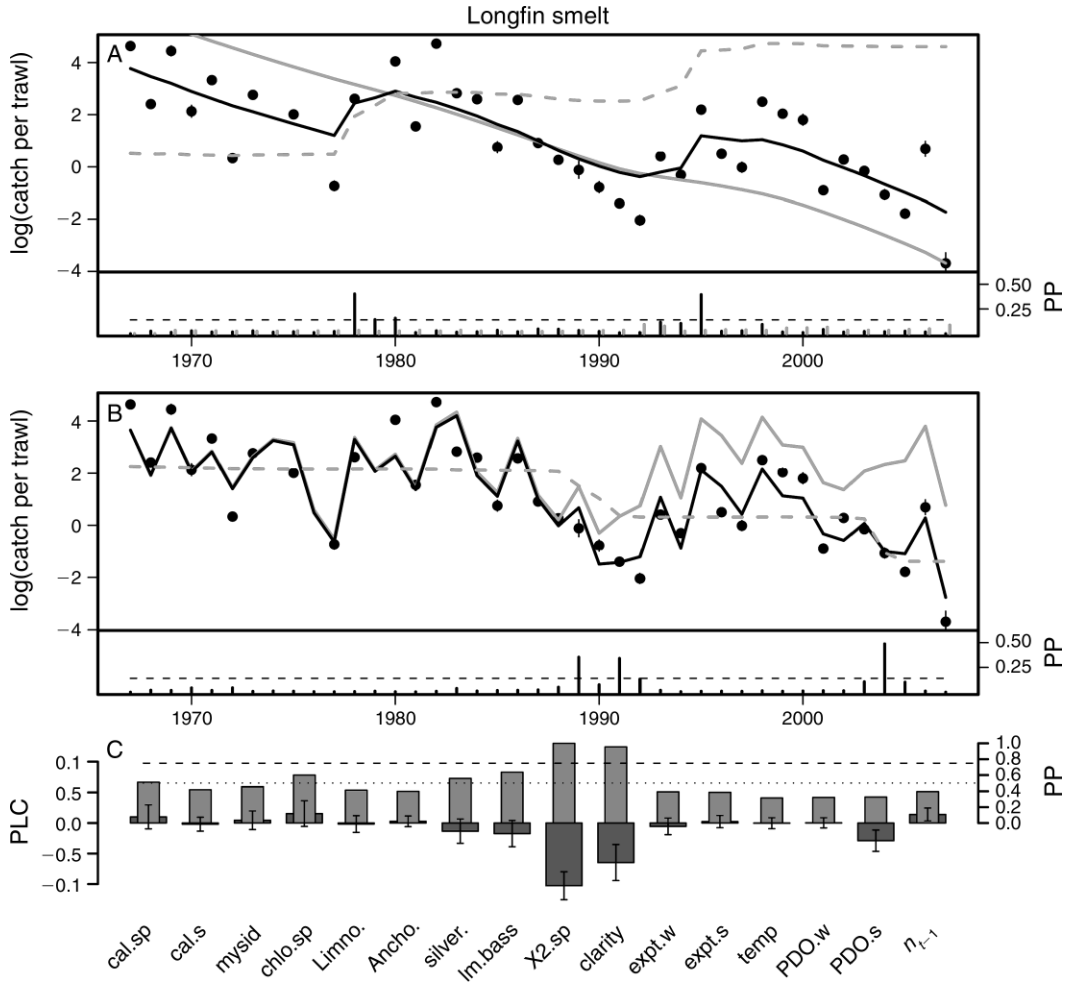

FIG. 6. Results of the models for longfin smelt. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(water clarity) + f(spring X2), but f(water clarity) was near zero, and including only f(spring X2) results in essentially the same figure as this.

apparent step increase in threadfin shad abundance in 1977 (Fig. 5A) was modeled as a response to low spring exports in that year (Fig. 8) in the covariate-conditioned models (note near-zero change point probabilities for 1977 in Figs. 5B and 7). The estimated relationship between winter exports and threadfin was weak in all models (Table 2), especially in the multispecies model that weighted 2002 step changes more heavily. The inclusion of summer calanoid biomass and an autoregressive term (both variables had $0.5 < \Pr(k > 0) < 0.75$) had no effect on posterior probabilities of change points for threadfin shad (estimated coefficients were close to zero in both cases).

DISCUSSION

Different model structures, particularly models for individual species compared with multiple species, yielded somewhat different sets of the more likely change points, but all models indicated sharp declines in abundance of delta smelt, longfin smelt, threadfin shad, and striped bass in the early 2000s. Post-2000 change points were evident in all covariate-conditioned models for all species, indicating that the covariates identified as the strongest predictors of abundance could not explain fully the recent declines. However, there was some evidence that increasing water clarity, winter exports, and spring X2 may have contributed to post-2000 declines in abundance of some species.

