Analysis of trawl efficiency at Chipps Island using coded-wire-tagged releases of juvenile Chinook salmon

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Executive summary

Midwater trawling in the estuary near Chipps Island has been conducted during the spring since 1978 to monitor Chinook salmon juveniles leaving freshwater en route to the ocean. Typically, some of these fish have been tagged with coded-wire tags (CWTs) prior to being caught. CWTs provide critical information about ocean distribution patterns, fishery impacts, and survival rates, amongst other things. In the context of this study, CWT data provide the basis for estimating the efficiency of Chipps Island trawl, which can then be used to expand juvenile salmon catches at Chipps Island to estimate total abundance. Estimating the efficiency of the Chipps Island trawl, however, has been difficult in the past due to extremely low catch rates.

In this report, we used three different datasets and analytical techniques to estimate Chipps Island trawl efficiency using CWT releases of juvenile Chinook salmon. First, a paired-release dataset spanning 27 years with 36 control groups (downstream releases) and 204 upstream releases was analyzed using Bayesian hierarchical models. The paired-release design provides estimates of upstream survival rates, which form the basis for estimating trawl efficiency. This analysis provided the most thorough examination of temporal patterns in trawl efficiency, as well as potential relationships between efficiency and factors such as juvenile fork length, water temperature, turbidity, and flow. Second, we used releases in close proximity to Chipps Island to estimate trawl efficiency. These data consisted of 34 releases at Jersey Point (approximately 19 km upstream of Chipps Island) and 26 releases at Sherman Island (approximately 13 km upstream of Chipps Island). In this analysis, measures of migration rate (e.g., median day of trawl capture after release) were used as surrogates for survival in regression models to estimate efficiency. Finally, we analyzed three releases at Pittsburg (approximately 4 km upstream of Chipps Island) and one at Sherman Island that were coupled with an intensive 24-hour sampling period following release. The intensive sampling periods increased initial capture rates of juveniles at Chipps Island, but required a detailed approach to account for changes in trawl effort across the full capture period.

The paired-release analysis indicated that there were large differences in trawl efficiency across years. However, we speculate that this apparent temporal variability in efficiency is largely spurious and results from the confounding effects of variable survival rates among control groups. There were two lines of evidence supporting this contention. First, estimates of upstream survival rates were highly variable and often exceeded 1.0 (i.e., biologically impossible and indicative of bias). Second, efficiency estimates were poorly correlated with factors that would be expected to affect trawl efficiency (e.g., turbidity, flow, etc.). We found consistently weak or uncertain relationships between efficiency and covariates across numerous sensitivity analyses that examined inclusive and restrictive paired-release datasets. In short, we could not account for the apparent high variability in efficiency estimates across years. Instead, we conclude that variation in efficiency may be largely due to unaccounted for differences in ocean recovery rates (e.g., survival rates) between control groups and upstream migrants passing Chipps Island, which violates a key assumption of the paired-release design. For these reasons, we recommend that trawl efficiency should be assumed constant across time and across run types until there is compelling evidence to the contrary.

In light of this, we examined several approaches to estimate a constant or "mean" efficiency (where efficiency is defined as the proportion of all fish migrating past Chipps Island trawl that would be captured if the trawl operated continuously at a volume-sampled rate of 1000 m^3/minute). Each dataset and analytical technique had its own strengths and weaknesses, and hence, a single best estimate of trawl efficiency cannot be recommended. We highlight three estimates of mean efficiency, ranging from low to high as follows: the paired-release estimate was 0.0064 (95% CI: 0.0053 – 0.0077); the Jersey Point estimate was 0.0088 (0.0058 – 0.0130); and the Pittsburg estimate was 0.0124 (0.0087 – 0.0151). By comparison, the "fish flux" method of Kimmerer (2008), which expands trawl catch based solely on trawl volumes and physical measures (e.g., channel width and assumed swimming speed of juveniles), has an implied efficiency of roughly 0.04. This efficiency greatly exceeds the "mean" estimates derived using CWT releases, which suggests that catch expansions based on the fish-flux method may severely underestimate true abundance. We recommend that any "expansion" method be avoided in favor of empirical estimates of trawl efficiency.

We provide numerous recommendations for future efficiency testing and additional analyses of existing data. Principal among these is an assessment of the feasibility/utility of a "hybrid" proximal-release design that allows for simultaneous estimation of (a) survival rate via acoustic tags, and (b) trawl-catch rates via CWTs. For example, at a location such as Jersey Point, a small number of acoustic-tagged juveniles (e.g., 200 fish) would be interspersed with a much larger CWT release. Such a design is the most promising approach we can conceive of for obtaining cost-effective, period-specific efficiency estimates that are not confounded by variation in survival rates.

Introduction

Two of the most important metrics for monitoring anadromous salmonid populations are the abundances of spawners and the number of juveniles they produce. In the Central Valley of California, the number of juvenile Chinook salmon leaving freshwater during the spring has been sampled annually since 1978 by means of midwater trawling in the estuary near Chipps Island (Brandes and McLain 2001). Chipps Island is located downstream from the junction of the Sacramento and San Joaquin rivers, and thus is located where all juvenile Chinook salmon produced in the two basins must pass enroute to the ocean. The area sampled near Chipps Island is relatively constricted (3/4 of a mile across the channel), which provides the most concentrated opportunity for sampling juveniles as they leave the Central Valley.

Since 1994, trawling has also occurred at Chipps Island in other months of the year to estimate juvenile abundance by run. The four runs in the Central Valley and more specifically the Sacramento River basin are fall, late-fall, spring, and winter run. The San Joaquin tributaries support only a fall-run population. The run is named for the season in which adults return to freshwater. The winter run is listed as endangered and the spring run is listed as threatened under the federal Endangered Species Act (ESA), and thus the distinction of these runs and estimation of their abundance is critical to gauging the success of management actions aimed at recovering these stocks. Abundance at Chipps Island has historically been estimated using two methods to expand catches: (1) using the proportion of time and channel width sampled to expand catches; and (2) using an estimate of trawl efficiency to expand catches. Trawl efficiency is based on the proportion of marked fish surviving to the trawl and recovered in the trawl from releases made upstream, corrected for sampling effort. Differences in abundance estimates between methods of catch expansion have raised uncertainty as to which method is most reliable.

In addition to uncertainty regarding catch expansion, genetic analyses indicate that length-at-date methods used to apportion total juvenile abundance into the various runs of Chinook salmon have been inaccurate. Those methods used length and date of capture to assign fish to a given race (Fisher 1992; and S. Greene, personal communication). Because the fall run composes over 90% of adult Chinook salmon returning to the Central Valley (www.fws.gov/stockton/afrp), small errors in classification of individuals from this run can cause large errors in the numbers assigned to other runs.

In recent years, genetic markers have been developed that make it possible to distinguish race of Chinook salmon with greater than 95% accuracy (Banks and Jacobson 2004). Fin tissue for DNA analysis was collected for 6 years from a subset of juveniles sampled at the Delta fish facilities, and results showed that true winter run (determined by DNA) composed between 4 to 84% (with an average of 49%) of the juvenile salmon that were designated as winter run based on length-at-date criteria (Hedgecock 2002). Although most genetic winter run were within their designated length-at-date range (95.5%), roughly half the Chinook salmon in that length range were actually of a different run (Hedgecock 2002). These results indicate that use of length-at-date criteria can result in large overestimates of juvenile winter run abundance. The length-at-date method may be even less accurate for spring run because their length and time of migration overlap considerably with the fall run.

To reduce these sources of uncertainty, the study reported here was designed with two objectives: (1) to determine the most reliable methods for expanding trawl catches to total abundance; and (2) to sample the genetic composition of juvenile Chinook salmon catches at Chipps Island and estimate the abundance that each genetically distinct group composed. The analyses and results for these two objectives were divided into two reports. In this report, we focus on trawl efficiency. In a separate report, Pyper et al. (2013) use several of the efficiency estimates reported here and results of genetic sampling of juvenile salmon catches from October, 2007 to June, 2011 to estimate run compositions and abundances.

Determining the efficiency of midwater trawling at Chipps Island is especially difficult because catch rates are very low. As noted above, two distinct approaches have been applied in past studies. First, simple expansion approaches have been used (e.g., Kjelson and Brandes 1989; Kimmerer 2008) based on trawl-net dimensions and measures of trawl effort (time or volume sampled). These "expansion" methods of estimating abundance assume a fixed (constant) trawl efficiency across time, and depend critically on assumptions that fish do not exhibit avoidance behaviors and are randomly distributed with respect to trawl location. The second approach has used paired releases of coded-wire-tagged fish (CWT releases) to provide empirical estimates of trawl efficiency (e.g., USFWS 2006). In theory, paired-release estimates have several distinct advantages: (1) they implicitly account for potential avoidance behaviors or distributional anomalies (e.g., depth of migrating juveniles) that affect trawl efficiency; (2) they provide period-specific estimates of trawl efficiency, which may vary seasonally or annually (USFWS 2006); and (3) they allow estimation of statistical uncertainty in efficiency estimates. However, past paired-release tests have been conducted primarily for fall run, and there has not been a comprehensive examination of historic data to determine if improved estimates could be developed by modeling relationships between trawl efficiency and key factors that might affect efficiency (e.g., fish length, water flow, temperature, turbidity, etc.). In particular, we were interested in developing improved models of trawl efficiency for spring and winter runs, which compared to fall run, exhibit seasonal differences in their migration timing and body size.

Thus, in this report, our primary objective was to examine relationships between trawl efficiency and potential covariates using historic paired-release data, and to determine how to best apply estimates to winter and spring run. To do so, we used Bayesian multilevel (hierarchical) models of paired-release data across years 1979-2005. However, because these analyses highlighted potential limitations of the paired-release data, we expanded our analysis to include "proximal" CWT releases (i.e., upstream releases that were made reasonably close to Chipps Island trawl) for estimating trawl efficiency. Estimates based on CWT data were also compared to the "fish flux" expansion method used by Kimmerer (2008).

Methods

In the remainder of this report, we define trawl efficiency as the proportion of available fish (i.e., potentially vulnerable fish that are occupying the channel trawl zone when sampling occurs) that are captured when the trawl is operating, which is consistent with previous analyses (e.g., USFWS 2006). Given assumptions of randomness, this is equivalent to defining efficiency as the proportion of all fish surviving to and migrating past Chipps Island trawl that would be captured if the trawl operated continuously.

Data

Midwater trawling has been conducted at Chipps Island between April and June since 1978. This sampling was initiated to gain abundance and survival information on juvenile salmon emigrating from the Delta towards the Pacific Ocean (Brandes and McLain 2001) (map provided in Appendix B). Generally, ten 20-minute tows were conducted three to seven days each week from April to June (Brandes and McLain 2001). Sampling was conducted seven days per week during recovery of experimental CWT releases of salmon (usually December-January and April-May) to increase the numbers recovered from these experimental fish released upstream and in the Delta. In October of 1993, sampling was expanded to continue through June of 1994, and since October of 1994, year-round sampling has been conducted to better understand the temporal patterns of juvenile salmon emigration downstream.

Trawls were conducted within a 3 km section of river upstream of the western tip of Chipps Island (Brandes and McLain 2001). Trawls were conducted in both directions (upstream and downstream) regardless of tide in three channel locations: north, south, and middle. Occasionally, inclement weather, mechanical problems, or excessive delta smelt or salmon catch reduced tow duration or number of tows per day.

Four key datasets spanning years 1978-2011 were compiled for this analysis: (1) CWT-release data by tag code (race, location, date, hatchery source, number released, etc.); (2) effort data for Chipps Island trawl by tow (minutes, volume, temperature, turbidity, etc.); (3) CWT-recovery data for Chipps Island trawl (tag code, tow, fish length, etc.); and (4) CWT-recovery data for ocean fisheries (tag code, fishery, expanded recoveries, etc.). Datasets for CWT releases, trawl effort, and trawl recoveries were obtained online from the US Fish and Wildlife Service (USFWS) data repository (www.fws.gov/stockton/jfmp/datamanagement.asp). Ocean recovery data were obtained for all CWT tag codes in the USFWS database from the Regional Mark Information System (RMIS), an online database query (www.rmis.org) for CWT data maintained by the Pacific States Marine Fisheries Commission. We also obtained two records of daily flow data (Rio Vista and estimated Delta Outflow) from the California Department of Water Resources Dayflow program (www.water.ca.gov/dayflow). These datasets were merged in various ways depending on the type of analysis or reporting conducted.

A key step in our data processing was to define unique "release groups" that combined, where applicable, two or more tag codes. Specifically, CWT releases with different tag codes but identical entries for release location, date, hatchery source and race were combined and given a unique release-group number (all further uses of "release group" refer to this definition). Data for CWT releases by tag code (i.e., USFWS data) included an entry for fork length at release. For our combined release groups, we computed a weighted mean for length at release, where weights were equal to the number of fish released by tag code. Before defining our final set of release groups, several tag-code groups were removed based on consultation with USFWS staff; these primarily consisted of releases that occurred over extended periods (> 5 days) or with unusual occurrences (e.g., high mortality during transportation). In addition, some tag-code groups had missing entries for race or fork length, which were resolved (when possible) by cross-checking the tag code with the RMIS database or by personal communication with USFWS staff.

For CWT-recovery data in the Chipps Island trawl, there were approximately ten fish for which we computed negative travel times (i.e., catch dates were earlier than the release dates for those fish). This was likely due to data entry errors or cases in which a group was released over multiple days. These records were removed from the database. Recovered fish with fork-length entries of zero were assigned missing values for fork length.

Ocean recoveries of CWT adult fish were restricted to observations in ocean and estuary fisheries (i.e., river fisheries were excluded). The RMIS dataset contained a unique record for each recovered fish that included the expanded number of recoveries based on the fraction of catch sampled for CWTs in that time/fishery stratum. This allowed us to compute total numbers of observed (*x*) and expanded ocean recoveries (*r*), and the overall sampling fraction ($f = x/r$), for each release group. The use of these quantities (*x*, *r*, *f*) is discussed below.

A final, important detail concerns the values of volume trawled per tow reported in the current trawl-effort dataset. These volume estimates (for all years) are based on an assumed effective-fishing mouth size of 18.5 m^2 for the trawl net fished at Chipps Island (Brandes and McLain 2001). However, measurements conducted in 2009 provided lower estimates of net-mouth areas, with mean effective-fishing mouth sizes of 12.7 m^2 for the Whitesel, which operated from 1986 to March 10, 2009, and 13.0 m^2 for the Confluence (March 11, 2009 to present) (P. Brandes, USFWS, pers. comm.). To be consistent with the existing USFWS database, we did <u>not</u> adjust trawl volumes to reflect these recent estimates of net-mouth area. As discussed below, a change in net-mouth area has very little consequence for our analysis of trawl efficiency (and abundance estimation), except in the case of the fish-flux method.

Paired-release studies

The paired-release design consists of one CWT group released downstream of Chipps Island that is paired with one or more upstream releases. The downstream release, referred to here as the "control" group, provides the basis for estimating the survival rate of the upstream group from point of release to passage at Chipps Island. In turn, this allows estimation of the abundance of juveniles passing Chipps Island and trawl efficiency. In the following sections, we describe the statistical modeling framework used to examine paired-release estimates of trawl efficiency.

