Drivers of pelagic fish abundance in the Sacramento-San Joaquin Delta

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ABSTRACT: Investigating the effects of environmental, biological, and anthropogenic variables on fish populations can aid interpretation of abundance and distribution patterns, contribute to understanding ecosystem functioning, and assist with management. Studies have documented recent declines in relative abundance of several fish populations in the Sacramento-San Joaquin Delta, a highly anthropogenically modified ecosystem on the west coast of the United States. This study extends previous research by applying zero-inflated generalized linear models to a 45-year time-series (1967-2012) of midwater trawl survey data collected in the Delta. The objectives were to evaluate effects of covariates synoptically measured with sampling, develop standardized catch-per-unit-effort (CPUE) indices, and compare the relative roles of several annualized variables (water flow, water quality, zooplankton abundance, and chl-*a*) in explaining CPUE patterns for four fishes (delta smelt, longfin smelt, age-0 striped bass, and threadfin shad). Model comparisons showed that along with year, the sampling covariates region, month, and Secchi depth were statistically important. An inverse relationship of CPUE with Secchi depth was detected for all species, which suggests water quality mediates localized fish abundance. When the year covariate was replaced by annualized biotic and abiotic variables, model comparisons strongly indicated total suspended solids (TSS) best explained CPUE trends for all species, which confirmed the importance of water quality at an annual time-scale. Predicted CPUE across TSS was positively related for all species except threadfin shad. Concurrent declines in TSS and volatile suspended solids with CPUE generally support a bottom-up control hypothesis of food limitation for fishes in the Delta.

INTRODUCTION

The dynamics of fish populations involve a complex suite of biological processes operating at different temporal and spatial scales. Abiotic and biotic variables modulate the intrinsic biological properties of individual fish species and structure the diversity and abundances of species within ecosystems. Such variables can be ecological, environmental, climatic, and anthropogenic, and they synthetically influence ecosystem dynamics. Ecological variables are often described in the context of bottom-up (Chavez et al. 1993, Frederiksen et al. 2006) or top-down (Cury & Shannon 2004, Hunt & McKinnell 2006) control of food webs, while environmental variables such as temperature, dissolved oxygen (Breitberg 2002), and others have been shown to influence early life history (Norcross et al. 1981) and the distribution of fishes within ecosystems (Craig 2012, Buchheister et al. 2013). Climate variability can have a multipronged impact, exerting influence on specific life stages, such as the formation of new year-classes (Houde 2009), or at the level of individual species (Hare et al. 2010) or whole ecosystems (Winder & Schindler 2004, Drinkwater et al. 2009). Numerous anthropogenic stressors such as pollution, nutrient enrichment and eutrophication, introduction of non-native species, and perhaps most notably, overexploitation have been documented to influence ecosystem structure and fish abundance (Islam & Tanaka 2004, Molnar et al. 2008, Diaz & Rosenberg 2008, Worm et al. 2009).

Globally, centuries of anthropogenic change have transformed estuarine and coastal waters into systems with reduced biodiversity and ecological resilience (Jackson et al. 2001, Lotze et al. 2006). Given the importance of these areas to marine life, efforts to remediate the cascading effects of anthropogenic stressors will undoubtedly require deep consideration of

principles inherent to ecosystem-based management (EBM; Link 2010). However, before strategic and tactical management policies can be effectively implemented, EBM rooted or otherwise, the relative roles of natural and anthropogenic factors that affect ecosystem structure and associated species abundances must be well understood.

San Francisco Bay is a tectonically created estuary located on the Pacific coast of the United States that has experienced considerable anthropogenic change (Nichols et al. 1986). The bay and its watershed occupies 1.63 x 10^7 ha and drains 40% of California's land area (Jassby & Cloern 2000). Water is supplied to the estuary from the Sacramento and San Joaquin rivers, which converge to form a complex mosaic of tidal freshwater areas known collectively as the Sacramento-San Joaquin Delta (referred herein as the Delta). Most naturally occurring wetlands in the estuary have been lost due to morphological changes to the system for agriculture, flood control, navigation, and water reclamation activities (Atwater et al. 1979). Other notable changes include modifications to the volume of freshwater entering the Delta and thus the delivery of sediment (Arthur et al. 1996), introduction and invasion of non-indigenous species (Cohen & Carlton 1998), input of contaminants (Connor et al. 2007), and reported decreases in chlorophyll-*a* (Alpine & Cloern 1992), zooplankton (Orsi & Mecum 1996), and fish abundance (Sommer et al. 2007).

A variety of tools can be used to understand the impacts of how specific changes to ecosystem components influence fish population dynamics. These include directed field studies, statistical analyses, and multidimensional process oriented modeling activities, with all often being required to develop a robust understanding of ecosystem dynamics. In the Delta, there has been a considerable focus on empirical analyses designed to examine how temporal

trends in metrics of fish abundance statistically relate to various abiotic and biotic variables. Specifically, water flow within the Delta has been noted as a key structuring variable of fish abundance (Turner & Chadwick 1972, Stevens & Miller 1983, Sommer et al. 2007) as has the salinity variable X_2, which is defined to be the horizontal distance up the axis of the estuary where the tidally averaged near-bottom salinity is 2 psu (Jassby et al. 1995, Kimmerer 2002, Kimmerer et al. 2009, McNally et al. 2010). However, the evidence supporting these inferences was based on relationships between indices of relative abundance and metrics of water flow and/or X_2, which can be limiting since collapsing many raw field observations of fish abundance into annual indices leads to a sizable loss of potentially valuable information. Feyrer et al. (2007, 2011) applied statistical models to base survey data collected from the Delta to quantify fish occurrences in relation to water quality variables, however, they did not examine fish abundance or consider variables at broader spatiotemporal scales.