Inferences about declines in abundance after 2000 depend partially on whether species were considered jointly or separately. When delta smelt and longfin smelt were modeled individually, the best-supported models largely associated the 2002 decline in abundance of delta smelt with high winter exports and the 2001 decline in abundance of longfin smelt with spring X2. In these models, sharp, unexplained declines in abundance did not occur until 2004. However, in the multispecies model all four species experienced unexplained declines in 2002, and the estimated effects of winter exports and spring X2 on delta smelt and longfin smelt, respectively,

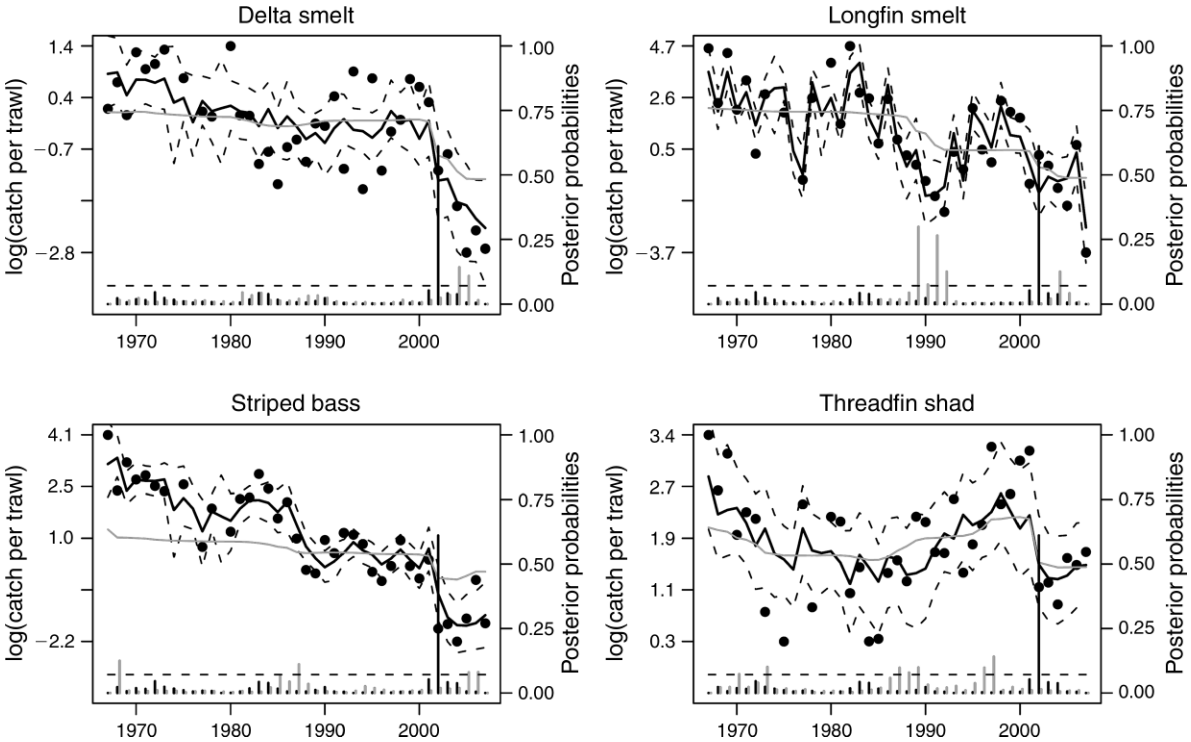

FIG. 7. Abundance [log(catch per trawl)] with fitted values (solid black lines; dashed lines are 95% credible intervals) and intercept parameters (gray solid lines) for delta smelt, longfin smelt, striped bass, and threadfin shad in the multispecies change point model. Intercept parameter = species-specific intercept plus common change point parameter. Bars show posterior probabilities (right axis) of common (black) and species-specific (gray) change points in each year.

were moderately reduced (Table 2). A similar reduction in the estimated effect of winter exports in the multispecies model was observed for threadfin shad. The increased probability of unexplained declines in 2002 and reduced covariate effects in the multispecies model, relative to the single-species models, reflect differences in the amounts of data (evidence) used to fit the different models. Combining data from all species in the multispecies model strengthened the evidence for an unexplained (by the covariates considered) step decline in 2002 for all species and led to a corresponding reduction in the estimated influence of variables that, in single-species models, might have explained 2002 declines for individual species. These results are consistent with a hypothesis that simultaneous, abrupt declines in abundances of multiple species are more likely to have been caused by a common but unknown factor than by different factors for each species (e.g., winter exports for delta smelt and threadfin shad, spring X2 for longfin smelt, another unknown factor for striped bass).

The covariate-conditioned models indicated step declines in abundance of age-0 striped bass in 1987 (evident in a model without autocorrelation) and step declines of longfin smelt in 1989–1991. These declines may be related to the effects of the introduced (ca. 1987) clam *Corbula amurensis*, which caused an ongoing decrease of ~60% in chlorophyll *a* concentration in the estuarine low-salinity zone (Alpine and Cloern 1992). There were concurrent declines in abundance of mysids and some species of copepods upon which striped bass and longfin smelt prey (Kimmerer and Orsi 1996, Orsi and Mecum 1996, Kimmerer 2006). These changes in prey abundance were evident in the diets of striped bass and other fish species (Feyrer et al. 2003). Although variable-selection models did not identify prey variables as strong predictors of fish abundances at the whole-estuary scale of this analysis, summer calanoids and mysid biomass were positively correlated with abundances of striped bass and longfin smelt (calanoids only) in a MAR model of this system (see Mac Nally et al. 2010). When those prey variables were included in covariate-conditioned models for striped bass, evidence for an unexplained step decline in 1987 was reduced greatly (to odds ratio <3), supporting the prey-availability hypothesis. Conversely, the inclusion of prey biomass did not alter substantially evidence for step declines in 1989 and 1991 in longfin smelt abundance.