<u>Single-study estimates</u>

The following is a brief synopsis of estimators for trawl efficiency based on a single paired-release test in which one control (downstream release) is paired with one upstream release. For our purposes, it was sufficient to develop approximate estimators for efficiency and variance, which were used primarily in exploratory analyses. Details of the derivation of estimators and their variances are provided in Appendix A.

Define as follows:

R = number of CWT fish released (subscript 1 = upstream, 2 = control)
r = number of actual ocean recoveries of R
x = number of observed ocean recoveries of R

q = probability of a fish (either an upstream release that passes Chipps Island or a control release) being captured in ocean fisheries (function of marine survival, ocean distribution, harvest rates)
f = overall fraction of catch sampled for CWTs in ocean fisheries
s = survival rate of upstream fish from point of release to Chipps Island
n = number of upstream fish captured by the Chipps Island trawl
E = trawl efficiency (proportion of available fish captured when the trawl is operating)
p = proportion of time (or standardized volume) trawled

As detailed in Appendix A, a key assumption underlying the estimation of survival (*s*) and trawl efficiency (*E*) is that control fish have the same probability of capture in ocean fisheries as upstream fish that migrate past Chipps Island trawl. This assumption (i.e., $q_1 = q_2$) leads to the following maximum-likelihood (ML) estimates for survival rate and trawl efficiency:

(1) $$\hat{s} = \frac{x_1 f_2 R_2}{x_2 f_1 R_1},$$

(2) $$\hat{E} = \frac{n x_2 f_1}{x_1 f_2 R_2 p}.$$

In Equations (1) and (2), the observed variables are the upstream captures at Chipps Island (*n*) and observed ocean recoveries (x_1, x_2). As discussed in Appendix A, we defined these equations in terms of observed ocean recoveries (*x*) rather than expanded recoveries ($\hat{r} = x/f$) to make explicit that uncertainty accrues from the actual observations (*x*).

The efficiency estimate (Equation 2) is standardized to account for the proportion (*p*) of time or volume sampled during the period in which upstream releases migrate past the Chipps Island trawl. This allows for direct comparisons across efficiency estimates computed at different periods and sampling intensities. Traditionally, *p* has been computed as the fraction of time trawled across the full capture period:

(3a) $$p = \frac{\sum_{d=1}^{D} M_d}{D * 1440}$$

where *d* denotes day, *D* is the number of days in the capture period (from first to last day of capture at Chipps Island), and *M* is the daily minutes trawled (total minutes in a day = 1440). In this case, trawl efficiency (*E*) represents the fraction of migrating fish that are captured when the trawl is operating. This assumes that trawl operation (e.g., trawl gear, speed, channel coverage, etc.) is consistent across all paired-release tests examined. However, there is clear evidence of a declining trend over years in volume per minute sampled (Figure 1). (Note that increased seasonal sampling since October of 1993 cannot readily account for the differences observed in Figure 1 because there is little to no overlap in the boxplots between early and later years.)

Assuming that volume is a better measure of sampling effort than time, we computed *p* as a standardized proportion of volume sampled:

(3b) $$p = \frac{\sum_{d=1}^{D} V_d}{D*1440*v} \ .$$

where *V* is daily volume sampled, and *v* is an arbitrary scalar defining a "standard" rate of volume sampled. For simplicity, we set *v* equal to 1000 m^3/minute (slightly less than the average rate observed in recent years; Figure 1), such that the "standardized" total daily volume sampled (for continuous 24-hour trawl operation) was 1440 minutes/day x 1000 m^3/minute = 1,440,000 m^3/day. In this case, trawl efficiency (*E*) is defined as the fraction of migrating fish that are captured when the trawl is sampling at a rate (*v*) of 1000 m^3/minute. Unless noted otherwise, we used volume-based *p* (Equation 3b) to standardize efficiencies in all analyses below.

The ML estimates (1)-(2) may be biased, in particular when the expected number of ocean recoveries is low (Appendix A). Approximately unbiased estimators, referred to here as "bias-corrected" estimates, are given by

(4) $$\hat{s}' = \frac{x_1(x_2-1) f_2 R_2}{x_2^2 f_1 R_1} \ ,$$

(5) $$\hat{E}' = \frac{n x_2 (x_1-1) f_1}{x_1^2 f_2 R_2 p} \ .$$

As reported below, differences between ML and bias-corrected estimates were typically trivial for the paired-release tests examined. Because the ML estimates are consistent with the multilevel modeling approach used here, we report ML point estimates of *s* and *E* (where applicable) unless noted otherwise.

<u>Multilevel models of trawl efficiency</u>
We examined factors affecting trawl efficiency by modeling relationships across all paired-release tests of adequate quality. There were two general sources of replication. First, the key source of temporal replication was the number of unique control groups across years. The second source of replication, where appropriate, was provided by pairing multiple upstream releases with a given control (a similar approach has been used by USFWS to compute "mean" annual efficiency estimates; e.g., USFWS 2006). Pairing each control with multiple upstream releases will (in theory) improve the reliability of efficiency estimates and inferences. However, efficiency estimates based on same control group are not statistically independent (i.e., all estimates depend on the same observation of control-group ocean recoveries, x_2). The upstream releases are essentially "subsamples" used to better estimate trawl efficiency during a narrow period when a control release is made. In contrast, true replication occurs at the level of the control group, both with respect to estimates of efficiency (statistical independence) and defining unique environmental conditions or factors that may influence efficiency.

From a multilevel (hierarchical) modeling perspective (Gelman and Hill 2007), we view controls as a "grouping variable" for upstream releases (i.e., upstream releases are nested by control group), and we are interested in modeling efficiency at the control-group level using "group-level" covariates. This modeling approach for paired-release tests is well suited to Bayesian methods (Gelman and Hill 2007). At the upstream-release level, each estimate of efficiency incorporates three observed variables (n, x_1, x_2) that can be modeled using separate distributions. These processes determine the observation error (i.e., sampling or measurement error) associated with a given efficiency estimate. Variation among efficiency estimates at the control-group level (analogous to the mean across upstream releases) will be due to observation error as well as process error (e.g., variation in efficiency due to environmental conditions such as flow). Our goal was to model efficiencies at this level to examine potential relationships between efficiency and several covariates.

We can express the multilevel model for paired-release data as follows, where upstream release i is nested in control group j:

(6)

$$
\begin{aligned}
x_i &\sim \text{Poisson}(R_i s_i q_{j[i]} f_i) \\
x_j &\sim \text{Poisson}(R_j q_j f_j) \\
n_i &\sim \text{Poisson}(R_i s_i E_{j[i]} p_i) \\
\log(E_j) &\sim \text{N}(\beta_0 + \beta_1 X_j, \sigma_E^2)
\end{aligned}
$$

In a Bayesian context, these distributions represent the likelihood functions for each variable. The model contains three observed variables (n_i, x_i, x_j) that are assumed to follow Poisson distributions (see Appendix A); known quantities for upstream releases (R_i, f_i, p_i) and control groups (R_j, f_j); and parameters for upstream survival rates (s_i), control-group ocean recovery rates (q_j), and control-group efficiencies (E_j). These efficiencies, which are assumed to follow a log-normal distribution, are modeled as a linear function of a covariate X, with intercept β_0, slope β_1, and standard deviation σ_E. These latter parameters (β_0, β_1, σ_E) are commonly referred to as group-level parameters or hyperparameters.

For controls that are paired with multiple upstream releases, the model (Equation 6) assumes that variation in upstream captures at Chipps Island (n_i) will be adequately described via Poisson distributions with a common efficiency (E_j). However, this is an unrealistic assumption, and there was clear evidence of "overdispersion" in the data (i.e., variances in observations of n_i exceeded those assumed under the Poisson distribution). There are numerous potential explanations for such overdispersion, including factors that might lead to differences among upstream releases in their efficiencies (e.g., subtle differences in migration timing relative to trawl sampling, conditions experienced, fish behavior, etc.) or ocean capture rates (e.g., differences in ocean survival and/or harvest rates). To account for overdispersion, the model was modified as follows (e.g., Gelman and Hill 2007, p. 325):

(7) $$n_i \sim \text{Poisson}(R_i s_i E_{j[i]} p_i \delta_i)$$

where δ_i denotes a random deviate at the upstream-release level, with a distribution given by

(8) $$\log(\delta_i) \sim N(0, \sigma_\delta^2) .$$

The standard deviation σ_δ (an additional hyperparameter) determines the degree of overdispersion, where $\sigma_\delta = 0$ corresponds to the Poisson model (i.e., no overdispersion).

The Bayesian hierarchical models were fit using WinBUGS; see Gelman and Hill (2007) for details. Diffuse (non-informative) priors were specified for all parameters to ensure that posterior probability distributions reflected the data-based likelihoods. For a given model, each of three randomly-seeded chains were simulated for 5000 iterations, which provided adequate convergence. The final 2500 iterations were thinned across chains to provide a sample (N ≈ 1000) of the joint posterior distribution of all parameters.

Selection of paired-release data

Careful selection of control-upstream pairs is warranted. The selection process is an attempt to best satisfy the critical assumption that control fish and upstream fish (i.e., those passing Chipps Island) have similar marine survival rates and distributions in ocean fisheries, such that capture probabilities may be assumed equal ($q_1 = q_2$ or $q_i = q_{j[i]}$). Thus, in terms of factors that likely influence ocean survival/recovery rates, we want to ensure that control groups are reasonably "representative" of upstream releases at the point of Chipps Island passage.

To begin, candidate control groups were defined as any release made at either Benicia (~ 22 km downstream of the Chipps Island trawl) or Port Chicago (~ 12 km downstream) (Appendix B). Candidate control-upstream pairs had to be of the same race (fall, late-fall, spring, or winter). In addition, we required that all candidate releases (control or upstream) have a minimum fork length (the reported sample average at release) of 70 mm and at least five observed ocean recoveries (x). Values of x less than five produce efficiency estimates with very high observation error; that is, they add a lot of "noise" with minimal information on actual efficiency. The above criteria remained fixed in all analyses.

We then established three "flexible" criteria for selecting candidate control-upstream pairs, where each criterion had two options (Table 1). These three criteria – fish source, migration timing, and fish size – are likely to be important determinants of marine survival rates and ocean distributions. Rather than limit our pairing selections to one or a few arbitrary sets of criteria, we examined the implications of all eight possible sets. The least restrictive set allowed for upstream releases to have a different fish source (i.e., "any") from the control group, a median capture date for upstream recoveries at Chipps Island within two weeks (± 14 days) of the control release date, and a median fork length for upstream recoveries within 10 mm (± 10 mm) of the control fork length (the reported sample average at release). In contrast, the most restrictive set required that upstream releases had the same hatchery source as the control release, had a median capture date within one week (± 7 days) of the control release, and had a median fork length within 5 mm of the control fork length. Summaries of the control and upstream releases defined by the eight alternative pairing sets are provided in the Results section.

Table 1. Options examined for three pairing criteria.

Pairing criterion	Option 1	Option 2
Fish source (hatchery)	Any (no restriction)	Same
Median day of upstream recoveries at Chipps Island versus control-group release day	± 14 days	± 7 days
Median fork length of upstream recoveries at Chipps Island versus control-group fork length	± 10 mm	± 5 mm

<u>Treatment of survival-rate estimates that exceed 1.0</u>

The paired-release design can result in survival-rate estimates ($\hat{s}$) greater than 1.0. Although such estimates are clearly invalid from a biological perspective, they can be valid from a statistical perspective. For example, the expected sampling distribution of $\hat{s}$ will contain a region of $\hat{s} > 1$ when the true survival rate is high (close to one) but precision is low because ocean recoveries are low. Furthermore, across multiple tests (control groups), we would expect random cases in which ocean recovery rates of control fish (q_2) were lower than for upstream releases (q_1), resulting in a higher frequency of $\hat{s} > 1$. Thus, we anticipate values of $\hat{s} > 1$ that are statistical valid even when assumptions are met (i.e., $q_1 = q_2$ for a single test, or $\bar{q}_1 = \bar{q}_2$ for multiple tests). Removing data in such cases (high $\hat{s}$ and low $\hat{E}$) would tend to bias mean efficiency estimates upward.

On the other hand, we are primarily interested in explaining "true" variation in efficiencies, and values of $\hat{s} > 1$ will introduce variation in $\hat{E}$ that is biologically invalid (known statistical "noise"). Moreover, it is reasonable to expect cases in which the assumption of equal (or close to equal) ocean recovery rates for control and upstream releases will be strongly violated. In such cases, values of $\hat{s} > 1$ may provide a compelling reason to exclude paired-release data associated with a given control group.

Our treatment of paired tests with $\hat{s} > 1$ was as follows. First, we removed control groups for which all paired upstream releases had $\hat{s} > 1$ (i.e., ML survival-rate estimates > 1.0; Equation 1). These data provided no insight into the possible validity of estimates. Many of the remaining control groups were paired with one or more upstream releases with $\hat{s} \leq 1$ but others with $\hat{s} > 1$. We then fit models using two datasets with (1) all upstream releases retained (referred to herein as the "all-upstream" dataset), and (2) only those upstream releases with $\hat{s} \leq 1$ (the "s < 1" dataset). Details of these datasets are provided below in the Results section.

In addition, we constrained all survival-rate estimates to a maximum of 1.0 when fitting multilevel models in WinBUGS (unless noted otherwise). Our rational was to reduce statistical “noise” (sampling error) given the primary objective of examining associations between “real” variation in efficiencies and environmental covariates.

Covariates examined

We examined relationships between trawl efficiency and five factors: fish race, fork length, turbidity, water temperature, and flow. As discussed below, most paired-release tests were for fall Chinook, with several late-fall tests and one spring-run test. Exploratory analysis revealed no substantive differences between the fall and spring tests, either in terms of efficiency or conditions experienced. Thus, examinations of potential differences in efficiency due to race were limited to comparisons between pooled fall/spring tests and late-fall tests.

The remaining covariates were computed in two stages. First, covariate measures were computed for each upstream release. The fork-length measure (units mm) was simply the median across observed captures (recoveries at Chipps Island trawl) for a given upstream release. As a measure of turbidity, we used secchi disc readings (depth in units m), which were recorded for most tows. Note that secchi measurements are inversely related to turbidity. We also used water temperature measurements (degrees C) by tow, and two daily measures of flow (cfs): Rio Vista flow and estimated Delta Outflow.