This study builds on previous empirical analyses by examining how measures of fish abundance in the Delta statistically relate to a broad suite of abiotic and biotic variables across multiple temporal scales, and exclusively from the perspective of raw field observations. The analyses presented here follow a two-step procedure that reflects the specific objectives of this study, (1) investigate the role of covariates measured synoptically at the time of fish sampling to elucidate their effects on localized abundance and ultimately develop standardized indices of abundance with associated measures of precision, and (2) modify the analytical framework used for the first objective to examine the relative role of various abiotic and biotic variables hypothesized to influence fish abundance at larger temporal scales. Specific variables included various annualized metrics of zooplankton density, chl-*a* concentration, water quality, and

water flow. These analyses contribute to the understanding of ecosystem dynamics within the Delta and thus aid the formulation of EBM strategies by providing foundational information of fish population responses to natural and anthropogenically modified system attributes.

MATERIALS AND METHODS

Focal fish species

Reported declines of fish abundance in the Delta have revolved primarily around four species: delta smelt *Hypomesus transpacificus*, longfin smelt *Spirinchus thaleichthys*, age-0 striped bass *Morone saxatilis*, and threadfin shad *Dorosoma petenense*. Accordingly, these species are the focus this study. The delta smelt is a relatively small (60-70 mm standard length, SL), endemic, annual, spring spawning, planktivorous fish that is distributed primarily in the Delta and surrounding areas (Moyle et al. 1992). Delta smelt were listed as threatened under the U.S. Endangered Species Act (ESA) in 1993 and endangered under the California Endangered Species Act (CESA) in 2010. In the San Francisco Estuary, the endemic longfin smelt is also a relatively small (90-100 mm SL), anadromous, semelparous, spring spawning fish with an approximate two-year life cycle that is broadly distributed throughout the estuary (Rosenfield & Baxter 2007). Longfin smelt were listed as threatened under the CESA in 2010. Striped bass is a larger (> 1 m SL), relatively long lived, anadromous, late-spring spawning species deliberately introduced to the San Francisco Estuary from the U.S. east coast in 1879 (Stevens et al. 1985). Although subadult and adult fish reside primarily in estuarine and coastal waters, age-0 fish can be found in lower salinity areas where they feed on zooplankton and macroinvertebrates. Threadfin shad was discovered in the Delta during the early 1960s (Feyer

et al. 2009) and is a relative small (< 100 mm SL), summer spawning planktivorous fish that primarily inhabits freshwater areas of the estuary.

Sampling covariates and standardized indices of abundance

Fish sampling: The California Department of Fish and Wildlife (CDFW) has been conducting the Fall Midwater Trawl (FMWT) survey in the Delta nearly continuously since 1967 (Stevens & Miller 1983; see http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT for additional details, including specific sampling locations). The survey was initiated to measure the relative abundance of age-0 striped bass, however, survey data have been used to infer patterns in relative abundance of a variety of species inhabiting the Delta (Kimmerer 2002, Sommer et al. 2007). Monthly cruises are conducted from September through December and the number of tows each month has increased from approximately 75-80 during the early years of the program to > 100 in more recent years. The survey follows a stratified fixed station design such that sampling occurs at approximately the same location within predefined regional (17 areas excluding areas 2, 6, and 9 per the CDFW's protocol; Fig. 1). At each sampling location, a 12 minute oblique tow is made from near bottom to the surface using a 3.7 m X 3.7 m square midwater trawl with variable mesh in the body and a 1.3 cm stretch mesh cod end. Each catch is sorted and enumerated by species and station-specific measurements of water temperature, electrical conductivity (specific conductance), and Secchi depth are recorded. Catch-per-unit-effort (CPUE) is defined as number of fish collected per trawl tow.

Statistical modeling: Generalized linear models (GLMs; McCullagh & Nelder 1989) were used to evaluate the effects of sampling covariates on relative abundance and to derive standardized indices. GLMs are defined by the underlying statistical distribution for the response variable and how a set of linearly related explanatory variables correspond to the expected value of the response variable (Maunder & Punt 2003). The relationship between explanatory variables and the expected value of the response variable is defined by a link function, which must be differentiable and monotonic.

Since CPUE was defined as fish counts per trawl tow, candidate distributions included the Poisson and negative binomial. Plots of the proportion of FMWT tows where at least one target animal was captured across the time-series for each species showed low values for many years, which gave rise to the possibility that these data were zero-inflated (Fig. S1). In general, zero-inflated count data implies that the response variable contains a higher proportion of zero observations than expected based on a Poisson or negative binomial process. Ignoring zero-inflation can lead to overdispersion and biased parameter and standard errors estimates (Zuur et al. 2009).

Zero-inflated distributions are a mixture of two distributions, a degenerate component that is zero with certainty and a second component that includes zeros and positive values (Maunder & Punt 2003). In effect, the data are divided into two groups, where the first group contains only zeros (termed false zeros) and the second group contains the count data which may include zeros (true zeros) along with positive values (Zuur et al. 2009, 2012). Diagnostics of preliminary model fits supported application of a zero-inflated negative binomial distribution, which can be expressed as:

$$\Pr(y_i) = \begin{cases} \pi_i + (1-\pi_i)\cdot\left(\dfrac{k}{\mu_i + k}\right)^k & y_i = 0 \\ (1-\pi_i)\cdot\dfrac{\Gamma(y_i+k)}{\Gamma(k)+\Gamma(y_i+1)}\cdot\left(\dfrac{k}{\mu_i+k}\right)^k\cdot\left(1-\dfrac{k}{\mu_i+k}\right)^{y_i} & \text{otherwise} \end{cases} \quad (1)$$

where y_i is the ith CPUE observation and π_i is the probability of a false zero. The top equation represents the probability of obtaining a zero CPUE value, which is a binomial process that can occur either as a false zero or a true zero count adjusted by the probability of not obtaining a false zero. The bottom equation is the familiar negative binomial mass function with parameters k and μ_i adjusted by the probability of not obtaining a false zero. GLMs were specified to model π_i and μ_i with logit and log link functions, respectively.