Covariate relationships and previous analyses

The covariates we identified as strongly associated with pelagic fish abundance, namely X2, water clarity, and export flows, previously have been hypothesized to affect abundance. Jassby et al. (1995) and Kimmerer (2002) identified a relationship between abundances of

TABLE 2. Summary of covariate effects in models of annual abundance of four species of pelagic fishes in the San Francisco Estuary.

Covariate	Pr	Single-species model: Mean slope (SD)	Single-species model: 95% CI	R^2
Delta smelt				0.65
Water clarity	0.81	−0.24 (0.29)	(−0.85, 0.29)	
Winter exports	0.77	−0.25 (0.18)	(−0.60, 0.09)	
Longfin smelt				0.88
Spring X2	1.00	−1.25 (0.18)	(−1.61, −0.88)	
Water clarity	0.96	−0.15 (0.43)	(−1.05, 0.58)	
Striped bass				0.88
Water clarity	0.99	−0.59 (0.24)	(−1.04, −0.06)	
ρ	0.98	0.38 (0.17)	(0.05, 0.69)	
Threadfin shad				0.45
Winter exports	0.51†	−0.14 (0.19)	(−0.52, 0.25)	
Spring exports	0.59†	−0.22 (0.14)	(−0.50, 0.06)	

Notes: We used a variable selection model (Eq. 5) to select covariates and included the covariates in subsequent models if their posterior probability of inclusion (Pr) exceeded 0.75 (see Figs. 3, 4, 5, and 6 for corresponding values for all variables). Mean slope is the posterior mean of the average linear slope over the full range of covariate values in a piecewise linear spline model with up to three knots (changes in slope). All fitted splines were monotonic, and departures from linearity generally were moderate and are described in the "functional response" column. Estimated covariate effects are conditional on the variable being a predictor but incorporate uncertainties about the number and timing of change points. R^2 shows the relative fits of the posterior medians of the fitted values (n_t's in Eq. 6) to the observed log abundance data. Corresponding R^2 values for trend models were: delta smelt, 0.74; longfin smelt, 0.69; striped bass, 0.85; threadfin shad, 0.69. Covariate ρ is the autocorrelation coefficient in Eq. 6.

† Winter and spring exports were included in models for threadfin shad because probabilities of inclusion were sensitive to prior distributions on linear coefficients. Probabilities exceeded 0.75 under certain more restrictive prior distributions (see *Results: Species-specific results* and Appendix).

several species of estuarine-dependent nekton and freshwater flow indexed as spring X2. An association between abundance of striped bass and X2 has been identified before, but the relationship with X2 was weaker than for longfin smelt and the relationship was affected by other factors (Jassby et al. 1995, Kimmerer 2002, Kimmerer et al. 2009). In these previous studies, X2 did not strongly affect the autumn abundance of delta smelt or threadfin shad. These results are consistent with our result that only longfin smelt had a strong (and negative) relationship with spring X2 (Table 2).

The association between water clarity and abundance that we identified also is consistent with previous analyses. Water clarity can affect composition of fish assemblages in large river and estuarine systems (Blaber and Blaber 1980, Quist et al. 2004) and can mediate predator–prey interactions (Abrahams and Kattenfeld 1997, Gregory and Levings 1998). Water clarity (measured by Secchi disc depth) has been related to distributions of several species of fish in the San Francisco Estuary. Delta smelt and striped bass, but not threadfin shad, were most likely to occur where water was turbid during autumn (Feyrer et al. 2007). Secchi depth also explained some of the variation in distribution of delta smelt in summer (Nobriga et al. 2008). Adding Secchi depth to nonlinear models of distribution based on salinity improved fits substantially for delta smelt, striped bass, and longfin smelt (Kimmerer et al. 2009). These effects of water clarity on distributions may translate to effects on abundance to the extent that the fish populations are limited by the availability of habitat. Laboratory experiments and observations suggest that young delta smelt cannot feed effectively unless particles are suspended in the water column (Baskerville-Bridges et al. 2004, Mager et al. 2004).

Export flows in winter and spring were negatively associated with abundance of delta smelt and threadfin shad, respectively, in our models. Previous analyses indicated that export flows can remove a substantial fraction of the delta smelt population in both winter and spring of dry years (Kimmerer 2008). Although previous analyses reported an effect of export flows on the abundance of young striped bass (Stevens et al. 1985), this effect was negligible if egg supply was taken into account (Kimmerer et al. 2001). Threadfin shad has been abundant relative to other species in freshwater zones of the Delta since monitoring began (1967). However, the proportional loss of the threadfin shad population to export operations has not been determined. Of the four species we examined, only threadfin shad occupies the freshwater portion of the Delta for its entire life cycle. The other three species move into brackish water during summer and autumn. Given that water diversions only export freshwater, threadfin shad may have been especially vulnerable to exports throughout the year.

TABLE 2. Extended.