We explored several options for computing upstream-release measures of secchi, temperature, and flow. These included (1) the median measure across observed recoveries; (2) the mean across recoveries; (3) the mean across all tows (or days in the case of flow) during the observed recovery period (i.e., first to last day of capture at Chipps Island); and (4) a weighted mean based on estimated daily catch-per-unit-effort (CPUE = daily captures / daily volume fished) across the recovery period. Note that measure (2) is a weighted mean in that tow- or day-specific measures are weighted by the number of observed recoveries (a crude approximation of the underlying distribution of migrating fish). In contrast, measure (3) computes means across all available records within the recovery period, regardless of when fish are recovered (assumes a more uniform distribution for migration). The CPUE measure has the potential advantage of weighting recovery-specific records by effort (volume fished), and hence, better approximating the underlying distribution of migrating fish. However, this approach was compromised by missing sampling days for some upstream release (see Discussion). In general, these four approaches provided similar (i.e., highly correlated) measures across upstream releases. Consequently, we selected measure (2) – the mean across records for each recovery – as the upstream covariate for secchi, temperature, and flow.

In the second stage, we computed covariate measures by control group (for controls paired with two or more upstream releases) as the mean across upstream-release measures. Because most controls were paired with multiple upstream releases, the potential influence of the computational form for upstream measures was further minimized by averaging across them.

To facilitate model comparisons, we standardized each continuous covariate (excluding race) to have a mean of zero and standard deviation of one. This standardization improves model convergence and allows for direct comparisons of model coefficients (β_0 and β_1; Equation 6), which are on the same scale regardless of the specific covariate units (Gelman and Hill 2007).

Baseline and sensitivity analyses

Multilevel models were fit a given dataset beginning with a "mean-only" model (i.e., omitting the covariate X in Equation 6), followed by all single-covariate models. The baseline analysis used the most inclusive (base) pairing set. Sensitivity analyses were then conducted by refitting all models to each of the seven more restrictive pairing sets. For each pairing set, models were fit to the "all-upstream" dataset as well as the "s < 1" dataset, which removed upstream releases with survival estimates greater than one. In total, 112 models were examined.

Additional models were then fit to examine the sensitivity of results to exclusion of late-fall releases. Late-fall releases had high fork lengths and were associated with low temperatures, so it was unclear to what extent these data might obscure relationships between these factors and efficiency for fall/spring releases. Thus, we removed late-fall releases from all pairing sets and refit the mean-only and single-covariate models. These analyses were limited to all-upstream datasets.

Finally, we tested the sensitivity of results to the choice of p (proportion of time or volume sampled) used to standardize efficiency tests across periods. The default was volume-based p (Equation 3b). To examine the influence of using time-based p (Equation 3a), we refit models using the base pairing, all-upstream dataset. We also examined an additional covariate (log[volume/minute]) to test for evidence of a linear relationship between efficiency and volume/minute sampled. We anticipate that efficiency would be roughly proportional to volume sampled, but the use of time-based p ignores the obvious trend in volume/minute sampled across years of paired-release tests (Figure 1). The volume/minute covariate was computed for each upstream release as $\sum V_d / \sum M_d$ (i.e., sums across the full capture period), and then averaged across replicate upstream releases for each controls group.

Proximal releases

As discussed below, the paired-release analysis provided evidence of potential bias in estimates of survival rate and efficiency. We therefore examined alternative approaches for estimating efficiency using "proximal" upstream releases that were made relatively close to Chipps Island. These included numerous releases made at Jersey Point and Sherman Island, as well as four "special" releases (three at Pittsburg and one at Sherman Island) that were associated with an initial 24-hour period of intensive trawl sampling.

Jersey Point and Sherman Island releases

The primary focus of this analysis was to estimate mean efficiency across releases. Releases at Jersey Point (roughly 19 km upstream of Chipps Island) and Sherman Island (13 km upstream) were selected because of their close proximity to Chipps Island and because numerous releases (> 20) were made at each location across years. A key assumption of our approach is that fish survival from point of release to passage at Chipps Island will be close to 100% for nearby releases that migrate rapidly downstream. Thus, the approach did not require use of control groups to estimate survival.

Presumably, release groups with relatively slow migration rates will tend to experience higher mortality prior to passage at Chipps Island (thus reducing abundance and apparent efficiency). To account for this possibility, we modeled efficiency as a function of two alternative measures of migration rate: (1) the number of days from release to first capture at Chipps Island (first-day models); and (2) the number of days from release to median day of capture at Chipps Island (median-day models). In other words, we treated these variables as potential surrogates of survival, with an assumed survival rate of 100% at "day 0" (rapid migration), and an implied decline in survival thereafter.

Statistical methods were as follows. For a given release, an estimate of efficiency (assuming 100% survival from release point to the Chipps Island trawl) is given by

(9) $$\hat{E} = \frac{n}{Rp} \ .$$

We used Bayesian multilevel models to estimate efficiency across multiple releases. The Bayesian models, which accounted for over-dispersion in captures *n*, had the general form:

(10) $$\begin{aligned} n_i &\sim \text{Poisson}(R_i E_i p_i \delta_i) \\ \log(E_i) &= \beta_0 + \beta_1 X_i \\ \log(\delta_i) &\sim \text{N}(0, \sigma_\delta^2) \end{aligned}$$

where log(efficiency) was modeled as a linear function of a migration-rate covariate (X = first day or median day of capture at Chipps Island) with parameters β_0 and β_1, and the hyperparameter σ_δ measured the degree of overdispersion. The key parameter of interest was the intercept (β_0), which provides an estimate of (log) mean efficiency at day 0. Details of model simulation were the same as those described above for paired-release models, except that chains were simulated for 20,000 iterations to provide adequate convergence.

Separate analyses were conducted for the Jersey Point and Sherman Island datasets. Three models were fit to each dataset: (1) a mean-only model, which excluded the covariate X in Equation 10; (2) a "first-day model" in which X was the number of days from release to first capture at Chipps Island; and (3) a "median-day model" in which X was the number of days from release to median day of capture.

Special releases

A final set of four proximal releases was examined. These release experiments included an initial 24-hr period of intensive trawling at Chipps Island, followed by regular or intermittent trawl activity in subsequent days. As detailed below, three of the releases (race designation = "hybrid") were made at Pittsburg (roughly 4 km upstream of Chipps Island) in 2009, while one late-fall release was made at Sherman Island in 2003.

We examined each of these releases separately to better account for the highly skewed patterns of daily trawl effort and captures across the recovery period. Tow-specific data were visually examined across the recovery periods. The patchiness of recoveries precluded the use of a simple parametric description (model) of the migration distribution at Chipps Island. We therefore used a simple period-based approach to account for migration, sampling effort, and missing days to compute efficiency for each special release. Our approach had the following assumptions and details:

(1) Survival rate from point of release to passage at Chipps Island was 100%.

(2) The migration timing (arrival) at Chipps Island began with the first (tow-specific) capture during the initial intensive-sampling period.

(3) The migration ended at midnight on the last day of recorded capture.

(4) The initial intensive-sampling period, which extended for roughly 24 hours from about noon of the release day until noon the next day, was divided into two periods. The first period extended from the tow of first capture and ended at the beginning of the final 10 tows of intensive sampling (the next day). The second period extended from the beginning of the final 10 tows through midnight of that day. All remaining periods were defined as daily 24-hr intervals.

(5) For each period, the proportion of the migration sampled was estimated based on the catch-per-unit-effort (CPUE) observed in that period.

(6) For days with no sampling, simple linear interpolation was used to estimate CPUE.

Formally, CPUE (denoted q) was computed for each period (d) as the catch per minute sampled at a standardized volume-sampled rate (v) of 1000 m^3/minute:

(11) $$\hat{q}_d = \frac{n_d}{M_d}\left(\frac{v}{(V_d / M_d)}\right)$$

where n, V, and M represent the total catch, volume sampled, and minutes sampled across tows in period d. (Note, to ignore potential differences in volume sampled and use only time-based effort, the right-hand term in Equation 11 would be omitted.) For days with no sampling, q was estimated by simple linear interpolation. To estimate catch under continuous trawling, we multiply CPUE by the total period minutes (M^*) available for sampling:

(12) $$\hat{c}_d = \hat{q}_d M_d^* .$$

Across the full migration (periods d = 1, 2, …, D), efficiency is estimated as

(13) $$\hat{E} = \frac{\sum_{d=1}^{D} \hat{c}_d}{R} .$$

Note that the estimated proportion of the migration sampled is given by $\sum n_d / \sum \hat{c}_d$. This is directly analogous to the definitions of p provided earlier (Equation 3). The crucial difference is that the latter are based on simple sums of effort (volume or minutes trawled) across the full recovery period regardless of the daily distribution of captures, whereas the approach used here for the special releases uses CPUE (a proxy for the migration distribution of fish) to weight sampling effort for each discrete period examined within the migration.

We used a bootstrap procedure to approximate the precision and confidence intervals for each special-release estimates of efficiency. In brief, the method randomly sampled tow-specific CPUE estimates by period and then re-computed estimates as above (Equations 11-13). Specifically, the procedure for a single bootstrap replicate was as follows:

(1) For each period of the migration ($d = 1, 2, \ldots, D$) that was sampled, we re-sampled (with replacement) the tow-specific estimates of CPUE, assigned the randomly selected values to each tow within the period, and computed a new observed (decimal) catch.

(2) Next, we computed the new period-specific CPUEs (across tows; Equation 11) and used linear interpolation to estimate CPUEs for missing days.

(3) Last, we computed new values of estimated catch (Equation 12) and trawl efficiency (Equation 13).

This procedure was repeated 2000 times to generate a bootstrap distribution $\{b\}$ of efficiency estimates for each release as well as for estimates of mean efficiency (across all four releases or only Pittsburg releases).

Expansion methods

We refer to "expansion methods" as any method that computes total abundance by expanding trawl catches based only on physical measures related to net dimensions and trawl effort. In other words, there is no empirical (e.g., mark-recapture) estimate of trawl efficiency associated with an expansion method. However, any such method has an "implied efficiency" underlying it, and we can directly compare this implied efficiency to estimates based on CWT releases. In general, it is not possible to rigorously estimate variances associated with the implied efficiencies of expansion methods because they are based on assumed constants.

For example, Kjelson and Brandes (1989) expanded marked catches to estimate survival to Chipps Island using an expansion approach. The expansion is based on the proportionate "space" occupied by the net in the channel, which is then further expanded to account for the proportion of time trawled (this approach has been referred to as a "space-time" expansion). In short, the method as detailed by Kjelson and Brandes (1989) has an implied efficiency equal to trawl net-mouth width (9.1 m) divided by mean channel width (1167 m), that is, an efficiency of 0.0078 (i.e., 0.78% of all fish migrating past the Chipps Island trawl would be captured under continuous trawling). Some of the implicit assumptions of this approach, which are not required of CWT-based estimates, include: (1) all fish migrate at depths vulnerable to trawling; (2) fish do not avoid the trawl net nor are they herded into it; (3) fish cannot pass through the net; and (4) trawling locations provide a representative sample of the spatial distribution of migrating fish (e.g., fish are randomly distributed across the channel).

As noted by Kimmerer (2008), however, the "space-time" expansion is only appropriate for a stationary sampler (i.e., the trawl net is not occupying a fixed proportion of the channel, but is actively moving up and down the channel). Instead, Kimmerer (2008) developed a "fish flux" expansion method that assumes that the fraction of fish captured will be directly proportional to the volume sampled. To appropriately expand trawl catch, the method requires a guesstimate of the volume of water that migrating fish occupy. Specifically, the fish-flux method was defined as follows (see Equation 7 of Kimmerer 2008; we have omitted subscript *c*, which denoted Chipps Island trawl):

(14) $$\hat{\Phi}_d = \frac{\sum_{p=1}^{P_d} N_{dp}}{\sum_{p=1}^{P_d} V_{dp}} WZu \ ,$$

where

d = subscript denoting day
p = subscript denoting tow (trawl "sample" in Kimmerer)
Φ = daily flux of fish passing Chipps Island (i.e., total abundance)
N = number of fish caught
V = volume sampled (m^3)
W = channel width (Kimmerer assumes 1000 m)
Z = depth over which fish migrate (Kimmerer assumes 4 m)
u = migration speed (Kimmerer assumes 6000 m/day)

The daily expansion from catch (N) to abundance (Φ) in Equation (14) is determined by the ratio of two volumes, that is, the volume of water occupied by migrating fish (= WZu) divided by the total volume of water sampled (trawled). We can define the implied trawl efficiency of the fish-flux method on a daily basis as follows:

(15) $$E_d = \frac{V_d^*}{WZu} \ ,$$

where V_d^* is the total daily volume sampled under continuous trawling. In Kimmerer's application, the daily volume of water occupied by migrating fish (= WZu) is 24 million m^3. As noted above, our "standardized" total daily volume sampled (i.e., assuming continuous trawling at a rate v of 1000 m^3/minute) is 1,440,000 m^3, which yields our first value for implied efficiency:

(16) $$E_1 = \frac{1{,}440{,}000}{24{,}000{,}000} = 0.060 .$$

Thus, at a volume sampling rate of 1000 m^3/minute, the fish-flux method assumes an efficiency of roughly 0.060 (6.0% of all fish migrating past Chipps Island would be captured in the trawl under continuous trawling).

The implied efficiency defined by Equation (16) is applicable to the trawl volumes currently reported in the USFWS database (and used by Kimmerer 2008). However, to make the most accurate comparisons between CWT-based efficiencies and the fish-flux method, we should account for the recent (improved) data on net-mouth area discussed in the Data section. Current trawl volumes are likely overestimated because they are based on an assumed net-mouth area of 18.5 m^2, whereas recent measures were 12.7 m^2 (Whitesel; used between 1986 and March 10, 2009) or 13.0 m^2 (Confluence; used between March 11, 2009 and present), depending on the vessel. To correct volumes using a net-mouth area of 12.7 m^2, for example, we multiply reported volumes by 0.686 (= 12.7/18.5). We apply this correction to Equation (16) to obtain our second value for implied efficiency for the fish-flux method:

(17) $$E_2 = \frac{1{,}440{,}000 \times 0.686}{24{,}000{,}000} = 0.041.$$

Note that a slightly higher value of 0.042 for implied efficiency is obtained using a net-mouth area of 13.0 m^2 (Confluence) instead of 12.7 m^2 (Whitesel).

To be clear, all we are doing in Equation (17) is acknowledging that when we specify a volume sampled rate of v = 1000 m^3/minute based on current trawl volumes in the USFWS database, the "actual" volume sampled rate should be 686 m^3/minute (i.e., assuming a true net-mouth area of 12.7 m^2 instead of 18.5 m^2). Equation (17) then provides the best estimate of implied efficiency for comparison with the CWT-based efficiencies we report. Note that a change in the volume scalar, which is applicable to all years of data (ignoring the ~ 2% difference in the Whitesel and Confluence estimates), has no influence on our CWT-based estimates because they depend on relative rather than absolute volumes. Only the definition of v or "standardized effort" changes (e.g., efficiency estimates are either defined based on continuous sampling at a rate of 1000 m^3/minute given a net-mouth area of 18.5 m^2, or a rate of 686 m^3/minute given a net-mouth area of 12.7 m^2).