The explanatory variables considered were year, month, area (all categorical), and the continuous variable Secchi depth, which was rescaled by subtracting the mean and dividing by its standard deviation. Levels of categorical variables with < 5% of the total catch of each species were deemed uninformative and excluded from the analysis. The variables surface water temperature and surface salinity were also considered, however, variance inflation statistics indicated that month/temperature and area/salinity were collinear. Month and area were chosen over temperature and salinity because an appreciable number of catch records did not have associated measures of temperature and/or salinity and thus analyses to be based on maximal information. Also, the variables month and area arguably have the potential to be more useful in a management context. Interaction terms were excluded because the high proportion of zeros in the data lead to many year/area and month/area combinations for which there were no positive CPUE observations. Model parameterizations for each species ranged

from inclusion of only a year covariate for the count and probability of false zero models to the saturated model with all four covariates specified for both components, including the possible combinations of unbalanced covariate specifications. Akaike's Information Criterion (AIC; Akaike 1973, Burnham & Anderson 2002) was used for model selection. Yearly indices of relative abundance were generated from the best fitting model using estimated marginal means (Searle et al. 1980) and associated coefficients of variation were estimated from standard deviations of 1000 nonparametric bootstrapped samples (Efron & Tibshirani 1993). Models were fitted to data from 1967-2012 with the exception of 1974, September 1976, December 1976, and 1979 when no sampling occurred.

Annual covariates

The explanatory variable year is included in models when the goal is to develop a time-series of estimated yearly abundance indices. However, the year covariate is simply a proxy for the ecosystem conditions over an annual time frame and thus has no direct relation to the vital rates of fish populations. Therefore, to more directly investigate factors potentially underlying interannual patterns in relative abundance for each fish species, the aforementioned zero-inflated GLM structure was modified by replacing the year covariate individually by time-series of several hypothesized annual-scale continuous covariates. Operationally, this implied that the yearly value of the annual-scale covariate was assigned to each observed CPUE corresponding to the same year. Broad categories of the annual covariates considered were biotic, which included the density of various zooplankton taxa and chl-*a* concentration as a proxy for phytoplankton biomass, and abiotic, which included various water quality parameters and

water flow. Preliminary model fits revealed that the month and area covariates were important in both components of the zero-inflated model structure, but that Secchi depth was collinear with several annualized covariates (e.g., water quality measures). Therefore a single parameterization that included the annualized covariate along with month and area was considered for all annualized biotic and abiotic variables. The years analyzed were 1976-2010, which was due to availability of chl-*a* data (began in 1976) and water flow measures (obtained through 2010). AIC was used to compare among the model parameterizations with annualized covariates for each species.

Biotic variables: The California Department of Water Resources (DWR) in collaboration with the CDFW have been compiling data on zooplankton density in the Delta since 1968 (see http://www.water.ca.gov/bdma/meta/zooplankton.cfm for additional details, including specific sampling locations). The zooplankton monitoring program was initiated to investigate the population trends of pelagic organisms consumed by young fishes, particularly age-0 striped bass. Although the initial focus was to evaluate seasonal patterns in mysid abundance, the program expanded shortly after its inception to assess population levels of other key zooplankton taxa. Sampling occurs monthly at approximately 20 fixed stations. The zooplankton sampling gear consists of a Clarke-Bumpus net mounted directly above a mysid net and the unit is deployed in an oblique fashion from near bottom to the surface. Each net is equipped with a flow meter and all samples are preserved for sorting in the laboratory. For each station, zooplankton taxa are expressed as the total number per cubic meter of water

sampled. Starting in 1976, chl-*a* concentration was recorded synoptically with zooplankton sampling.

The zooplankton taxa examined were adult calanoid copepods, adult cyclopoids, a combination of the two, and mysids. Annual estimated mean densities of zooplankton and chl-*a* were based on lognormal GLMs fitted to data from the core sampling locations and first replicate sample. The categorical explanatory variables considered were year, survey (which is approximately equivalent to month), and area along with the continuous variable Secchi depth, which was again rescaled. Levels of categorical variables with < 5% of the total zooplankton density of each group were deemed uninformative and excluded from the analysis. Collinearity was assessed using variance inflation statistics and bias corrected predicted (Lo et al. 1992) time-series were generated from the best fitting model using estimated marginal means.

Abiotic variables: The DWR has been monitoring water quality parameters at discrete sampling locations in the Delta since 1970 (see http://www.water.ca.gov/bdma/meta/discrete.cfm for additional details, including sampling locations). The program was established to provide information for compliance with flow-related water quality standards for the Delta set forth in the series of formalized Water Right Decisions, and to provide abiotic data that could aid the interpretation of results from concurrent biological monitoring programs. Samples are taken at approximately 1 m depth and roughly within a one hour window of the expected occurrence of high tide from 19 fixed stations. Sampling frequency is bimonthly during the rainy season (October/November to February/March) and monthly during the dry season (March/April to September/October).

Water quality variables considered were mean summer (Jul-Sep) and winter (Jan-Mar) water temperature, total suspended solids (TSS) or filterable solids, volatile suspended solids (VSS) as a measure of the organic component of TSS, and turbidity. Water temperature metrics were estimated from a Gaussian GLM while annual mean TSS, VSS, and turbidity estimates were obtained from bias-corrected lognormal GLMs. The explanatory variables considered were categorically defined year, month, and area. Variance inflation statistics were again used to assess collinearity, and predicted mean values were based on estimated marginal means from the best fitting model.