Multispecies model			
Mean slope (SD)	95% CI	R^2	Functional response
		0.63	
−0.24 (0.26)	(−0.74, 0.30)		single-species model: weak at values >2 SD from mean, multispecies model: stronger at values > 1 SD
−0.22 (0.17)	(−0.55, 0.11)		weaker at values < −1 SD
		0.85	
−1.20 (0.18)	(−1.55, −0.83)		stronger at values > mean
−0.27 (0.41)	(−1.14, 0.48)		stronger at values > 1 SD
		0.89	
−0.57 (0.27)	(−1.06, −0.03)		linear
0.40 (0.13)	(0.11, 0.66)		
		0.46	
−0.10 (0.18)	(−0.45, 0.28)		single-species model: weak at values < mean, multispecies model: linear
−0.23 (0.14)	(−0.48, 0.03)		single-species model: weaker at values < −1.5 SD, multispecies model: linear

The variable-selection results suggest that, at the estuary scale, abiotic factors (water clarity, X2, exports) may have more influence on interannual variation in abundances of the four species than do biotic variables. This result is consistent with a MAR analysis of an expert-elicited model of this system that included species interactions among several trophic groups as well as abiotic covariates (Mac Nally et al. 2010). In the MAR analysis, abiotic variables explained 50% more variation than did trophic interactions. Trophic interactions were still important (Mac Nally et al. 2010), but the strongest effects generally were "top-down," with fish apparently having more influence on prey biomass than vice versa. These results suggest that targeted manipulation of abiotic variables such as water clarity, freshwater flow, and water exports could be used to influence fish abundances in this system, but greater understanding of the interactions between abiotic variables and trophic interactions is required before scientifically robust management alternatives can be formulated. Identification of the factor(s) that caused the post-2000 declines remains an important challenge; attempts to reverse declines are unlikely to succeed unless the main drivers of those declines are understood.

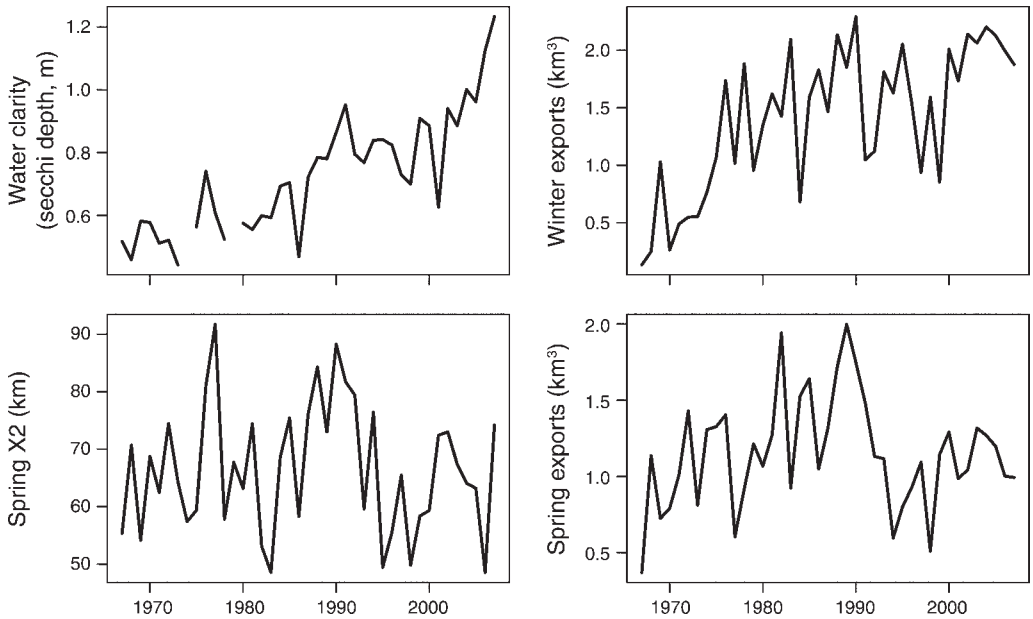

FIG. 8. Trends in covariates used in covariate-conditioned change point models. See Table 1 for explanations of covariates.

Our results confirm that the four species of pelagic fish experienced abrupt declines around 2002 and suggest that all potential drivers not considered in our analyses warrant further investigation.

Strengths of hierarchical Bayesian modeling

The hierarchical Bayesian modeling approach has several advantages over other approaches, such as multiple regression models (Cressie et al. 2009). The hierarchical structure allows sampling or measurement error to be separated from actual variation in underlying abundances, which can improve estimation of the underlying biological processes (Clark 2005). Hierarchical Bayesian models allow considerable flexibility in modeling of biological processes, so a wide variety of process models can be formulated and fitted within a common framework. The availability of public domain software such as WinBUGS, combined with an add-on developed by Lunn et al. (2006) for reversible jump MCMC (Green 1995), makes it increasingly feasible to fit and compare complex hierarchical models within a consistent estimation framework. We examined nonparametric trend models with change points for step and trend changes (Eq. 2), nonlinear variable selection models (Eq. 5), nonlinear covariate models with step changes (Eq. 6), and multiple-response models (Eq. 7), which all included temporal autocorrelation as appropriate. Within each of these general model classes were large sets of special cases that differed with respect to the particular change points and covariate effects included. Many models of a given class were compared or combined for inference on the basis of marginal likelihoods, which inherently penalize model complexity. For example, the capacity to treat the number and location of "knots" (i.e., change points) in linear splines as unknown parameters allowed the relative evidence for change points in specific years to be evaluated by formal comparison of a very large number of possible models (all possible combinations of up to four change points per parameter) while simultaneously estimating other parameters of interest (e.g., covariate effects) and accounting for data uncertainties (e.g., observation errors and missing covariate values).

Future work

Three areas of future research could help reduce uncertainty about drivers of abundance of pelagic fishes in the San Francisco Estuary. One is to pursue, in greater depth, simultaneous modeling of multiple species and interactions among species and covariates. The multiple-species change point models did not consider interactions among the four species of interest (but see Mac Nally et al. 2010), and interactions among covariates were not investigated. Some preliminary work (J. R. Thomson, *unpublished data*) fitting Bayesian additive regression trees (BART; Chipman et al. 2008) included interactions among covariates, but initial results did not yield substantial improvements in fits, and the post-2000 declines were not modeled adequately.