Results

Paired-release studies

<u>Initial pairing set, point estimates, and data removal</u>

A summary of the initial candidate pairings is shown in Table 2. A total of 40 candidate control groups were paired with 215 upstream releases. (Note that throughout, control-group names designate a two-digit year of release and within-year replicate, such that "96-2" denotes the second control release for 1996.) Across years, 22 of the control groups were released at Port Chicago and 18 at Benicia. However, as discussed below, four control groups were subsequently removed because survival estimates exceeded 1.0 or the test data were a clear outlier (see shaded rows in Table 2). Note that in recent years, there were significant harvest restrictions in ocean fisheries off the coast of California, and consequently, numbers of observed ocean recoveries (x) were too limited to define valid candidate pairings.

Point estimates of survival rate and trawl efficiency for upstream release groups (N = 215, initial pairings in Table 2) are shown in Figure 2. A total of 45 (21%) of the ML survival estimates exceeded 1.0. There was little difference between ML and bias-corrected estimates of either survival or efficiency (Figure 2). The median coefficient of variation was 23% for survival estimates and 36% for efficiency estimates (Figure 3).

Upstream survival estimates varied widely, both within and among control groups (Figure 4A). All survival estimates exceeded 1.0 for three control groups (88-2, 90-2, and 90-3). Efficiency estimates also varied widely among controls (Figure 4B). In particular, estimates for the 2008 control group (08-1) were all extremely low.

Exploratory mean-only models were used to estimate group-specific efficiencies for the initial pairing set (Table 2). Estimates are presented in Figure 5, with no constraint placed on survival (top panel) and a constraint of $s \leq 1$ (bottom panel). The three control groups for which all upstream survival estimates exceeded 1.0 had group efficiencies that were reasonably consistent with the other control groups, in particular for the model in which survival was constrained to $s \leq 1$ (Figure 5B). Nevertheless, these data provide no guidance as to what reasonable survival estimates may have been (i.e., all estimates are biologically invalid), and hence, these groups were removed from further analysis.

The efficiency estimate for the 2008 control group (08-1) was a clear outlier with very low efficiency, regardless of the constraint placed on survival (Figure 5). There were no obvious differences among the five 2008 upstream releases and the remaining fall releases for variables such as release date, fork length, secchi (turbidity), temperature, and flow (Figure 6). However, the 2008 releases were associated with anomalously low sampling effort, both in terms of the proportion of volume sampled and number of days not sampled during the Chipps Island recovery period (Figure 6). Thus, it seems unlikely that this outlier reflects important evidence of environmental processes affecting trawl efficiency. Instead, the data suggest that sampling variation related to sparse trawl activity (Figure 6) and poor survival estimation (Figure 4) warrants removal of this data point. Given that four of the five upstream releases had survival estimates greater than 1.0 (Table 2; Figure 4), and the obvious discrepancy in the 2008 efficiency estimate, this group was also removed prior to further analysis.

<u>Final datasets</u>

Tables 3-5 provide summaries of the final control-upstream pairings across the eight alternative pairing sets. Specifically, Table 3 shows pairings in which all upstream releases were included regardless of survival estimate ("all-upstream" datasets), while Table 4 shows pairings after removal of upstream releases with survival estimates greater than 1.0 ("$s < 1$" datasets). For each pairing set, Table 5 shows total numbers of control and upstream releases by race. The number of controls ranged from 36 for the base set to a low of 25 for the most restrictive pairing criteria (set 8; Table 5). For all-upstream datasets, total upstream releases ranged from 204 for the base set to only 55 for set 8. For $s < 1$ datasets, upstream releases ranged from 169 (base) to 46 (set 8). Of the 36 base control groups, 29 were fall releases, six were late-fall releases, and one was a spring-run release (group 03-2).

Sampling conditions varied widely by control group (Figure 7 and Figure 8) and race (Figure 9). Late-fall releases were characterized by high fork lengths (Figures 7C and 9) and low temperatures (Figure 8B and Figure 9). There was also considerable contrast in secchi and flow measures across control groups (Figure 8). The conditions experienced by the single spring-run release were similar to those for fall releases (Figure 9).

Baseline models

The first models we fit to the base pair sets contained no covariates (mean-only models). These models provided control-group estimates of efficiency, as well as (hyperparameter) estimates of (1) the mean efficiency across control groups, (2) the standard deviation (σ_E or "SD efficiency") for the between-group variability in efficiency among controls, and (3) the standard deviation (σ_δ or "SD dispersion") of the within-group variability (over-dispersion) in efficiency among upstream releases. The control-group efficiency estimates are shown in Figure 10 for the all-upstream dataset (top panel) and the s < 1 dataset (bottom panel). Posterior probability distributions for hyperparameters are shown in Figure 11 (also see summaries for Set 1, Table 6).

Results for the two datasets may seem counterintuitive at first. For the all-upstream dataset, the posterior median for mean efficiency was 0.0058 (Figure 11). After removing upstream releases with survival estimates exceeding 1.0, mean efficiency declined slightly to 0.0051. As noted above, releases with estimated $s > 1$ are expected to have low efficiency estimates, so after their removal, we might expect mean efficiency to increase rather than decline. The apparent reason for this discrepancy lies in the internal constraint placed on survival during model fitting: all survival estimates were constrained to a maximum of 1.0. As a result, upstream releases with $s > 1$ provided higher efficiency estimates when max(s) = 1. For example, suppose that five upstream releases (i) are paired with a given control (j), but in all cases, survival estimates are biased high because $q_i > q_j$, and hence, efficiency estimates are biased low. If releases with inadmissible survival estimates ($s > 1$) are removed, group efficiency remains biased low. But when they are retained and s is constrained to ≤ 1.0, the overall group efficiency increases.

This effect of removing upstream releases was most pronounced for control groups 00-1, 01-1, and 02-2 (Figure 10). These controls were paired with numerous upstream releases, many of which had survival estimates exceeding one (e.g., Table 2). When inadmissible ($s > 1$) upstream releases were removed, the group efficiency estimates were comparatively low (Figure 10B); however, with all releases retained, the group efficiencies were considerably higher and more similar to those for other control groups (Figure 10A).

The choice of dataset also influenced estimates of SD efficiency and SD dispersion (Figure 11). The posterior median for SD efficiency was considerably lower for the all-upstream dataset (0.046) than for the s <1 dataset (0.57). This reduced SD efficiency (between-group variation) was due in large part to the higher (and more similar) efficiencies of control groups 00-1, 01-1, and 02-2 for the all-upstream dataset (Figure 10). In contrast, SD dispersion (within-group variation) was greater for the all-upstream dataset (median = 0.46) than for the s < 1 dataset (0.37) (Figure 11). This was also largely due to the three controls (00-1, 01-1, and 02-2), which exhibited much greater within-group variation in efficiencies when all releases were retained and survival was constrained to ≤ 1.0.

Our primary objective was to better explain (account for) the between-group variation in efficiencies observed across control groups (Figure 10). To visually explore potential factors affecting these efficiencies, we plotted the all-upstream estimates (Figure 10A) against each covariate, as shown in Figure 12. The single efficiency estimate for spring run was very similar to the median estimate across fall groups (Figure 12). Late-fall groups tended to have slightly higher efficiency estimates. Estimates were reasonably similar across months, although there was a tendency for higher estimates in December (late-fall groups). Across all control groups, there was little visual evidence of a strong relationship between efficiency and either fork length, secchi, temperature, or flow (Figure 12).

Results for single-covariate models provided only weak evidence of associations between efficiency and the factors examined (Figure 13; Table 7 and Table 8, Set 1). Parameter estimates were reasonably consistent for the all-upstream and s < 1 datasets (Figure 13), and thus, reporting of results is limited to estimates for the all-upstream dataset (unless noted otherwise). The strongest relationships was between efficiency and secchi measurements (median $\beta_1 = 0.15$; SD(β_1) = 0.09). However, the secchi coefficient was only marginally "significant" (Figure 14; Table 7); the 80% probability interval (0.03, 0.26) excluded zero (no relationship), whereas the 95% interval included zero (-0.03, 0.32). In addition, from a biological perspective, we would expect a negative rather than positive relationship between efficiency and secchi (i.e., water visibility). Increasing turbidity (decreasing secchi) should reduce fish avoidance behavior and increase efficiency, but the opposite relationship is implied by these data.

For fish race, late-fall groups were estimated to have efficiencies 1.27 (= exp[β_1]) times greater than for fall/spring groups; however, this estimate was highly uncertain (95% interval: 0.76 – 2.16). Coefficients for fork length, temperature, and flow were all relatively weak (Figure 13; median $\beta_1 < 0.08$; SD(β_1) > 0.08).

Sensitivity analysis

Key model estimates were reasonably consistent across the eight pairing sets examined (Figures 15-18; Tables 6-8). For example, estimates of mean efficiency were similar across pairings for either all-upstream datasets (Figure 15) or *s* < 1 datasets (Figure 16). Likewise, coefficients for covariate models were reasonably similar across pairing sets (Figure 17 and Figure 18).

The strongest relationships were observed for secchi measures, followed by fish race. Again, however, the positive relationships between efficiency and secchi were uncertain; all 95% intervals for β_1 included zero (no effect) except for one borderline case (Set 3, s < 1 dataset; Table 8). The strongest race differences were estimated for Set 1, and in particular, Set 5 (Table 7 and Table 8). These were the only pairing sets that retained all six late-fall control groups (see Table 5). Again, estimates were uncertain. For example, for Set 5, late-fall efficiencies were estimated to be 1.37 (95% interval: 0.83 – 2.23) times greater than fall/spring efficiencies for the all-upstream dataset (Table 7), and 1.47 (95% interval: 0.93 – 2.43) times greater for the s < 1 dataset (Table 8).

We refit models using only fall/spring releases (analysis limited to all-upstream datasets) to examine potential confounding of relationships due to late-fall data, which had a tendency toward higher efficiency but markedly higher fork lengths and lower temperatures. Results for mean-only models are provided in Table 6 and Figure 19; results for covariate models are provided in Table 9 and Figure 20.

After removing late-fall releases, estimates of mean efficiency declined slightly, as expected (e.g., Table 6). Estimated coefficients (β_1) for fork length declined for all pairings sets and tended to be negative for fall/spring releases (e.g., Figure 20, compare with Figure 17), though length relationships with efficiency remained weak. Secchi coefficients remained positive and were typically the strongest coefficients observed across covariates and pairing sets (Table 9; Figure 20). Temperature coefficients went from generally negative estimates for all races (Figure 17) to positive estimates for fall/spring releases (Figure 20), with relatively strong relationships for Sets 5 and 6 (Table 9). Flow estimates changed little and remained weak.

Using time instead of volume to standardize efficiency estimates had little influence on estimated relationships between efficiency and covariates. Estimates for single-covariate models fit to the base pairing, all-upstream dataset are shown in Table 10 and Figure 21. Relationships between efficiency and race, temperature, flow, or fork-length were all weak. The relationship for secchi was positive though uncertain (median β_1 = 0.13, SE(β_1) = 0.10), consistent with results using volume-based *p* to standardize efficiency (e.g., Table 7, Set 1). Notably, the strongest relationship observed was between time-based efficiency and volume/minute sampled (median β_1 = 0.16, SE(β_1) = 0.10). Though uncertain, this relationship (Figure 22) closely approximated the expected 1:1 relationship between efficiency and volume/minute that would occur if trawl efficiency was directly proportional to volume sampled. Thus, to the extent relative differences in volume/minute sampling rates across years (Figure 1) are accurate, it seems most reasonable to account for these changes and use volume-based *p* to standardize efficiency estimates.

Proximal releases

Jersey Point and Sherman Island releases

As noted above, 21% of the paired-release estimates of survival rate for upstream releases exceeded 1.0 (biologically impossible). This high proportion suggests that there may be a tendency across paired-release tests for survival rates to be overestimated, which would in turn bias efficiency estimates low (a more complete discussion is provided below). In particular, Jersey Point releases tended to have the highest survival estimates compared to other locations with multiple releases (Figure 23). Of the 19 Jersey Point releases used in the paired-release analysis, 12 had survival rates greater than 1.0 (median = 1.25 across all 19 releases). Given this tendency, it seems reasonable to assume that Jersey Point releases experience relatively high survival rates from point of release to Chipps Island (especially when fish migrate rapidly, as assumed in the covariate models below). In contrast, there was only one Sherman Island release used in the paired-release analysis (a 2005 release with a survival estimate = 0.53).

The releases examined for Jersey Point (N = 34) and Sherman Island (N = 26) are summarized in Tables 11 and 12, respectively. All Jersey Point releases were fall run. Note that four of these releases, which were made in October of 2002, had high average fork lengths at release (> 160 mm) (Table 11, releases 24-27). Of the 26 Sherman Island releases, 24 were fall run and two were late-fall releases (Table 12). Most of the Sherman Island releases occurred in recent years (2009-2011).

There were clear differences in efficiency estimates between the two datasets (Figure 24). In particular, Jersey Point releases tended to have higher efficiencies and stronger (visually apparent) trends between efficiency and measures of migration speed (either “first day” or “median day” of capture at Chipps Island after release).

These differences were confirmed by the modeling results. First, we compare results for mean-only models fit to each dataset (Table 13; Figure 25). The mean efficiency (expressed as exp[β_0]) for Jersey Point releases (median posterior = 0.0046) was roughly double that for Sherman Island releases (0.0024). The Jersey Point efficiencies were also much less variable (median SD dispersion = 0.59) than those for Sherman Island (1.04). Next, relatively strong and precise relationships between efficiency and surrogates of migration speed were found for Jersey Point releases, whereas for Sherman Island, relationships were highly uncertain (Figure 26). As hypothesized, negative relationships were evident between Jersey Point efficiencies and both first day of capture (median β_1 = -0.22; 95% interval = [-0.32, -0.13]) and median day of capture (median β_1 = -0.09; 95% interval = [-0.15, -0.03]) (Table 14; bottom panels of Figure 27 and Figure 28). In contrast, for Sherman Island releases, there was a negative but uncertain relationship for first day of capture and a weak positive relationship for median day of capture (Table 14; bottom panels of Figure 27 and Figure 28).

Our primary interest lies in the intercept estimates of efficiency for the covariate models (i.e., the day-0 estimates where it is assumed that survival rate = 100%) (Table 13; top panels of Figure 27 and Figure 28). For Jersey Point releases, the efficiencies implied by the intercepts were similar for the first-day model (median exp[β_0] = 0.0080) and median-day model (0.0076) (Table 13). In the case of Sherman Island, we have little confidence in the interpretation of the intercepts given the high uncertainty in the covariate relationships.

The discrepancies in results between Jersey Point and Sherman Island releases was likely due in large part to differences among years in efficiencies and/or sampling intensities. In particular, Sherman Island efficiencies in 2011 (N = 15; Table 12) were much lower than in previous years (Figure 29), with a median efficiency of only 0.0014. In contrast, the median efficiency across the previous 11 Sherman Island releases was 0.0055. This latter value was consistent with Jersey Point efficiencies, which had a median of 0.0046. Thus, the large difference in mean efficiency for the two datasets (e.g., Figure 25A) was driven primarily by the 2011 Sherman Island releases. In addition, sampling effort (e.g., proportion of volume sampled and days sampled during the capture period) was considerably lower for Sherman Island releases than for Jersey Point releases (Figure 30). Reduced effort and daily frequency of sampling would tend to increase uncertainty in efficiency estimates as well as the surrogate measures of migration speed (first day and median day of capture) used in the covariate models as a proxy for survival rate. Note that other conditions (e.g., fork length, temperature, and flow) were reasonably similar among Jersey Point and Sherman Island releases, though secchi measures tended to be higher for Sherman Island releases (Figure 30).