The water flow variables considered were classified into two groups, 'historical', which refers to measured flows taken from monitoring equipment located at various points in the Delta, and 'unimpaired', which is a estimated reference quantity intended to represent broader watershed-level hydrology. For each group, monthly inflow and outflow time-series were assembled. Historical inflow included combined measurements from the Sacramento River, Yolo Bypass, and Eastern Delta (San Joaquin River and adjacent areas; Fig. 1), while historical outflow is a net quantity of inflow and an estimate of Delta precipitation less total Delta exports and diversions. All historical flow time-series were based on DAYFLOW, which is a computer program designed to estimate daily average Delta outflow (see http://www.water.ca.gov/dayflow/ for more details). Unimpaired inflow is an estimate of water entering the Delta from the expansive watershed while unimpaired outflow is a net value adjusted for natural losses (e.g., evaporation and vegetation uptake). Flow data were provided courtesy of W. Bourez (MBK Engineers, Sacramento, CA).

For each flow variable, a single value was calculated by averaging monthly flow values four different ways: (i) from Jan-Jun within the year of sampling, (ii) from Mar-May within the year of sampling, (iii) from Jan-Jun of the preceding sampling year, and (iv) from Mar-May of the preceding sampling year. This approach gave rise to 16 annual flow covariates. Lagged flow variables were considered to investigate possible delayed effects of flow on the relative abundance of fish populations. For the best fitting annual covariate, 95% prediction intervals of counts and probabilities of false zeros were based on 1000 nonparametric bootstrapped model fits (Efron & Tibshirani 1993). All statistical analyses were performed with the software package R (version 2.15.1, R Development Core Team 2012).

RESULTS

Fish sampling summary

Complete tow, month, area, and Secchi depth information was available for 15,273 stations sampled during monthly fall cruises from 1967-2012 (excluding 1974, Sep 1976, Dec 1976, and 1979 when no sampling occurred). Data summaries by month indicated that all levels contained adequate nonzero CPUEs for inclusion in the analysis. However, spatial data summaries showed CPUEs were variable and low in some areas, which led to the inclusion of only areas 12-16 for delta smelt, 11-14 for longfin smelt, 12-16 for YOY striped bass, and 15-17 for threadfin shad (Fig. 1). Total numbers of tows analyzed for each species were 8,802 for delta smelt (max. catch of 156 animals in December 1982), 6,582 for longfin smelt (max. catch of 3,358 animals in September 1969), 8,733 for age-0 striped bass (max. catch of 1,100 animals in September 1967), and 5,019 for threadfin shad (max. catch of 4,012 animals in December

2001). Although high CPUE values did occasionally occur, the data for each species were strongly skewed toward zero and very low CPUE values. Mean percent of nonzero catches across the full time-series was 28.1% for delta smelt, 50.2% for longfin smelt, 52.1% for age-0 striped bass, and 47.1% for threadfin shad (Fig. S1).

Sampling covariates, standardized indices of relative abundance

Based on AIC statistics, the full zero-inflated negative binomial GLM (model M_4) provided the best fit to the survey data for each species (Table S1). For delta smelt, model M_5 received modest empirical support (ΔAIC=5.9), and no other parameterizations provided comparably plausible fits for the other three species. The superior fit of model M_4 suggested that all covariates were statistically important structuring variables and that CPUEs and the probabilities of false zeros varied considerably by year, month, area within the Delta, and across the domain of observed Secchi depths.

The model predicted standardized indices of yearly relative abundance showed differing patterns for each species (Fig. 2). For delta smelt, higher predicted indices generally occurred in the early 1970s, 1980, and also for various years during the 1990s. The highest index value occurred in 1991, and low relative abundance occurred for much of the 1980s and 2000s. The indices of longfin smelt abundance were variable and high during the late 1960s, early 1970s, and for a few years during the early 1980s. Since 2000, abundance indices have been consistently low with 2007 marking the lowest index value on record. Age-0 striped bass relative abundance consistently declined throughout the analysis time period. The first year in the survey (1967) marked the highest age-0 striped bass index value on record while 2002

marked the lowest value. Indices of threadfin shad relative abundance declined in the late 1960s, rebounded to higher but variable levels from the mid-1980s to early 2000s, and declined to the lowest value on record in 2012. Average species-specific CPUE across the time-series was as follows: 1.24 fish/tow for delta smelt, 13.4 fish/tow for longfin smelt, 5.34 fish/tow for age-0 striped bass, and 22.9 fish/tow for threadfin shad. The precision of the estimated indices for all species was quite good, as bootstraped estimated yearly CVs predominately ranged between 0.15 and 0.45 with occasional values greater than 0.5.

Peak estimated monthly CPUE occurred in October for delta smelt, December for longfin smelt, September for age-0 striped bass, and November for threadfin shad (Fig. 3). Delta smelt CPUEs for November and December did not differ considerably from its peak month nor did the threadfin shad December CPUE when compared to its peak. Spatially, highest CPUE occurred in area 15 for delta smelt, area 12 for longfin smelt, area 15 for age-0 striped bass, and area 17 for threadfin shad. Age-0 striped bass CPUE for areas 12 and 14 were comparably similar in magnitude to its peak. The response in estimated CPUE across the range of observed Secchi depths was strong and consistent across each species, as higher predicted CPUEs corresponded to low observed Secchi depths. This result emerged because the estimated Secchi depth coefficients associated with the count component of model M_4 were consistently negative across species. Related were the consistently positive estimated coefficients for the false zero model component of each species. Therefore, predicted CPUE declined with increased water clarity (higher Secchi depth) and the probabilities of false zeros increased with water clarity. In terms of actual water quality conditions in the Delta, the minimum observed Secchi depths for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad were 0, 0, 0, 0.12 m,

respectively, while the maximum were 2, 1.6, 2, 2.09 m. Relative to the maximum predicted CPUE for each species, the observed Secchi depth at which estimated CPUE decreased by 25, 50, and 75%, respectively, was approximately 0.07, 0.17, and 0.35 m for delta smelt, 0.10, 0.25, and 0.50 m for longfin smelt, 0.11, 0.23, and 0.53 m for age-0 striped bass, and 0.4, 0.74, and 1.12 m for threadfin shad. Collectively, these results suggest that an increase from virtually no water clarity to roughly 0.5 to 1 m of water clarity corresponded to a 75% or greater reduction in estimated CPUE for all species.