Another area of future work that may clarify mechanisms is to fit process models that include multiple life history stages of the fish species using data available from surveys that complement data from autumn midwater trawl surveys used here. For example, adult delta smelt are sampled from January through April throughout the estuary with a Kodiak trawl (a surface-oriented trawl), and small juveniles are sampled from March through July in the "20-mm survey" (Dege and Brown 2004). In summer, juvenile delta smelt are sampled with tow net surveys. A life history model that linked the abundances of each life stage would provide a more continuous picture of the delta smelt population and would capitalize more fully on available data. The approach to change point identification used here could be applied to any parameter(s) of interest (e.g., population growth parameters) within almost any model structure (Lunn et al. 2006), which may allow identification of important changes in key processes.

A third potential means to elucidate drivers of abundance is to carry out formal statistical comparisons of some of the models formulated by Sommer et al. (2007) and Baxter et al. (2008) to explain declining abundances of pelagic fishes in the San Francisco Estuary. These authors considered many hypotheses for declines in abundance, including changes in stock–recruitment relationships and food webs, mortality from predation and water diversions, contaminants, and changes in the physical environment. Multispecies models with explicit life history submodels could be used to compare the relative likelihood of these alternative hypotheses conditional on the available data. Formal model selection procedures, such as reversible jump MCMC (Green 1995), could be used to estimate posterior probabilities for the models corresponding to different hypotheses.

It is possible, however, that the change points were caused by variables that have not been measured or have not been measured long enough to provide data useful in statistical analyses. For example, of the potentially contributing variables listed by Sommer et al. (2007; Fig. 6), only a few could be included in the models. The effects of toxic algae, for example, have only recently been measured and may have increased. Contaminants are too numerous and dispersed, and effects too sporadic and subtle, for any monitoring program to provide useful information for correlative analyses. Thus, these effects must be investigated through more detailed, mechanistic studies.

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APPENDIX

Details of prior distributions used in change point and associated regression models (*Ecological Archives* A020-051-A1).

SUPPLEMENT

WinBUGS and R code to fit change point and variable selection models (*Ecological Archives* A020-051-S1).

Ecological Archives **A020-051-A1**

J. R. Thomson, W. J. Kimmerer, L. R. Brown, K. B. Newman, R. Mac Nally, W. A. Bennett, F. Feyrer, and E. Fleishman. **2010. Bayesian change-point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications* 20: 1431–1448.**

Appendix A. Details of prior distributions used in change-point and associated regression models.

Priors for the number, timing and magnitude of change-points.

We specified binomial prior distributions for the number of step changes k_α and the number of trend changes k_β: $k_\alpha \sim \mathrm{Bin}(k_{max}, \pi)$, $k_\beta \sim \mathrm{Bin}(k_{max}, \pi)$., where k_{max} is the maximum possible number of each type of change, and π is the binomial probability. Under these priors, the prior probability that there will be k_α step changes was

$$p(k_\alpha) = \binom{k_{\max}}{k_\alpha} \times \pi^{k_\alpha}(1-\pi)^{(K_{\max}-k_\alpha)} = \frac{k_{\max}!\pi^{k_\alpha}(1-\pi)^{(K_{\max}-k_\alpha)}}{k_\alpha!(k_{\max}-k)!}.$$

The priors for the timing of change-points δ(step) and θ(slope) were conditional on k_α and k_β, respectively. All models with a given number of change-points were equally probable a priori. That is, all combinations of k_α step changes were treated as equally probable. For step changes, the prior probability of a specific combination of k_α change-points (e.g. in 1973 and 1999, given that $k_\alpha=2$) was

$$p(\delta \mid k_\alpha) = \binom{T}{k_\alpha}^{-1} = \frac{k_\alpha!(T-k_\alpha)!}{T!},$$

where T is the number of possible change points (= number of survey years – 1).

Therefore, the prior probability for a particular combination of step changes was

$$p(\delta) = p(\delta \mid k_\alpha).p(k_\alpha) = \frac{k_\alpha!(T-k_\alpha)!}{T!} \cdot \frac{k_{\max}!\pi^{k_\alpha}(1-\pi)^{(K_{\max}-k_\alpha)}}{k_\alpha!(k_{\max}-k)!} = \frac{k_{\max}!(T-k_\alpha)!\pi^{k_\alpha}(1-\pi)^{(K_{\max}-k_\alpha)}}{T!(k_{\max}-k)!}$$

.

The probability that any specific year y is included in the vector δ of k_α change-points is k_α / T. Accordingly, the prior probability for a change-point at any give year y was

$$p(y) = \int_{k=1}^{K_{\max}} p(y \mid k_\alpha).p(k_\alpha).dk_\alpha = \sum_{k=1}^{K_{\max}} \left(\frac{k_\alpha}{T} \cdot \frac{k_{\max}!\pi^{k_\alpha}(1-\pi)^{(K_{\max}-k_\alpha)}}{k_\alpha!(k_{\max}-k)!} \right) = \frac{\pi K_{\max}}{T}.$$

These model priors are uninformative about the timing of change-points, but are somewhat informative about the number of change-points. A maximum number of change-points is specified, and there is a prior expectation of πk_{max} step and slope changes. We used π = 0.5 and k_{max} = 4. Importantly, the prior also allows for no change points. In fact, the model with no change-points has higher prior probability ($=0.5^4 \times 0!(T-0)!/T! = 0.5^4$) than any other single model (i.e., any specific combination of ≥ 1 change-points).