<u>Special releases</u>

A summary of release and trawl data for the four special releases is provided in Table 15. The Sherman Island release was captured over a 21-day period in which only one day was not sampled. The capture periods for Pittsburgh releases were shorter and contained more days with no sampling.

The number of captures by tow of each release are shown across the full capture periods in Figure 31, and for the initial intensive-sampling periods in Figure 32. These plots illustrate several important features of the data that were common to all the releases. First, the intensive periods began with several or many (in the case of Sherman Island) tows with no catch followed by high catches in subsequent tows (Figure 32). Thus, the data appear to depict a clear onset of migration passage at Chipps Island, which is why we used the tow of first capture to define the start of the first "catch period." Second, for Pittsburgh releases, there were one or two initial tows with very high catches, indicating a tendency for early (rapid) migrants to travel in schools, which created a "clumpy" or "patchy" distribution of catches in the intensive period. Third, catches generally declined towards the end of the intensive sampling period. For this reason, we used the final ten tows to define the start of the second catch period, which extended until midnight of that day. Fourth, in addition to the irregular distributions of catches within the initial intensive-sampling periods, the distributions observed across the full capture period (Figure 31) were highly skewed (long tailed). For these reasons, we adopted a period-specific approach to expand catches rather than attempt to characterize the underlying distributions using parametric models.

Period-specific summaries of trawl data, CPUE, and estimated catch are provided for the four special releases in Tables 16-19. For example, the Sherman Island release had a total of 53 captures ("observed catch") across 21 days (Table 16). The observed catch during initial intensive sampling (the first two periods in Table 16) was 33, accounting for 62% of the total captures. The estimated catch (i.e., under continuous sampling) across the 21-day period was 188.2, but only 48.1 (26% of the total) for the first two periods. Thus, our period-specific calculations suggest that a majority (74%) of fish released passed Chipps Island after the intensive sampling period, even though most captures (62%) occurred during intensive sampling. The Sherman Island release had relatively complete sampling coverage; there was only one day (day 15) with no trawl sampling, which had no effect on estimated catch because the CPUE for that day (estimated by linear interpolation) was zero (Table 16).

By comparison, the three Pittsburgh releases had shorter capture durations, higher proportions of observed catch during intensive sampling, and more days with no sampling (Tables 17-19). The proportions of observed catch during intensive sampling (the first two periods in each table) were 72%, 95%, and 91%, whereas proportions of estimated catch during intensive sampling were only 23%, 71%, and 56%. In addition, the proportions of estimated catch derived for missing sampling days (via interpolation of CPUE) were 42%, 14%, and 26%, respectively (i.e., across shaded rows of Tables 17-19).

Point estimates of trawl efficiency for each special release are shown in Table 20. The estimates (volume based) ranged from a low of 0.0073 for the Sherman Island release to a high of 0.0157 for the first Pittsburgh release. For comparison, efficiencies based on minutes sampled (time) are also shown in Table 20; these estimates were very similar to the volume-based estimates because volume sampling rates across periods for each release (Tables 16-19) were similar to the value used to standardize volume (1000 m^3/minute). All remaining results pertain to volume-based estimates only.

As expected, there was considerable uncertainty in the special-release efficiency estimates (Table 21; Figure 33). Note that the bootstrap distributions provide a minimum estimate of uncertainty, in part because of the arbitrary division of the initial intensive-sampling period (i.e., use of the final ten tows to represent the second period through midnight of that day), and because the true migration distribution of releases was sporadically sampled in all cases (e.g., non-random daily trawl times and missing days). Nevertheless, estimates of mean efficiency were relatively precise (e.g., CVs of approximately 13%). The point estimate of mean efficiency across all four releases was 0.0111 (Table 20) with a 95% bootstrap confidence interval of (0.0082, 0.0132) (Table 21). The mean efficiency across the three Pittsburg was slightly higher (0.0124) with a 95% bootstrap confidence interval of (0.0087, 0.0151).

Discussion

We used several alternative methods and datasets of CWT releases to derive estimates of trawl efficiency at Chipps Island. Our ultimate objective was to develop, if possible, improved estimates of efficiency for computing total abundances of juvenile Chinook salmon captured by the Chipps Island trawl, in particular for the winter and spring runs (Pyper et al. 2013). However, as detailed below, our results suggest the following: (1) there is no compelling evidence of relationships between efficiency and environmental variables based on paired-release data; (2) paired-release estimates of efficiency are likely biased and confounded by variation in ocean survival rates; (3) trawl efficiency should be assumed constant (across time and across runs) until there is compelling evidence to the contrary; (4) alternative estimates of "mean" efficiency differ appreciably, and it is unclear which of the estimates is preferred; and (5) expansion methods for estimating abundance should be avoided, and in particular, the fish-flux method of Kimmerer (2008) is likely to greatly underestimate abundance.

Paired-release tests

We suspect that paired-release estimates of efficiency tended to be biased low, and that variation among efficiency estimates was largely due to unaccounted for variation in ocean capture rates. Specifically, the critical assumption that control fish and upstream fish passing Chipps Island trawl have equal (or very similar) marine survival rates is likely to be routinely violated. From a biological perspective, there is a strong contrast between control fish and upstream fish passing Chipps Island trawl. Initial mortality of hatchery releases may be substantial and variable, and would be most relevant to control fish. Control fish were comprised of new releases made over a short duration (hours) at either of two discrete locations downstream of Chipps Island trawl (Benicia ~ 30 km downstream or Port Chicago ~ 15 km downstream). By comparison, upstream fish passing Chipps Island trawl were typically released several or many days before arrival at Chipps Island trawl. These fish had already survived to the point of passage at Chipps Island, and were presumably better acclimated and distributed in time and space (i.e., from an individual fish's perspective) for seaward migration and subsequent survival.

Thus, it seems reasonable to expect potentially large differences in survival rates (and hence, ocean recovery rates) between control fish and upstream migrants passing Chipps Island trawl. Such differences could yield two effects. First, if mortality rates of control releases tend to be higher than for upstream migrants passing Chipps Island, efficiency estimates will tend to be biased low. Specifically, ocean capture rates of control fish be will lower than for upstream migrants ($q_{control} < q_{upstream}$), resulting in upstream survival estimates (from point of release to passage at Chipps Island trawl) that are biased high ($\hat{s} > s$) and efficiency estimates that are biased low ($\hat{E} < E$). Evidence of this possible form of bias was examined and discussed as a "shock effect" by Newman (2003). There was also evidence of such bias in the paired-release data we examined. For example, in the initial candidate pairing groups, 21% (45 of 215) of the upstream survival estimates ($\hat{s}$) exceeded 1.0. While some values of $\hat{s} > 1.0$ may be expected due to chance alone, this high frequency raises suspicion. More conclusively, the fact that the 19 Jersey Point releases used in the paired analysis had a median $\hat{s} = 1.25$ suggests that systematic bias was present in the paired-release data (these 19 releases were distributed among 11 different control groups, and values of $\hat{s} > 1.0$ occurred for seven of those controls).

The second effect of differences in marine survival rates would be spurious variation in efficiency estimates. Ordinarily, we would interpret the high between-group variability (σ_E) in paired-release efficiency estimates as indicating real and large differences in efficiencies over time (e.g., see Figure 10A). However, the efficiency estimates were poorly correlated with factors that would be expected to affect trawl efficiency. Consistently weak or uncertain relationships were found between efficiency and covariates across numerous sensitivity analyses. The strongest associations we found were positive relationships between efficiency and secchi measurements; however, from a biological perspective, we would expect a negative rather than positive relationship between efficiency and secchi (i.e., water visibility). Increasing turbidity (decreasing secchi) should reduce fish avoidance behavior and increase efficiency, but the opposite relationship was implied by the data. In sum, we could not account for the apparent high variability in efficiency estimates observed across years.

We should be cautious in our interpretation of the covariate analysis. We cannot conclude that the factors examined (e.g., fish size, water flow, temperature, etc.) have little influence on trawl efficiency (important relationships could well exist). Rather, we found no compelling evidence of such relationships using paired-release tests, which we suggest are thoroughly confounded by differential marine survival rates. Other aspects of the paired analysis were quite rigorous, including: (1) the use of multiple (replicate) upstream releases per control to better estimate group efficiency; (2) the use of Bayesian multilevel models to incorporate the sampling distributions of observed variables and within-group overdispersion; and (3) extensive sensitivity analysis to examine the influence of pair-selection criteria, whereby more restrictive criteria reduced available pairs but increased (presumably) the likelihood that control and upstream releases would have similar marine survival/harvest rates.

Thus, given the lack of compelling covariate relationships, in combination with evidence of highly variable upstream survival estimates ($\hat{s}$) both among control groups (e.g., Figure 4) and within selected locations (e.g., Figure 23), we conclude that variation in efficiency estimates across years may be largely due to differential marine survival rates (i.e., unreliable controls). It was beyond the scope of this study to further investigate this hypotheses (some additional analyses are suggested below), though it seems well supported by biological arguments. In short, observing real two-fold or four-fold differences in trawl efficiency (especially when considering all migrating juveniles and not just isolated CWT releases) across relatively similar environmental conditions (e.g., Figure 12) seems much less likely than observing such differences in marine survival rates of control fish relative to upstream migrants (i.e., two-fold or four-fold differences in the true ratio $q_{control}/q_{upstream}$ between paired-release tests). In any case, it is impossible to distinguish between real variation in efficiency and variation due to differential ocean capture rates ($q_{control}/q_{upstream}$) using paired-release tests.

For these reasons, we recommend that trawl efficiency should be assumed constant across time and across runs until there is compelling evidence to the contrary. We provide additional discussion of temporal variation below. With respect to run type, there were relatively small differences in efficiency estimates between late-fall and fall releases despite strong contrast in release conditions. Late-fall releases had somewhat higher efficiencies (e.g., 30% greater on average) than fall releases, but estimated differences were highly uncertain. Given the lack of late-fall tests (N = 6) and potential confounding in the paired-release design, we cannot make strong inferences about potential differences in run-specific efficiency. The body size and conditions experienced by migrating juveniles of the winter and spring runs are more similar to fall run than late-fall run, so we consider the estimates developed in this report as generally applicable to all runs.

Comparison of selected estimates of "mean" efficiency
Our conclusions regarding potential bias and confounding in paired-release data prompted us to examine other methods for estimating "mean" efficiency using proximal (nearby) releases. Here, we refer to "mean" efficiency in general terms as an underlying average or constant efficiency applicable to all time periods and runs.

To facilitate further discussion, we provide a summary of four selected estimates of "mean" efficiency in Table 22. These estimates were used by Pyper et al. (2013) to compute total abundances and assess the sensitivity of abundance estimates to the choice of efficiency estimate.

Table 22. Selected estimates of mean efficiency for (A) paired-release tests (base pairing for the "all-upstream" dataset); (B) Jersey Point proximal releases (median-day model); (C) Pittsburg special releases; and (D) the implied fish-flux efficiency. LCI and UCI denote the lower and upper 95% confidence intervals, respectively. Estimates (A)-(C) assume continuous trawling at a standardized volume rate of 1000 m^3/minute. The fish-flux estimate was adjusted using recent measurements of net-mouth area to provide a more realistic comparison with estimates (A)-(C). See text for details.

		Median	Median	Expected mean efficiency		
Method	Dataset	$\exp(\beta_0)$	σ_E or σ_δ	Estimate	LCI (95%)	UCI (95%)
A	Paired releases	0.0058	0.462	0.0064	0.0053	0.0077
B	Jersey Point	0.0076	0.521	0.0088	0.0058	0.0130
C	Pittsburg			0.0124	0.0087	0.0151
D	Fish flux			0.041		

The estimates in Table 22 include a mean estimate for the paired-release tests (base pairing of the "all-upstream" dataset), the day-0 estimate for the "median-day" model fit to Jersey Point releases, the mean for Pittsburg special releases, and the implied efficiency of the fish-flux method (Equation 17). Note that point estimates of mean efficiency previously reported for the paired-release tests (Table 6) and Jersey Point models (Table 13) were based on posterior medians (= $\exp[\beta_0]$). Because the assumed distributions for efficiency were log-normal, the expected (average) efficiency is computed in Table 22 as $\exp[\beta_0 + \sigma^2/2]$ to account for variability in efficiencies as formulated in the model. For paired-release tests, σ is the point estimate of σ_E, while for Jersey Point releases, σ is the point estimate of σ_δ.

The three CWT-based estimates of "mean" efficiency (Table 22) ranged from a low of 0.0064 for paired releases to a high of 0.0124 for Pittsburg releases (a two-fold difference), while the estimate for Jersey Point releases was intermediate (0.0088). Given the very different datasets and approaches applied in each case, it is difficult to assign confidence in any particular estimate. Note that the relative precisions of the estimates (Table 22) do not inform us as to which estimate is most "reliable" (e.g., there may be biases present in each estimate). Rather, each dataset and/or approach has advantages and disadvantages.

The paired-release dataset was the most comprehensive and allowed for estimation of upstream survival rates when computing efficiencies. Mean efficiency estimates were similar across all paired-release datasets examined, so the choice in Table 22 is sufficient. However, as previously discussed, we suspect that paired-release efficiencies tend to be biased low because control releases may experience (in general) higher initial mortality rates than upstream migrants passing Chipps Island (e.g., Newman 2003). Thus, we consider the paired-release estimate of 0.0064, which was notably lower than the Jersey Point and Pittsburg estimates, to be a minimum estimate of "mean" efficiency. We can easily compute the implications of higher control mortality (i.e., $q_1 < q_2$) on the paired-release mean. If control fish experienced, on average, 30% greater mortality than upstream migrants, this would imply a "true" paired-release mean similar to the Jersey Point estimate (~0.009). With 50% greater mortality, the implied "true" mean would be similar to the Pittsburg estimate (~0.013). Note that such additional mortality among controls is consistent with estimates provided by Newman (2003). He examined a subset of the paired-release data used here, with a focus on modeling upstream survival rates as a function of covariates. That framework allowed estimation of a "shock" parameter (ψ), which in our context, is analogous to defining $q_1 = \psi q_2$. Depending on the model examined, estimates of ψ ranged from 0.4 to 0.8, which implies additional control-group mortality ($1 - \psi$) ranging from 20% to 60% (i.e., on average across all paired-release tests; see Table 5 of Newman 2003).

The Jersey Point dataset had a moderate sample size (34 release groups) and revealed the negative relationships between efficiency and measures of migration rate that would be expected if mortality was a function of time at large. In Table 22, we reported the day-0 estimate for the median-day model because the median day of capture should be a more robust measure of migration rate than the first day of capture (the first-day model had a very similar, but more precise, estimate of mean efficiency; Table 13). The extrapolation of efficiency to passage at day-0 might be a reasonable (albeit indirect) approach for accounting for effects of survival on efficiency estimates, though simulations and/or auxiliary data are needed to confirm this.