Annual covariates analysis

Biotic variables: Predicted trends of the annualized biotic and abiotic variables showed differing patterns through time. Adult copepod density (calanoid, cyclopoid combined) has been variable but generally decreasing in the Delta, with this trend being largely driven by taxa within the calanoid group (Fig. 4A-E). In contrast, the predicted trend in cyclopoid copepod density has been increasing since the mid-1990s, however, the comparably low density of cyclopoid copepods marginalized the impact of this group on the combined copepod trend. Estimated mysid density has been fairly stable since 1990, but much reduced from peak and moderate levels in the mind 1980s and late 1970s, respectively. The predicted trend of chl-*a* was relatively high and variable in the early part of the time-series, but considerably lower and more stable since 1987, which is when the lower trophic level food web of the Delta changed in response to impacts by the introduced clam *Cobubula amurensis* (Kimmerer 2002). The CVs of the estimated zooplankton densities and chl-*a* levels were generally low and indicative of good precision.

Abiotic variables: Trends in predicted summer and winter water temperatures were generally stable over time, with estimated winter temperatures being slightly more variable than annual or summer temperatures (Fig. 4F-J). Predicted trends of TSS, VSS, and turbidity in the Delta were similar in that they showed considerable declines since the mid-1970s. Patterns in the various water flow variables showed distinct periods of 'wet' and 'dry' Delta hydrology over time. Peak flow events occurred in 1983, the mid 1990s, and more recently in 2006, while low flows were observed in mid 1970s, early 1990s and late 2000s (Fig. 5). As expected, comparisons of type-specific (historical, unimpaired) patterns of inflows and outflows were the same qualitatively, with the latter simply reflecting reductions in water volume due to utilization. For the historical inflows and outflows, the two chosen averaging periods yielded virtually the same yearly volumes, however, there were notable differences in yearly volumes of unimpaired inflow and outflow depending on the monthly averaging period. The precision of all estimated annual water quality variables was very good as evidenced by consistently low CVs.

Modeling results: Based on AIC statistics, the best fitting annualized variable was TSS for all species (Table S2). Comparatively, there was no empirical support for any other annualized variables considered. The predicted CPUE responses and probabilities of false zeros across the range of TSS were similar for all species with the exception of the trend in predicted CPUE for threadfin shad (Fig. 6). Over the range of TSS, predicted delta smelt, longfin smelt, age-0 striped bass CPUE increased, while the CPUE trend for threadfin shad showed an inverse relationship. For all species, the predicted trends in probabilities of false zeros were fairly

pronounced and decreasing with TSS. In terms of precision, the bootstrapped prediction intervals for both model components were generally narrow for all species.

DISCUSSION

Sampling covariates, standardized indices of relative abundance

Patterns in Delta fish abundance derived from FMWT survey data have been the focus of numerous investigations, particularly over the past several years (see Jassby et al. 1995, Kimmerer 2002, Sommers et al. 2007, among others). However, contemporary studies of fish populations have generally relied on abundance indices developed by the CDFW, which are derived from an analysis protocol that has several technical limitations (see http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT for methodological information). Newman (2008) reviewed these limitations and described an advancement in the form of a sample design-based procedure for estimating total abundance (applied to delta smelt), and also suggested the use of model-based procedures. The present study was partially motivated by that suggestion.

Although the survey indices of relative abundance in this study do not substantially differ qualitatively from those reported by the CDFW, there are distinct advantages to the use of a model-based approach. First, each index value represents a standardized estimate of the mean annual CPUE, provided the assumptions of the modeling approach were not violated. For each species, plots of residuals for the count and false zero models across the observed domains of the covariates showed no distinct patterns or nonlinearities, and overdispersion was adequately handled by the zero-inflated model structure. Diagnostically, the means of the

negative binomial and binomial distributions appear to be well estimated, however, the degree to which the estimated indices track true population abundance depends on the representativeness of FMWT samples. Second, model-based procedures support relatively straightforward uncertainty estimation, and as a general rule, measures of precision for indices of relative abundance should be routinely reported. Bootstrapped CVs of the indices were fairly low for all species and likely due to the relatively high sampling intensity of the FMWT survey and the high proportion of consistently low observed CPUEs. Since the inception of the FMWT survey, the number of monthly sampling locations has grown considerably (~25%), yet accompanying studies of potential gains/losses in bias and precision of indices are absent from the literature. In general, model-based approaches can be useful in the design of fisheries-independent surveys (Peel et al. 2013), and the methods in this study could support optimization studies to evaluate design elements, appropriate sample sizes, and thus allocation of resources for future FMWT surveys. Third, the non-year effects in a model-based procedure can yield potentially valuable information about how CPUE responds to different structuring variables. The estimated monthly, area-specific, and Secchi depth effects for the four species showed relatively unique CPUE responses, which is important foundational information for future hypothesis driven field studies and mechanistic based modeling activities.

The annual frequency of zero CPUE observations over the course of the entire FMWT survey was appreciably high for all species (Fig. S1). As a means of coarsely evaluating the temporal pattern of zero-inflation in the FMWT data, model M_4 and its non-zero-inflated counterpart (intercept only parameterization for the false zero component) were sequentially fitted to subsets of the FMWT data set truncated by decade for each species. That is, the two

models were applied to only 1960s data, then to 1960s-1970s data, then to 1960s-1980s data, and so on through the full time-series. With the exception of the 1960s data for longfin smelt, AIC statistics strongly supported the zero-inflated parameterization for all species and time periods. Therefore, it appears that the FMWT survey data have almost always contained more zero CPUE observations than would otherwise be expected given a negative binomial count process, which raises the question, why?