The uninformative priors used for all other model parameters are shown in Tables A1 through A3.

TABLE A1. Parameters and their prior distributions for trend models.

The model

$$y_t \sim Normal(n_t, \sigma_{Ot}^2) \quad \text{(A.1)}$$

$$n_t \sim LogNormal(\alpha_t + f_t(t), \sigma_p^2) \quad \text{(A.2)}$$

$$\alpha_t = \alpha_1 + \sum_{j=1}^{k_\alpha} \chi_j I(t \geq \delta_j) \quad \text{(A.3)}$$

$$f_1(t) = \beta_1 t + \sum_{j=1}^{k_\beta} \beta_{[j+1]}(t-\theta_j)_+ \quad \text{(A.4)}$$

Parameters	Description	Prior	Comments
σ_{0t}^2	Variance of observation error at time *t*:	Point estimate calculated from catch	uncertainty of estimated

		data	abundance y_t
σ_p^2	Variance of process error	IG(0.001,1000)	Uninformative
α_1	Estimated initial abundance	N(0,10000)	Uninformative
k_α	Number of step changes in abundance.	Bin(4, 0.5)	Maximum of 4 step changes, prior expectation of 2.
$\delta_j, j = 1,\ldots,k_\alpha$	year when the jth step change occurred	$p(\delta_j \mid k_\alpha) = \frac{k_\alpha!(T-k_\alpha)!}{T!}$ T= survey years –1.	Prior is conditional on k_α. All possible combinations of k_α Step changes are equally likely
$\chi_j, j = 2,\ldots,k_\alpha$	Vector of step change sizes occurring at the k_α change-points	N(0, σ_α^2)	Uninformative, exchangeable prior
σ_α^2	Variance of the normal distribution of step change sizes	$\frac{(\ln y_{\max} - \ln y_{\min})}{1.96}$	Point estimate derived from data range
k_β	Number of changes in the slope; number of times linear trend in abundance changes	Bin(5, 0.5)	Maximum of 5 changes-in-slope. Prior expectation of 2.5.
$\theta_j\ j = 1,\ldots, k_\beta$	year when the jth trend change (change in slope) occurred	$p(\theta_j \mid k_\beta) = \frac{k_\beta!(T-k_\beta)!}{T!}$	All possible combinations of k_β changes-in-slope are equally likely
$\beta_j, j = 1\ldots, k_\beta$	Slope of linear trend	N(0, σ_β^2)	Uninformative, exchangeable prior
σ_α^2	Variance of the normal distribution of linear trend parameters	$\frac{(\ln y_{\max} - \ln y_{\min})}{4 \times 1.96}$	Point estimate derived from data range

Distributions: N= Normal, Bin = Binomial, IG = inverse Gamma. In WinBUGS, Normal distributions are specified with precisions (1/variance) and Gamma distributions with inverse scale parameters, e.g., Gamma(0.001,1000) is specified as dgamma(0.001,0.001).

TABLE A2. Parameters and their prior distributions for variable selection models.

The model

$$y_t \sim Normal(n_t, \sigma_{Ot}^2)$$

$$n_t \sim Lognormal\left(\alpha + \sum_{j=1}^{Q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt} - \phi_{jm})_+ + \rho \log n_{t-1}, \sigma_p^2\right) \quad \text{(A.5)}$$

Parameters	Description	Prior	Comments
σ_{0t}^2	Variance of observation error at time *t*:	Point estimates calculated from catch data	uncertainty of estimated abundance y_t
σ_p^2	Variance of process error	IG(0.001,1000)	Uninformative
α	Estimated initial abundance	N(0,10000)	Uninformative
$k_j, j = 1,\ldots,Q$	Number of linear segments in piecewise linear spline for variable *j*	Cat(p_0, p_1, p_2, p_3) $p_0 = 0.5$, $p_1 = 0.3$, $p_2 = 0.1$, $p_3 = 0.1$ p_n is probability of *n* segments.	$p_0 = 0.5$ is prior probability of no effect of variable *j* Max. segments (knots) is 3
ϕ_{jm} $m=1,..,k_j$. $j = 1,\ldots,Q$	Knot value for m^{th} segment of linear spline for variable *j*	Cat($p_1,\ldots,p_{10}$) $p_n = 0.1$is probability of knot at n^{th} candidate value. There were 10 evenly spaced candidate knot values starting at min(x_j).	Categorigal prior with 10 discrete knots used to limit model space (hence increase speed of MCMC) in variable selection

$\beta_{jm,}$ $m=1,..,k_{j.}$ $j = 1,\ldots,Q$	Linear coefficient for m^{th} segment of linear spline for variable j	N(0, σ_β^2)	Uninformative, exchangeable prior for non-zero coefficients
k_{Q+1}	Binary indicator for inclusion of autocorrelation term ρ	Bin(1,0.5)	
ρ	Autocorrelation coefficient	N(0, σ_β^2)	
σ_β	Standard deviation of the non-zero coefficients.	$\sigma_\alpha = \lvert\zeta\rvert \times \sigma_z^{-0.5}$ ζ~N(0, A) σ_z ~G(0.5,2) A=0.5	Half-Cauchy prior

Distributions: N= Normal, Bin = Binomial, IG = inverse Gamma, Cat = Categorical (equivalent to Multinomial with n = 1).