For example, a recent study (SJRGA 2013) of acoustic-tagged juveniles (fall run smolts at roughly 105 mm fork length and released at Durham Ferry) yielded an estimate of survival rate from Jersey Point to Chipps Island of 0.69 (approximate 95% CI: 0.43 – 0.95) (Rebecca Buchanan, personal communication). The average travel time (harmonic mean, based on seven fish) from Jersey Point to Chipps Island was 0.86 days. Although this survival estimate is highly uncertain, we can compare the estimate (survival ~ 70% with median travel time ~ 1 day) to the survival curve implied by our median-day model for Jersey Point (Figure 26). The median-day model, which assumes 100% survival at day 0, declines somewhat slowly, implying survival rates of 92% at day 1, 84% at day 2, 77% at day 3, and 70% at day 4 (i.e., an implied release-group survival rate of 70% when the median day of capture in the Chipps Island trawl was 4 days after release). Thus, the curve depicts a higher survival rate at day 1 (92%) than the acoustic estimate (70%), which suggests that our approach may underestimate efficiency somewhat. That is, the curve may be much steeper close to the day-0 intercept, but there were no releases with median days to capture less than 3 days to provide such insight (Figure 26).

In general, the combination of evidence (high survival estimates in paired-release tests and significant negative relationships between efficiency and measures of migration rate) and replication across years suggest that the Jersey Point data may provide a reliable estimate of "mean" efficiency. On the other hand, analyses of Sherman Island releases did not provide consistent patterns or estimates. This appears to be largely due to the 2011 releases, which had much lower efficiencies than in previous years, but further analysis is warranted.

Potential advantages of the Pittsburg releases include high survival (close proximity) and high capture rates through use of an initial intensive-sampling period. Even though we assumed 100% survival, which is improbably high and would tend to bias efficiency estimates low, the mean efficiency estimate for Pittsburg releases (0.0124) was substantially greater than the day-0 estimate for Jersey Point releases (0.0088). However, there were only three Pittsburg releases and they all occurred in April/May of 2009. In addition, initial trawl captures were very clumpy, indicating a tendency for fish to school (poor dispersal). It is unclear if the distribution of Pittsburg releases at Chipps Island trawl is representative of run-of-the-river migrants, either in terms of channel cross-section or depth relative to trawl sampling. It is quite possible that catch rates of Pittsburg releases may be inflated (or reduced) compared to typical upstream migrants due to the close proximity and channel location of their release.

In contrast, the implied efficiency of the fish-flux method is considerably higher at 0.041 (the estimate for the Whitesel, or similarly, 0.042 for the Confluence). This efficiency is roughly 3 times greater than the Pittsburg estimate and 6 times greater than the paired-release estimate (Table 22). Because catch expansions are inversely proportional to efficiency, we expect the fish-flux method to provide abundance estimates of roughly 1/3 to 1/6 of those derived using CWT-based efficiency estimates. Note that the fish-flux method as employed by Kimmerer (2008) used current database trawl volumes with an implied efficiency of 0.060, and hence, in this case we would expect even lower abundance estimates ranging from roughly 1/5 to 1/9 of those based on CWT releases.

In short, the fish-flux method has an implicit efficiency that greatly exceeds the "mean" estimates derived using CWT releases. The latter estimates are based on actual data, and although biases may be present, they could not account for such discrepancies (e.g., see discussion above for paired-release tests). In contrast, the fish-flux method is a simple "conceptual model" that contains several questionable assumptions, perhaps the most important being (1) fish do not avoid the trawl net, and (2) trawling locations provide a representative sample of the spatial distribution of migrating fish. Even if we double migration speed at Chipps Island from 6 km/day to 12 km/day, we still have an implied fish-flux efficiency (now ~ 0.02 or

2%) that is considerably larger than currently indicated by actual CWT-test data. In contrast, the implied efficiency of 0.0078 for the "space-time" expansion of Kjelson and Brandes (1989) is similar to the CWT-based estimates (Table 22). We regard this as coincidental; the space-time expansion relies on similarly questionable assumptions and we recommend that any "expansion" method be avoided in favor of empirical estimates of trawl efficiency.

In summary, we have three different CWT-based estimates of "mean" efficiency, and it is unclear which estimate should receive the most confidence (though we interpret the paired-release estimate as a minimum value). It makes little sense to try to combine these disparate methods and estimates by use of a weighted average, for example. Rather, for the purposes of abundance estimation, Pyper et al. (2013) compared results using all four estimates provided in Table 22.

Temporal variation in efficiency and overdispersion

As discussed above, we largely reject the evidence of high inter-annual variation in efficiency indicated by the paired-release tests (i.e., between-group variation reflected by σ_E). The current approach (e.g., USFWS 2006) of estimating and applying annual efficiencies based on one or two control releases is suspect, and we would caution against it given the likely shortcomings of the paired-release design. Yet there is undoubtedly some degree of seasonal/annual variation in efficiency, which if large enough, will have important implications when estimating abundances. For example, when computing variances for abundance estimates, Pyper et al. (2013) assumed that efficiency was constant and used the standard errors reported in Table 22, but these terms only account for estimation error in "mean" efficiency estimates. Adding a variance term for seasonal or annual variability in efficiency might greatly increase variances of abundance estimates.

Thus, a key goal of future efficiency testing should be to quantify levels of seasonal/annual variation and likely causal relationships. To this end, we propose using a "hybrid" release design for efficiency testing (see recommendations below). The outcome of rigorous testing will be either a conclusion that seasonal/annual variation is minimal and adequately accounted for via variance terms in abundance estimators, or that variation is sufficiently important to warrant replicate testing under general or specific conditions (e.g., replication within each year or perhaps only when key environmental conditions are anomalous).

There may also be fruitful avenues for further investigation of seasonal/annual variation in the current data. The greatest insight may be gained by exploring the extremes observed in efficiency estimates, or more generally, in trawl catch rates. For example, the two highest paired-release estimates (1991 and 1992; see Figure 10) occurred at the lowest measures for Rio Vista flow (Figure 12). Although there was no evidence of an overall flow-efficiency relationship based on the linear form modeled (i.e., $\log(E) \sim \log(\text{flow})$), the data could be indicative of threshold effects (e.g., profound slowing of migration rate, dominant tidal influences, etc.) that might be supported by other lines of evidence not considered here. In contrast, an extremely low paired-release efficiency was estimated for 2008 (Figure 5) and very low catch rates of Sherman Island releases were observed in 2011 (Figure 29). We dismissed these results in part because of low sampling effort (even though we accounted for sampling effort in our estimation of efficiency), but a detailed examination of these data is warranted (e.g., what mechanisms underlying low effort, or environmental factors, could account for such discrepancies?).

There may also be considerable short-term variation in efficiency and/or overdispersion in trawl catches. Daily differences in efficiency could arise from subtle differences in trawl operation (channel location, direction, trawl speed, etc.) or environmental conditions (tidal currents). But even if trawl efficiency was constant across days, we would expect trawl catches to exhibit some degree of overdispersion (i.e., greater variance than assumed by the Poisson distribution) if migrating fish exhibit patchy spatial and/or temporal distributions. Distinguishing between sources of short-term variation in efficiency and overdispersion in catches would be difficult, and so we refer to them collectively as producing overdispersion in trawl catches. In any case, if such overdispersion were large, then it should be accounted for when estimating variances of abundance estimates (Pyper et al. 2013). Although there was strong evidence of overdispersion for paired-release tests (i.e., high estimates of σ_δ), this could be largely due to differences in the ocean capture rates of upstream releases. Thus, we would avoid using paired-release estimates of σ_δ unless they are treated as an upper bound for exploratory purposes. In the recommendations below, we suggest further analyses to better quantify overdispersion and operational factors that may affect efficiency.

Recommendations for efficiency testing

1. We strongly recommend an assessment of the feasibility/utility of a "hybrid" proximal-release design that allows for simultaneous estimation of (a) survival rate using acoustic tags, and (b) trawl-catch rates via CWTs. Such a design is the most promising approach we can conceive of for obtaining cost-effective, period-specific efficiency estimates that are not confounded by variation in survival rates. For example, at a location such as Jersey Point, a small number of acoustic-tagged juveniles (e.g., 200 fish) would be interspersed with a much larger CWT release (*R*). While the primary purpose of the acoustic tag component would be to estimate survival rate (*s*) from the point of release to Chipps Island trawl, useful auxiliary information would include data on temporal patterns (e.g., timing of passage or residency time in the trawl zone). Trawl recoveries (*n*) of CWTs would provide the second metric needed to compute efficiency ($E = n/Rsp$). It is straightforward to determine appropriate sample sizes for the acoustic tag and CWT components to achieve a desired precision for efficiency estimates given assumptions regarding true *s*, *E*, trawl effort (*p*), detection probabilities for acoustic tags, etc. Ideally, the choice of release location would satisfy two objectives: (a) juveniles passing Chipps Island trawl have spatial and temporal (diel) distributions representative of run-of-the-river migrants; and (b) releases have high survival rates, which increases the precision of estimates (at a given cost). For example, Pittsburg releases (~ 4 km upstream of Chipps Island) likely have high survival rates but it is unclear if fish are sufficiently dispersed at passage to achieve the first objective. Initially, several release locations could be tested to determine suitability.
2. If Pittsburg releases continue to be used in a similar manner (i.e., associated with an initial intensive-sampling period and without an auxiliary acoustic tag component), we suggest the following: (a) Individual tests may be combined to estimate "mean" efficiency as done here, but differences among tests should not (in general) be used to

assess temporal variation in efficiencies due to confounding effects of survival. In the three tests examined, an estimated 29% to 77% of passage occurred after the 24-hr intensive period, suggesting that potentially large and variable mortality rates (prior to passage at Chipps Island) could be associated with such tests. (b) Spatial and temporal patterns of trawl catches (e.g., patchiness, channel location, and time of day) should be compared to baseline expectations (i.e., distributions for run-of-the-river migrants during a similar period). (c) After the initial intensive-sampling period, attempt to maintain a moderate to high daily trawl effort for several more days to reduce uncertainty in period-specific expansions of total catch (see Methods).

3. We are skeptical that paired-release tests can provide reliable efficiency estimates because of potential bias and confounding derived from lower survival rates of control groups. Further, ocean harvest rates may continue to be restricted, thus limiting ocean recoveries of CWTs that are crucial to the estimation and precision of paired-release estimates. Nevertheless, if paired releases continue to be used, we recommend the use of multiple control releases for a given test. Increasing the spatial and temporal replication of control releases should increase the likelihood of meeting the assumption that $q_{\text{control}} = q_{\text{upstream}}$ and reduce the chance that a single control release provides unrepresentative ocean recovery rates. For example, three control releases could be made at different downstream locations and on different days within a given week. Ideally, there would be multiple upstream releases that could be reasonably compared with these controls. In the context of a multilevel model, the control releases would be modeled as a group (with potential overdispersion in ocean recoveries), providing a mean q_{control} for estimating upstream survival rates and group efficiency E. Again, however, we emphasize that considerable bias may always be present in the paired-release design if control fish tend to experience higher mortality rates than upstream migrants passing the Chipps Island trawl. To this end, any feasible release strategy that may improve initial survival of controls (e.g., acclimation in net pens) should be implemented.
4. Conduct multiple tests within a given year. Temporal replication is required to reliably estimate either "annual" efficiency or seasonal differences in efficiency. This recommendation would apply to "hybrid" releases or paired releases, though the paired design is much more constrained temporally (a single test may require three or four weeks worth of upstream pairings to achieve good group replication). Conducting a test every month during the key migration period (April through June) might be sufficient. Ideally, an appropriate number of annual tests would be based on statistical considerations of expected seasonal variability in efficiency and precisions of estimates. For example, our multilevel framework, or an approximate analytical version thereof, would provide a useful basis for examining alternative paired-release strategies (e.g., determining numbers of tests and replicate controls per test to achieve a desired precision for efficiency estimates). Key variance parameters would include σ_E, σ_δ, and potential overdispersion in ocean capture rates of replicate control releases.

Recommendations for further analysis

5. Additional analyses could provide greater insight into potential bias and confounding in paired-release tests: (a) Comparisons of ocean capture rates for Benicia and Port Chicago releases, in particular for releases made within a few days of each other. (b) Similar

comparisons for upstream releases. Strong differences in ocean recovery rates of replicate upstream releases (i.e., with essentially the same attributes but slightly different release times, say within a week of each other) only emphasizes the possibility of unreliable controls. (c) Comparisons of ocean capture distributions (fishery strata) of paired control-upstream releases. (d) Use of a more comprehensive paired-release model, applied to current data, that models covariate relationships for survival rates of upstream releases and allows estimation of a "shock effect" (e.g., Newman 2003).

6. Additional analyses could provide greater insight into potential seasonal/annual differences in efficiencies. In particular, it would be useful to further assess the anomalies noted here, including the high paired-release efficiencies for 1991 and 1992 that occurred at extreme lows for Rio Vista flow (possible threshold effects, tidal influences, effects on control group survival), and the low efficiencies observed in 2008 (paired-release data) and 2011 (Sherman 2011 releases).
7. Our analysis of Jersey Point releases provides a promising approach to estimating "mean" efficiency. We recommend two avenues for additional analysis. First, it would be useful to conduct simulations to explore the appropriate structural relationship between measures of migration rate and survival rate, which is essential to the accurate estimation of "mean" efficiency (in our case, the day-0 or intercept estimate). Second, the modeling framework could be extended to include virtually all release locations, with potential grouping variables (e.g., location, year, etc.) for shape parameters to account for some of the variation due to survival differences. Again, the approach depends on an assumed functional relationship between a measure of migration rate (e.g., median day of capture post release) and survival rate, and alternative flexible models should be explored (e.g., multilevel GLMs and GAMs). The possible benefits of such an approach would be large-sample inferences and insight into a "generic" (across time and space) mortality function for releases.
8. For some upstream releases, a parametric function (e.g., Zabel and Anderson 1997) could be used to characterize the distribution of migrants passing Chipps Island trawl. This may provide more accurate estimates of period-specific trawl effort (p) or point measures of migration rate in cases where there are missing days of sampling or large changes in daily sampling effort within the capture period of a release.
9. We recommend a comprehensive analysis of daily tow-specific trawl data for run-of-the-river migrants across all years (e.g., using models that account for variation in abundance implicitly via day-specific means or a time-series component). Such an analysis could be used to (a) characterize spatial patterns (e.g., channel location) and temporal patterns (e.g., time of day) in catch rates, which would serve as a baseline for assessing the representativeness of test releases; (b) standardize catch rates (CPUE) to account for daily (or seasonal/annual) differences in aspects of trawl sampling that affect efficiency/catch rates (e.g., channel location, direction, time of day, and seasonal interactions thereof); and (c) quantify overdispersion in daily catch rates by modeling the error structure for tow-specific data (e.g., overdispersed Poisson or negative binomial distributions).
10. Insight into size selectivity of trawl sampling can be gained by comparing the average fork length at release (admittedly, based on a small and potentially non-random sample) to the mean or median fork length of CWT recoveries in the Chipps Island trawl. We did a preliminary analysis across roughly one thousand upstream releases (data not shown) and found little evidence of differences between length at release and length at capture

when time at large was minimal (i.e., when most captures at Chipps Island occurred within a few days of release). However, as migration time increased, there was increasing trend toward higher lengths of captures at Chipps Island compared to average length at release. Collectively, the evidence was consistent with growth and/or delayed size-selective mortality but not size-selective trawl capture. We recommend a formal analysis along these lines.