Failing to successfully encounter target populations can arise because they are rare, samples are taken in suboptimal habitats (true zeros), or because samples are taken in optimal habitats but reduced survey catchability across time, space, and/or ecosystem conditions prevent successful collections (false zeros). Species rarity does not seem likely for Delta fishes since ESA and CESA listings of delta smelt and longfin smelt occurred decades after the survey began, estimated adult striped bass abundance exceeded 1 million fish in the early 1970s (Stevens et al. 1985) thus requiring considerable age-0 production, and threadfin shad have been viewed as highly abundant since appearing in the Delta (Feyer et al. 2009). The FMWT survey does follow a fixed station sampling design, which raises the possibility that samples are consistently taken at locations that do not support high localized fish abundance. Additionally, if habitat utilization of fishes in the Delta has systematically changed over time in response to morphological alterations of the estuary and/or sustained regimes of ecosystem conditions, differences in relative abundance and distribution become confounded. The relatively high spatiotemporal sampling intensity of the FMWT survey may somewhat mitigate these concerns, but the four focal species are schooling pelagic fishes and thus variable distributions through time and space should be expected.

The consistency of the model estimated responses to Secchi depth for all species warrants deeper consideration, especially in the context of false zeros. Feyer et al. (2007) analyzed raw FMWT survey data to evaluate fish occurrences (presence/absence of delta smelt, age-0 striped bass, and threadfin shad) in relation to various environmental variables and documented an inverse response with Secchi depth. The results of this study generalize that finding to include localized fish abundance. For delta smelt, Feyer et al. (2007) noted that higher presence/absence at lower Secchi depths could be due to required turbidity for feeding and/or turbidity mediated top-down predation impacts. A third potential explanation is that catchability of the FMWT survey sampling gear changes with Secchi depth. In general, Secchi depth is a coarse measurement of water clarity, and it is not possible to distinguish among constituent groups causing low measurements. If those constituent groups are largely organic material, then a positive fish CPUE response to food availability is possible. Conversely, if those constituent groups are not largely organic, then higher CPUE at lower Secchi depths could be due to compromised foraging impacts of visually oriented piscivores such as larger striped bass (Horodysky et al. 2010). However, all of the fishes in this study are pelagic, planktivorous feeders, and thus it is reasonable to assume that vision plays a central role in their sensory ecology. Animals could be more effective at gear avoidance under higher Secchi depths than at lower Secchi depths simply because of a larger field of visibility for gear detection.

Although experimentally testing the variable catchability hypothesis is challenging, flume trials to assess gear behavior under various hydrographic conditions and gear attached video equipment could be informative. In terms of the bottom-up hypothesis, characterization of water column constituents synoptic with fish stomach content analysis could assist in

understanding trophic interactions and prey selectivity, which could assist in determining if the inverse relationship of CPUE and Secchi depth is a response to food availability (more on this topic below). Regarding top-down impacts, results of striped bass and other fish predator diet composition studies in the Delta have shown very little consumption of delta smelt and longfin smelt, and modest consumption of age-0 striped bass and threadfin shad (Nobriga & Feyer 2007, Nobriga & Feyer 2008). However, these studies were temporally abbreviated and each acknowledged potential biases due to spatial limitation of predator stomach collections. Therefore, systematic temporal and spatial diet composition studies of piscivorous fishes could be helpful in more fully understanding predation impacts of larger fishes.

Annual covariates analysis

The annualized covariates considered were chosen in an effort to evaluate hypothesized drivers of fish abundance that were potentially operating at broad temporal scales. The choice to focus on the annual time-scale was motivated from the notion that yearly environmental conditions have the potential to impact early life history and thus new year-class formation. However, the analytical approach taken to evaluate annual covariates can be used for variables aggregated across other potentially meaningful scales. For example, biotic or abiotic variables summarized monthly or seasonally could be used to more directly explore drivers of within-year CPUE patterns, and variables could be aggregated spatially to investigate drivers of fish distribution within the Delta. Studies of this type represent fruitful areas of future research.

The strong empirical evidence supporting TSS as the best fitting annualized covariate for all species is consistent with the importance of Secchi depth documented in the analysis of

sampling covariates. Trends in the model predicted CPUEs and probabilities of false zeros across TSS were analogous to those associated with Secchi depth, with the exception of predicted threadfin shad CPUE which showed a modest decline with TSS perhaps due to the influence of a few high observed CPUE values at lower TSS values (Fig. 6K). The results for the other three species confirm the general effect that more turbid water yields higher CPUE and suggest that it is also detectable at an annual time scale. The bottom-up, top-down, and variable gear catchability hypotheses are again in play, however relative to the Secchi depth results, the variables TSS and VSS afford additional insights. By definition, TSS is a measure of the actual weight of particulate material present in a water sample, and it includes both sediment and organic constituents. VSS is a measure of the solids within TSS that are lost upon ignition, and thus it approximates the amount of organic material present in a TSS sample. VSS is likely comprised of phytoplankton, zooplankton, and detritus, but since relative ratios of those groups are not known, it is difficult to assess the amount of nutritional organic material available to fishes. Yearly ratios of VSS to TSS ranged from 13-28% and have been generally increasing over time, most appreciably since 1999. However, despite the notion that the organic component of TSS is increasing recently, predicted trends of VSS show a decline since the 1970s and a stabilization since the mid-1990s near the lowest levels in the time-series (Fig. 4). Under the assumption that trends in the indices represent changes in true fish abundance, which is a key assumption that should be formally evaluated, the results of the annual covariate analysis lend support to the bottom-up hypothesis that declines in fish abundance may be due to food limitation and/or poor food quality.