TABLE A3. Parameters and their prior distributions for covariate-conditioned change-point models.

The model

$$y_t \sim Normal(n_t, \sigma_{Ot}^2)$$

$$n_t \sim Lognormal\left(\alpha_t + \sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt} - \phi_{jm})_+ + \rho \log n_{t-1}, \sigma_p^2\right) \quad \text{(A.6)}$$

In the single species model,

$$\alpha_t = \alpha_1 + \sum_{j=1}^{k_\alpha}\chi_j I(t \geq \delta_j)$$

In the multi-species model, α_t for species s (denoted α_{st} in text), was

$$\alpha_t = \alpha_{s1} + \sum_{j=1}^{k_{s\alpha}} \chi_{sj} I(t \geq \delta_{sj}) + \sum_{l=1}^{k_{C\alpha}} \psi_l I(t \geq \zeta_l) \qquad \text{(A.7)}$$

Parameters	Description	Prior	Comments
σ_{0t}^2	Variance of observation error at time *t*: relative uncertainty of estimate, $y.obs_t$	Point estimates calculated from catch data	
σ_p^2	Variance of process error	IG(0.001,1000)	Uninformative
α_1	Estimated initial abundance	N(0,10000)	Uninformative
k_α ($k_{s\alpha}$ in multi-species model)	Number of step changes in abundance.	$k_\alpha \sim$ Bin(4, 0.5) $k_{s\alpha} \sim$ Bin(2, 0.5)	Maximum of 4 (2) step changes, prior expectation of 2 (1)
$\delta_j, j = 1,\ldots,k_\alpha$	year when the jth step change occurred	$p(\delta_j \mid k_\alpha) = \frac{k_\alpha!(T-k_\alpha)!}{T!}$ T= survey years –1.	Prior is conditional on k_α. All possible combinations of k_α Step changes are equally likely
$\chi_j, j = 2,\ldots,k_\alpha$	Size of jth step change	N(0, σ_α^2)	Uninformative, exchangable prior
σ_α^2	Variance of the normal distribution of step change sizes	$\frac{(\ln y_{\max} - \ln y_{\min})}{1.96}$	Point estimate derived from data range
kj , $j = 1,\ldots,Q$	Number of linear segments in piecewise linear spline for variable *j*	1+ κ_j $\kappa_j \sim$ Bin(3,0.3)	At least 1 segment (linear effect), up to 3 changes in slope
ϕ_{jm} $m=1,..,kj$. $j = 1,\ldots,Q$	Knot value for m^{th} segment of linear spline for variable *j*	U(min(x_j), max(x_j))	Uniform prior for continuous knots

β_{jm}, $m=1,.., kj$. $j = 1,\ldots,Q$	Linear coefficient for m^{th} segment of linear spline for variable j	N(0, σ_β^2)	Uninformative, exchangeable prior for non-zero coefficients
ρ	Autocorrelation coefficient	N(0, 0.001) for striped bass 0 for all other species	Uninformative. Included only for striped bass
σ_β	Standard deviation of the non-zero coefficients.	$\sigma_\beta = \lvert\zeta\rvert \times \sigma_z^{-0.5}$ ζ~N(0, A) σ_z ~G(0.5,2) A=0.04	Half-Cauchy prior
$k_{C\alpha}$	Number of step changes common to all species	Bin(2, 0.5)	Multi-species model only
ζj, $j = 1, ,kC\alpha$	year when the jth common step change occurred	$p(\psi_j \mid k_{C\alpha}) = \frac{k_{C\alpha}!(T-k_{C\alpha})!}{T!}$ T= survey years –1.	Multi-species model only
ψj, $j = 1, ,kC\alpha$	Size of jth common step change	$\frac{(mean(\ln y_{\max}) - mean(\ln y_{\min}))}{1.96}$	Multi-species model only

Distributions: N= Normal, Bin = Binomial, IG = inverse Gamma, U = Uniform, G= Gamma (note G(0.5,2) is equivalent to a χ^2 distribution with 1 d.f.)

Sensitivity of change-point detection to prior distributions

Absolute posterior probabilities of change-points obviously will be sensitive to the prior distributions on the numbers of change-points k_α and k_β (in trend models). Posterior probabilities for change-points in particular years will generally increase with the prior expectation for the number of change-points. Clearly it is important to use prior distributions that reflect appropriate definitions of change-points and plausible expectations about the numbers of such change points (e.g., priors that allowed up to 40 change-points would not be sensible). Across a range of sensible priors for k_α and k_β (e.g. k_{max} = 4 vs. k_{max} = 2) the relative probabilities of change-points and odds ratios (which mostly remove the influence of prior

model probabilities) generally should be consistent. Therefore, inferences about the timing of change-points will rarely be sensitive to the exact choice of priors for k_α or k_β (within reasonable limits). This was certainly true in sensitivity tests for our trend models in which we fitted models with k_{max} = 1, 2, 4 and 6 (for both k_α and k_β).

The prior variances σ_α^2 and σ_β^2 control the possible magnitudes of any change-points in trend models (and covariate-conditioned change-point models for σ_α^2). Posterior model probabilities can also be sensitive to these parameters, because the degree to which integrated likelihoods penalize complexity largely depends on the prior variance for model parameters. Larger prior variances will tend to favor less complex models, and vice versa. In regression models, the prior variance essentially specifies the expected magnitudes of effects. Thus, large prior variances will favor models with few large effects, whereas small prior variances will favor models that include a greater number of variables with relatively small effects. For change-point models, this equates to a choice between favoring few large change-points, or relatively many (up to k_{max}) smaller changes.