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Figures

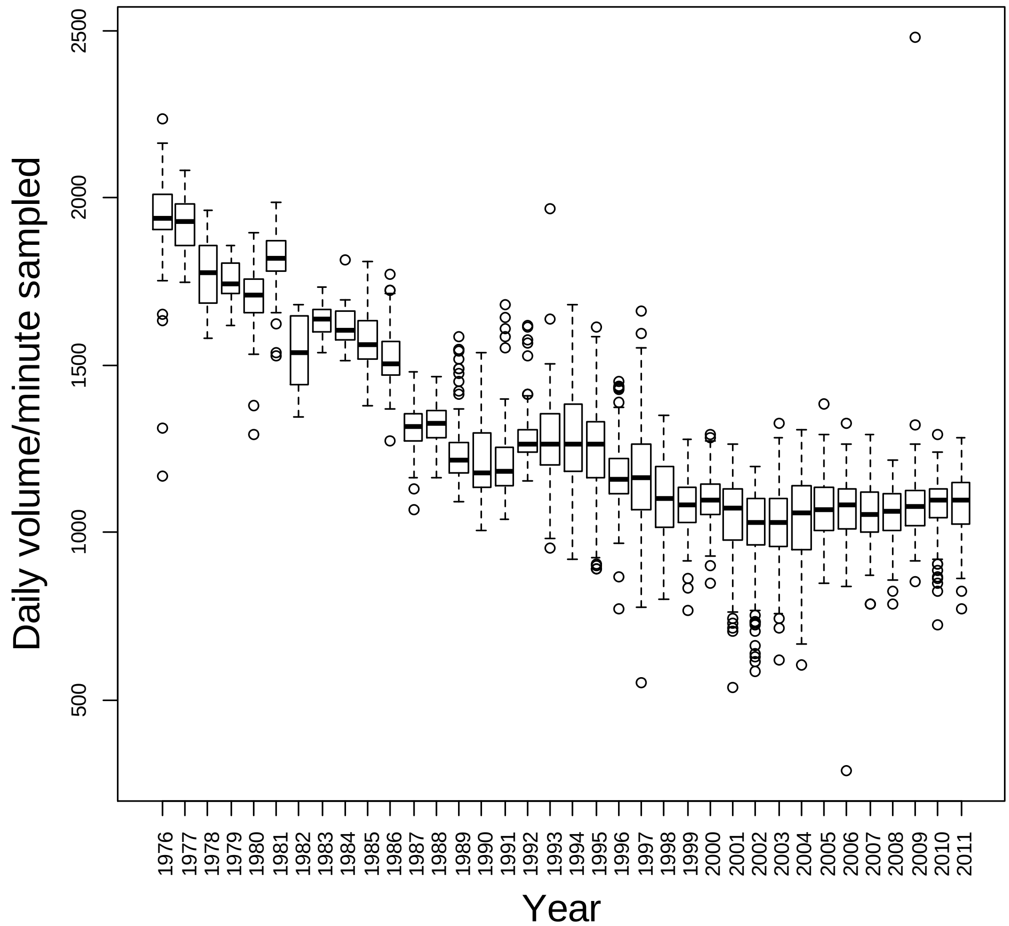


Figure 1. Boxplots of daily values of volume sampled (m^3) per minute fished (Chipps trawl).

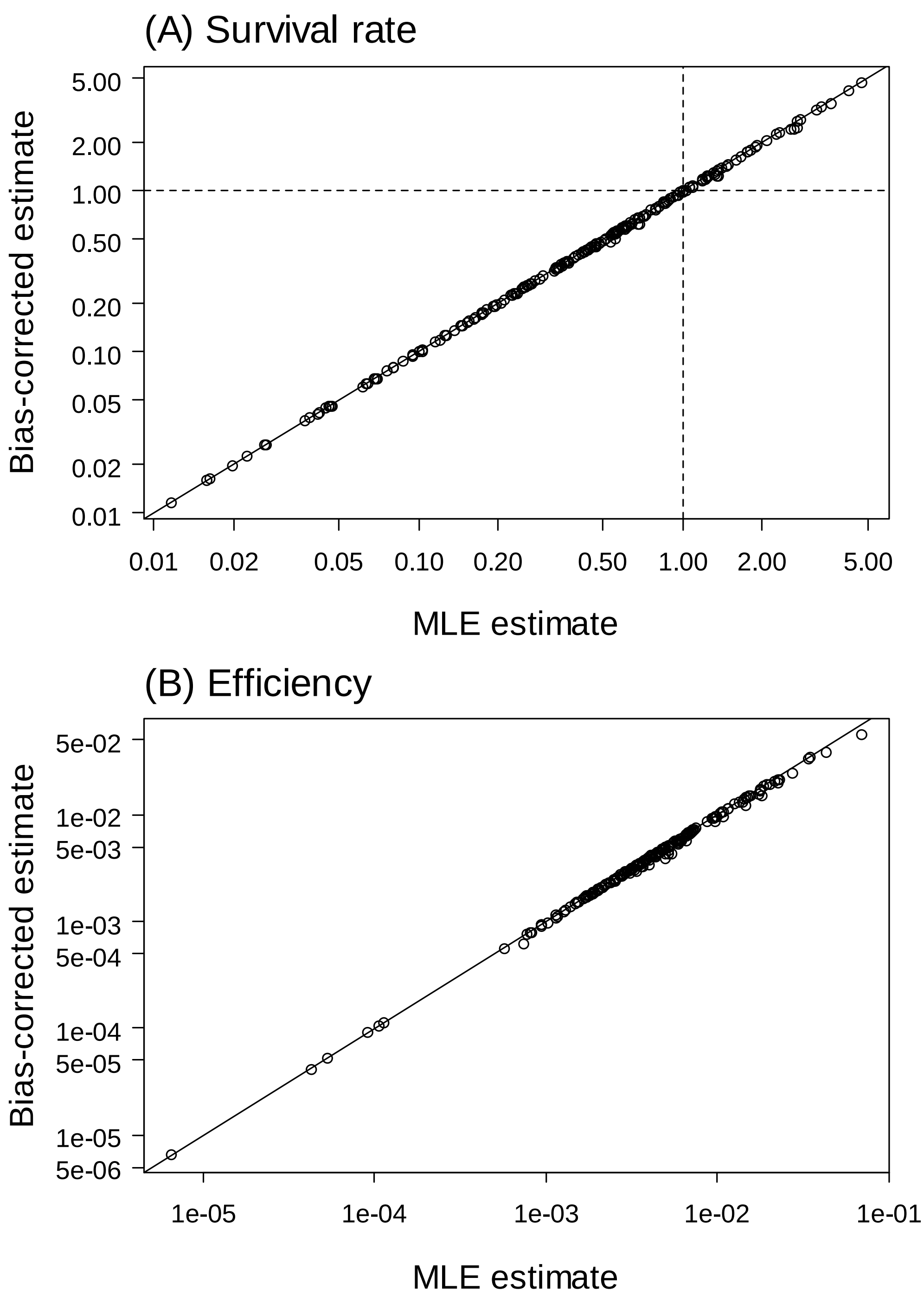


Figure 2. Comparison of ML and bias-corrected estimates of survival rate (A) and efficiency (B) across the initial candidate upstream release groups (N = 215; Table 2).

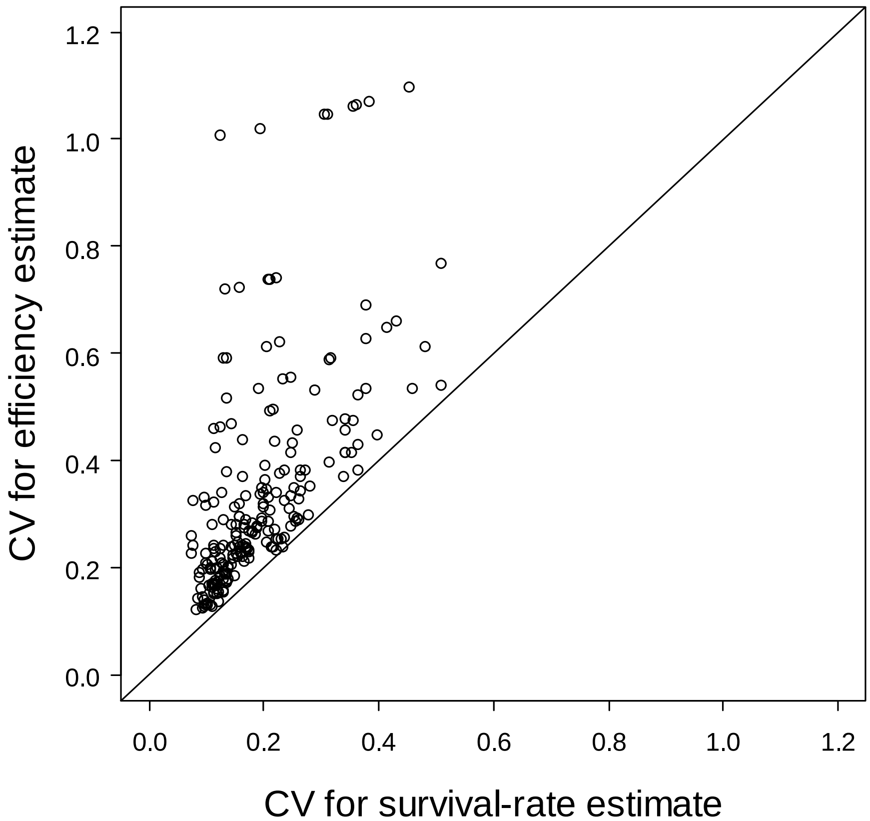


Figure 3. Coefficients of variation (CV) for survival estimates versus efficiency estimates for the initial candidate upstream release groups (N = 215; Table 2).

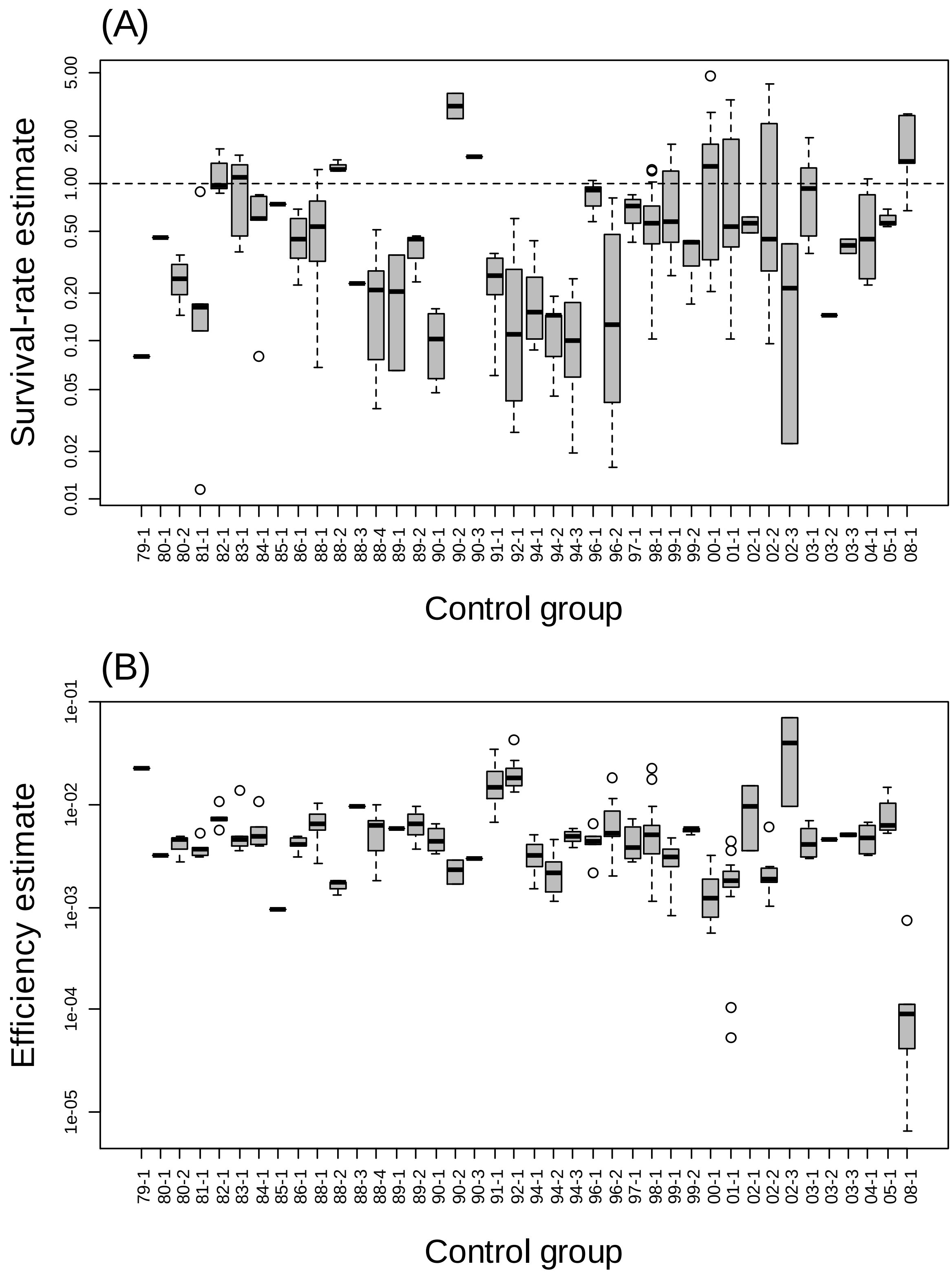


Figure 4. Boxplots of survival-rate estimates (A) and efficiency estimates (B) for upstream releases across the 40 candidate control groups (Table 2).