Much of the contemporary understanding regarding drivers of fish abundance in the Delta has revolved around flow, particularly outflow and the location of X_2. In this study, X_2 was not considered largely because it is highly variable, often moving significant distances within a single tidal cycle, and because it is a proxy variable directly influenced by flow. Thus, inclusion of the various flow variables constitutes a more direct evaluation of system hydrology. Compared to several of annualized plankton and water quality variables considered, the results of this study indicated that the flow variables received virtually no empirical support. If model comparisons are restricted to only the flow variables, historical outflow averaged January-June provided the best fit for delta smelt and threadfin shad, and historical inflow averaged January-June and the same variable averaged March-May provided the best fit for longfin smelt and age-0 striped bass, respectively (Table S2). There was competing empirical support for delta smelt related to historical inflow averaged January-June (ΔAIC = 1.3) and for age-0 striped bass related to historical outflow averaged January-June (ΔAIC = 3.1). These results fail to confirm the dominant influence of one single flow variable on fish abundance in the Delta, which is not overly surprising since the underlying dynamics of the focal fish species are likely shaped by intersections of a complex suite of biological, ecological, and environmental processes.

Management implications

Estuarine habitat is comprised of brackish water influenced by contributions from the marine environment through tides and weather patterns, riverine inputs in the form of flows of freshwater and the delivery of allochthonous material, and effects of geographic features such as levees, system channels, and connectivity to adjacent wetlands. The low salinity zone (LSZ)

of the San Francisco Bay-Delta estuary, which is defined to be the inland edge of the estuarine habitat where daily salinity ranges between 1-6 psu, has been an area of focused research and management because of perceived benefits it affords to fishes through turbidity mediated refugia and the supply of food. The LSZ is centered around X_2 with more westerly locations being positively related to fish survival and abundance (Jassby et al. 1995, Kimmerer 2002, McNally et al. 2010). This relationship was codified in 1995 through a formalized adoption of X_2 as a water quality standard by the State Water Resources Control Board of California. The associated regulatory requirements are designed to maintain expansive estuarine habitat by ensuring westerly springtime X_2 locations through combined effects of natural hydrology (indexed flows into reservoirs on the eight largest rivers) along with reservoir releases and/or decreased water exports.

During the first few years following implementation of the X_2 water quality standard, fish abundance indices showed a variable but generally increasing pattern (Fig. 2), which provided some indication that the approach to flow management was achieving its desired objectives. However, beginning in the early 2000s, fish abundance indices declined dramatically and maintained historically low levels (exception 2011) thus giving rise to a phenomenon deemed the pelagic organism decline (POD; Sommer et al. 2007). Again, assuming the indices track true fish abundance, the persistence of the POD for what has now been over a decade suggests the currently implemented X_2 water quality standard is an ineffective strategy for achieving healthy fish population abundances in the Delta. Further inspection of the unimpaired flow data (Fig. 5C,D) show that the late 1990s were relatively wet years in terms of watershed-level hydrology, and thus the associated improvements in fish

relative abundance could be more related to broader watershed-level inputs (which pushes X_2 west as a result) rather than the one-dimensional and absolute X_2 locations themselves. Watershed-level inputs imply the successful delivery of water over land nutrients, detritus, and other organic material which are all vital to stimulating basal food web processes. Management of X_2 locations through straightforward releases of largely clear and fresh reservoir water and/or reduced exports will certainly influence the area of the LSZ, but doing so likely fails to ensure the delivery of constituents necessary to maintain or enhance the ecological health of the Delta food web. The lack of watershed-level input in recent years is evident in the time-series of VSS, which has remained relatively low and stable since enactment of the X_2 water quality standard (Fig. 4I).

If the abundance indices are taken as representative of true abundance, the results of this study draw attention to the bottom-up hypothesis and suggest that fish populations in the Delta may be food limited. When evaluating the base of an estuarine food web, flow is certainly a variable that must be acknowledged since it represents the mechanism by which requisite nutrients, detritus, and other organic material are supplied to the system. Moving forward, though, a modification in management objectives to include a more direct focus on land derived inputs to the Delta may be warranted. Perhaps general flow criteria can be structured to include water diversions that traverse more expansive land cover thus re-establishing water interactions with remaining flood plains. Additionally, the importance of organic contributions to Delta food web processes derived from the now absent wetlands cannot be overstated, and efforts could be directed toward rehabilitating these emergent habitats that once formed an extensive mosaic in the Delta. Adopting strategies like these will

require drawing on approaches inherent to EBM, and although implementation of EBM can be daunting, the rewards afford an opportunity for ecosystem recovery that could benefit far more than just fishes.

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LITERATURE CITED

Alpine AE, Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946-955

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary

Arthur JF, Ball MD, Baughman SY (1996) Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta Estuary, California. In: Hollibaugh JT (ed) San Francisco Bay: The Ecosystem. Pacific Division American Association for the Advancement of Science, San Francisco, CA

Atwater BF, Conrad SG, Dowden JN, Hedel CW and others (1979) History, landforms and vegetation of the estuary's tidal marshes. In: Conomos TJ (ed) San Francisco Bay: The Urbanized Estuary. Pacific Division American Association for the Advancement of Science, San Francisco, CA

Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on

coastal fishes and fisheries. Estuaries 25: 767−781

Buchheister A, Bonzek CF, Gartland J, Latour RJ (2013) Patterns and drivers of the demersal fish community in Chesapeake Bay. Mar Ecol Prog Ser 481:161-180

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY

Chavez, FP, Ryan J, Lluch-Cota SE, Niquen M (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299: 217-221.

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555-558

Connor MS, Davis JA, Leatherbarrow J, Greenfield and others (2007) The slow recovery of San Francisco Bay from the legacy of organochlorine pesticides. Environ Res 105:87-100.