We tested the sensitivity of posterior probabilities for change-points to prior variances by fitting models with point priors set at 0.5, 1, and 2 times the data-range values described in the main text (and table A1). We also fitted models with hyper-priors on the variances or standard deviations σ_α and σ_β. This approach reflects prior uncertainty (ignorance) about the expected magnitudes of any effects (e.g., change-points, covariate effects). We fitted models using three different hyper-prior specifications discussed by Gelman 2006 (inverse uniform on standard deviations, inverse Gamma on variances, and Half-Cauchy priors), each with 3 different scale parameters that define the credible effect sizes (Table A4). Results generally were consistent in relative probabilities and odds ratios for change-points in particular years, and invariably led to consistent inferences about the most probable change-points. The absolute probabilities of change-points were generally lower with the hyper-priors because these placed relatively more prior weight on large effect sizes, including some extreme values.

TABLE A4. Priors used in sensitivity analysis for change-point parameters.

Prior name	Details	Scale parameters for σ_α	σ_β scales
point	$\sigma_\alpha^2 = (scale / 1.96)^2$	*scale*=*range*/2, *range*, 2×*range*	*scale/4*
Gamma	σ_α^2~InverseGamma(a,1/a)	a = 0.1, 0.01, 0.001	a
Uniform	σ_α ~Uniform(0, 0.8×*scale*)	*scale*=*range*/2, *range*, 2×*range*	*scale/4*

Half-Cauchy	$\sigma_\alpha = \lvert\zeta\rvert \times \sigma_z^{-0.5}$ $\zeta \sim N(0, 100/scale^2)$ $\sigma_z \sim Gamma(0.5,2)$	*scale*=*range*/2, *range*, 2×*range*	*scale/4*

range = ln y_{max}-ln y_{min}

Sensitivity of variable selection model to prior distributions

In variable selection models, posterior model probabilities can be sensitive to the prior on regression coefficients $\boldsymbol{\beta}$. We used a Half-Cauchy prior (see Table B2) with scale parameter chosen so that ca. 90% and 95% of the prior probability mass was in the interval (-1,1) and (-2,2) respectively. This prior puts most weight on more plausible coefficients while still allowing larger effects. We tested sensitivity of model posterior probabilities to the prior on $\boldsymbol{\beta}$ by fitting models with a range specifications for the prior variance σ_β^2 of the regression coefficients (the jump interface in WinBUGS allows only exchangeable normal priors for the vector of coefficients $\boldsymbol{\beta}$). We varied the scale parameter of the Half-Cauchy prior and fitted models with a range of different priors on σ_β^2, including point estimates (0.25, 0.5, 1,2), uniform on σ_β with upper limits (0.5, 1, 2, and 5). and inverse Gamma (0.01,0.01). We also implemented an approximation to the unit information prior (corresponding to Bayesian Information Criterion penalty when all models are equally probable, George and Foster 2000). Posterior model probabilities (hence probabilities of variable inclusion, Pr($k_j > 0$)) varied predictably with the prior (more diffuse priors yielded lower probabilities), but the relative values among variables were consistent. Pr($k_j > 0$) values for variables with strongest effects (e.g., spring X2 for longfin smelt, water clarity for striped bass) always were high (> 0.9) regardless of the prior used, and the set of variables with Pr(k_j >0)> 0.75 was generally consistent among different prior specifications (though Pr($k_j > 0$) for some variables varied between 0.7 and 0.85). Pr($k_j > 0$) values for winter exports in the delta smelt and winter and spring exports in threadfin shad models were the most sensitive to prior specifications. This sensitivity to priors suggests that only relatively small effects of winter exports on abundances of fishes are supported by the data.

We also tested the sensitivity of odds ratios to prior probabilities of inclusion (i.e., to prior Pr(k_j >0) by increasing the probability of 0 in the categorical prior for the number of linear segments in nonlinear variable selection models. A consistent set of variables with odds ratio > 3 emerged from each analyses.

Note on change-point detection in autoregressive models

The inclusion of an autoregressive term, ρn_{t-1}, in change-point models alters the interpretation of parameters and therefore complicates the detection and interpretation of change-points. In the covariate condition change-point model (Eq. A.6), if $\rho = 0$, then e^{α} is the initial abundance, and a step change in year *y* is modelled well by a new intercept value for year *y* <u>and all subsequent years</u> (as in Eq. A.3). But if $\rho = 1$, then e^{α} is the proportional change in abundance from year *y*-1 to year *y*, and a sustained change in α (Eq. A.3) would model a trend change (a change in the annual rate of change in *y*). With $\rho = 1$ a step change in year *y* is better modelled by a change in α at year *y* only, which can be achieved by modifying the α submodel:

$$\alpha_t = \alpha_1 + \sum_{j=1}^{k_\alpha} \chi_j I(t = \delta_j) \qquad \text{(A.8)}$$

Either or both types of change-point (Eqns. A.3 or A.8) can be included in change-point models. But when $0 < \rho < 1$ it is not clear which model is most appropriate because the interpretation of α, and any change in it, is difficult. This difficulty of interpretation makes the specification of appropriately bounded priors (i.e., credible effect sizes) difficult, which in turn may affect the probability of detecting change-points.

LITERATURE CITED

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