Craig JK (2012) Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar Ecol Prog Ser 445:75-95

Cury P, Shannon L (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Prog Oceanogr 60:223-243

Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. Science 321:926-929

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S and others (2009) On the processes linking climate to ecosystem changes. J Mar Sys 79:374-388

Efron B, Tibshirani RJ (1993) An Introduction to the Bootstrap. Chapman & Hall, New York, London.

Feyer F, Nobriga ML, Sommer T (2007) Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci 64: 723-734

Feyer F, Sommer T, Slater SB (2009) Old school vs. new school: status of threadfin shad (*Dorosoma petenense*) five decade after its introduction to the Sacramento-San Joaquin Delta. San Fran Estua Water Sci 7(1)

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259-1268

Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD (2010) Forecasting the dynamics of a coastal fishery species using a coupled climate-population model. Ecol Appl 20:452-464

Horodysky AZ, Brill RW, Warrant EJ, Musick JA, Latour RJ (2010) Comparative visual function in four piscivorous fishes inhabiting Chesapeake Bay. J Exp Biol 213:1751-1761

Houde ED (2009) Recruitment variability. In: Jakobsen T, Fogarty M, Megrey BA, Moksness E (eds) Reproductive Biology of Fishes: Implications for Assessment and Management. Blackwell Publishing, Malaysia

Hunt GL, McKinnell S (2006) Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Prog Oceanogr 68:115-124

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732

Islam MS, Tanaka M (2004) Impacts of pollution on coastal and marine ecosystems including coast and marine fisheries and approach for management: a review and synthesis. Mar Pollut Bull 48:624-649

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637

Jassby AD, Kimmerer WJ, Monismith SG, Armor C and others (1995) Isohaline position as a habitat indicator for estuarine populations. Ecol Appl 5:272-289

Jassby AD, Cloern JE (2000) Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). Aquatic Conserv Mar Freshw Ecosyst 10:323-352.

Kimmerer WJ (2002) Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser 243:39-55

Kimmerer WJ, Gross ES, MacWilliams ML (2009) Is the response of estuarine nekton to freshwater flow in the San Francisco estuary explained by variation in habitat volume? Estua Coas 32:375-389

Lo NCH, Jacobson LD, Squire JL (1992) Indices of relative abundance from fish spotter data based on delta-lognormal models. Can J Fish Aquat Sci 49:2515-2526

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation and recovery potential of estuaries and coastal seas. Science 312:1806-1809

MacNally R, Thomson JR, Kimmerer WJ, Feyer F, and others (2010) Analysis of pelagic species

decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol Appl 20:1417-1430

Maunder MN, Punt AE (2003) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141-159

McCullagh P, Nelder JA (1989) Generalized Linear Models. CRC Press, Boca Raton, FL

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Front Ecol Environ 6:485:492

Moyle PB, Herbold B, Stevens DE, Miller LW (1992) Life history and status of delta smelt in the Sacramento-San Joaquin Estuary, California. Trans Am Fish Soc 121:67-77

Munch SB, Snover ML, Watters GM, Mangel M (2005) A unified treatment of top-down and bottom-up control of reproduction in populations. Ecol Lett 8:691-695

Newman K (2008) Sample design-based methodology for estimating delta smelt abundance. San Fran Estuar Water Sci 6(3)

Nichols FH, Cloern JE, Luoma SM, Peterson DH (1986) The modification of an estuary. Science 231:567-573

Nobriga ML, Freyer F (2007) Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Fran Estuar Water Sci 5(2)

Nobriga ML, Freyer F (2008) Diet composition in San Francisco Estuary striped bass: does trophic adaptability have its limits. Environ Biol Fish 83:495-503

Norcross BL, Austin HM (1981) Climate scale environmental factors affecting year class fluctuations of Chesapeake Bay croaker, *Micropogonias undulatus*. Special Scientific Report No. 110, Virginia Institute of Marine Science, Gloucester Point, VA

Orsi JJ, Mecum WL (1996) Food limitation as the probable cause of a long-term decline in the abundance of Neomysis mercedis the opossum shrimp in the Sacramento-San Joaquin Estuary. In: Hollibaugh JT (ed) San Francisco Bay: The Ecosystem. Pacific Division American Association for the Advancement of Science, San Francisco, CA

Peel D, Bravington MV, Kelly N, Wood SN, Knuckey I (2013) A model-based approach to designing a fishery-independent survey. J Agricul Biol Environ Stat 18:1-21

Rosenfield JA, Baxter RD (2007) Population dynamics and distribution patterns of longfin smelt in the San Francisco Estuary. Trans Am Fish Soc 136:1577-1592

Searle S, Speed F, Milliken G (1980) Population marginal means in the linear model: An alternative to least squares means. Am Stat 34:216-221

Sommer T, Armor C, Baxter R, Breuer R and others (2007) The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries 32:270-277

Stevens DE (1977) Striped bass (Morone saxatilis) year class strength in relation to river flow in the Sacramento-San Joaquin Estuary, California. Trans Am Fish Soc 106:34-42

Stevens DE, Miller LW (1983) Effects of river flow on abundance of young Chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin River system. N Am J Fish Manage 3:425-437

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW (1985) The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Trans Am Fish Soc 114:12-30

Turner JL, Chadwick HK (1972) Distribution and abundance of young-of-the-year striped bass, Morone saxatilis, in relation to river flow in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 101:442-452

Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100-2106

Worm B, Hilborn R, Baum JK, Branch TA and others (2009) Rebuilding global fisheries. Science 325:578-585

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY

Zuur AF, Saveliev AA, Ieno EN (2012) Zero Inflated Models and Generalized Linear Mixed Models with R. Highland Statistics Ltd, Newburgh, United Kingdom.