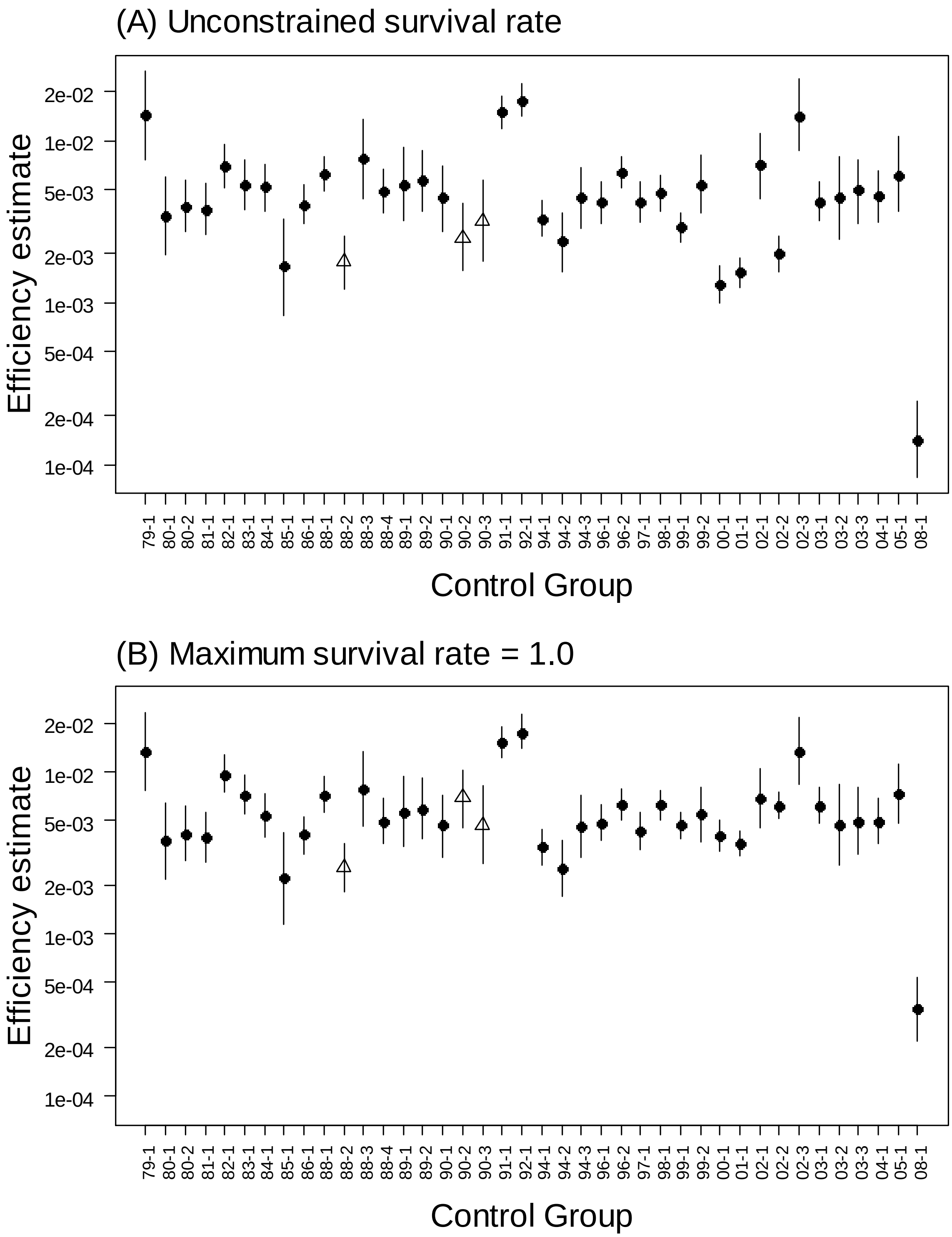


Figure 5. Efficiency estimates (posterior medians) with no constraint on upstream survival (A) and a maximum constraint of 1.0 (B) for the 40 candidate control groups (Table 2). Open triangles denote control groups for which all upstream survival estimates exceeded 1.0. Error bars denote 80% intervals.

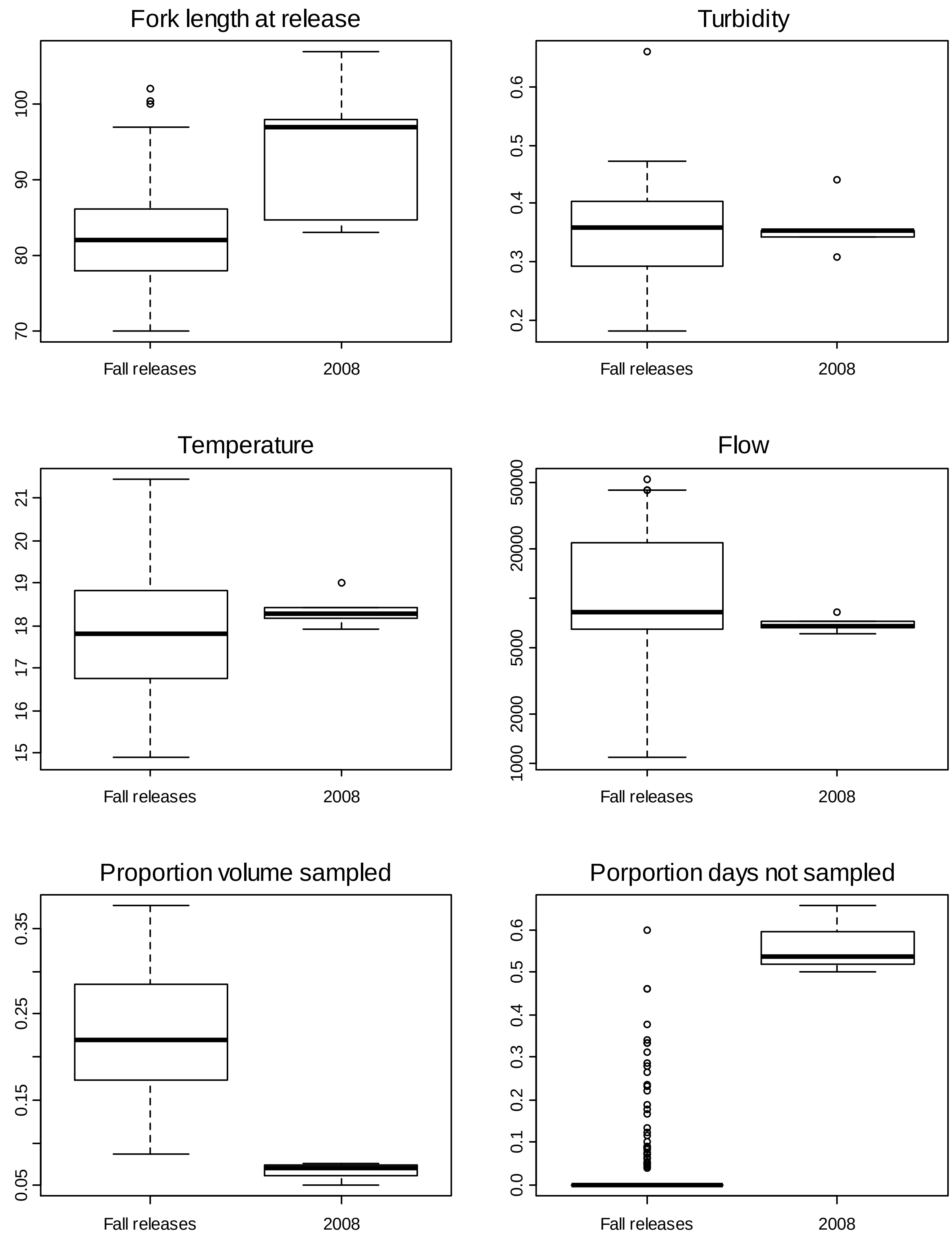


Figure 6. Boxplots of variables for all fall upstream releases (excluding 2008) versus 2008 fall upstream releases (N = 5) paired with control group 08-1.

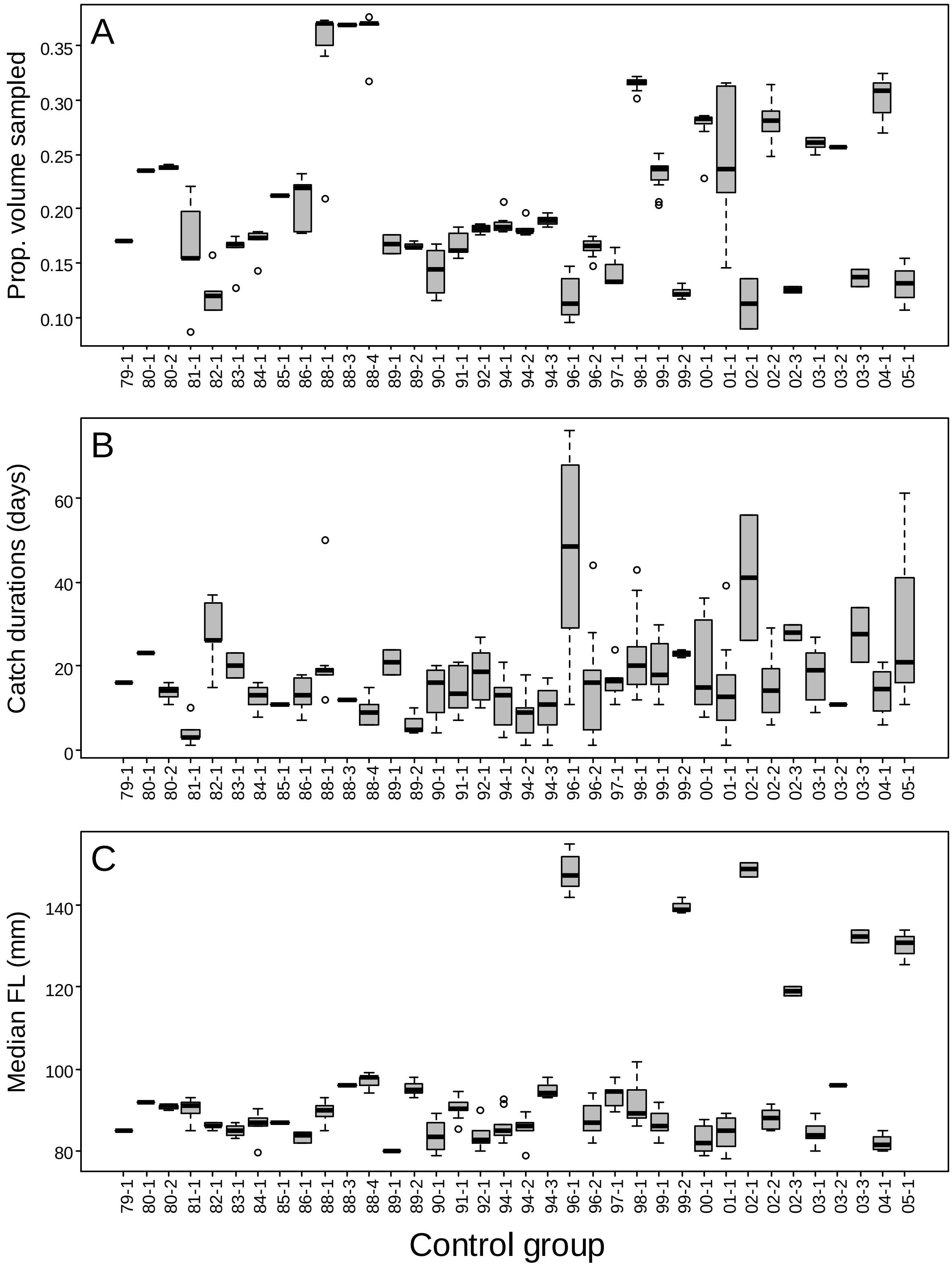


Figure 7. Boxplots of proportion volume sampled (A), catch duration (B) and median fork length (C) for upstream releases across the 36 baseline control-group pairings (Table 3).

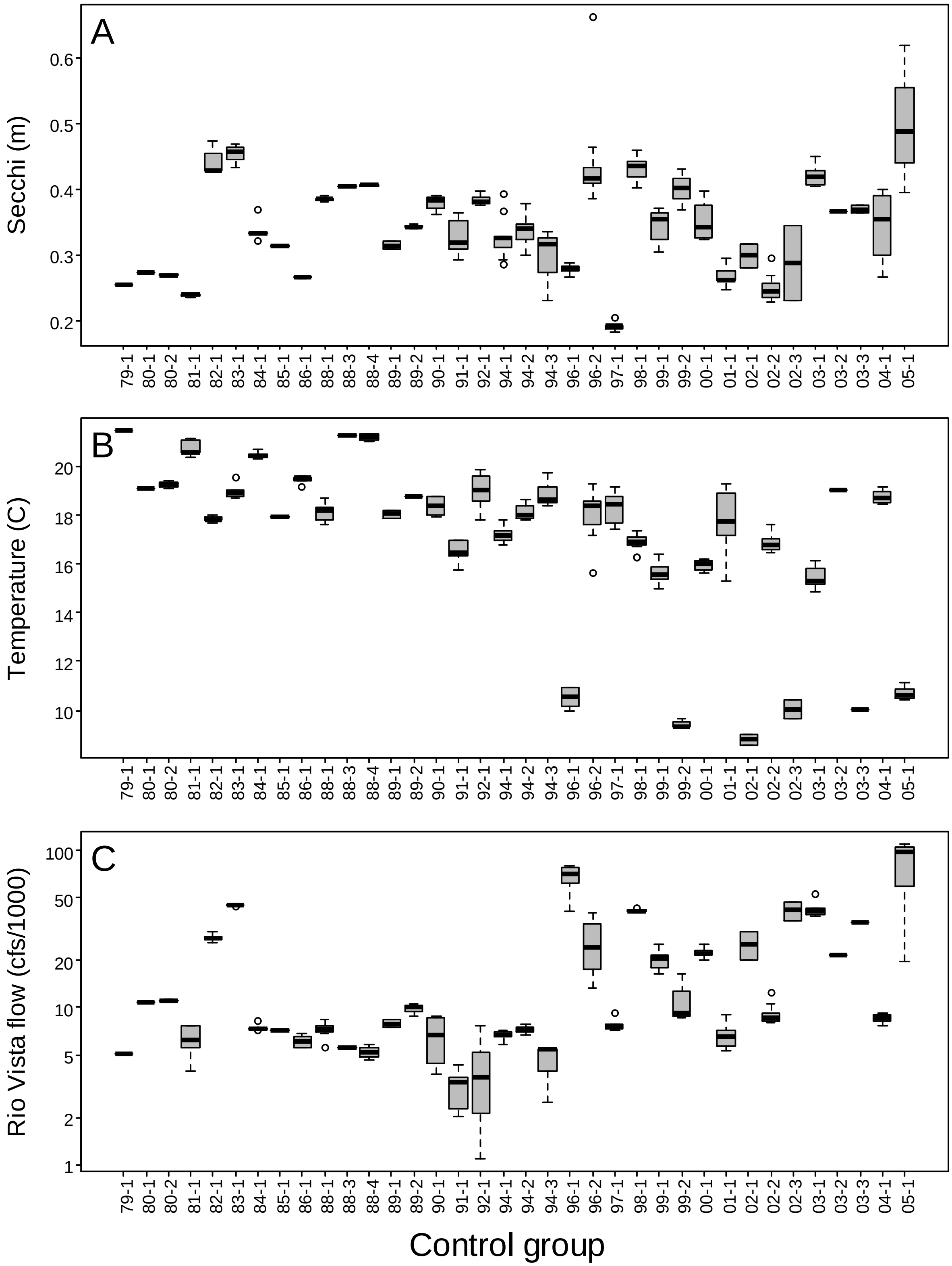


Figure 8. Boxplots of secchi (A), water temperature (B), and flow (C) measurements for upstream releases across the 36 baseline control-group pairings (Table 3).

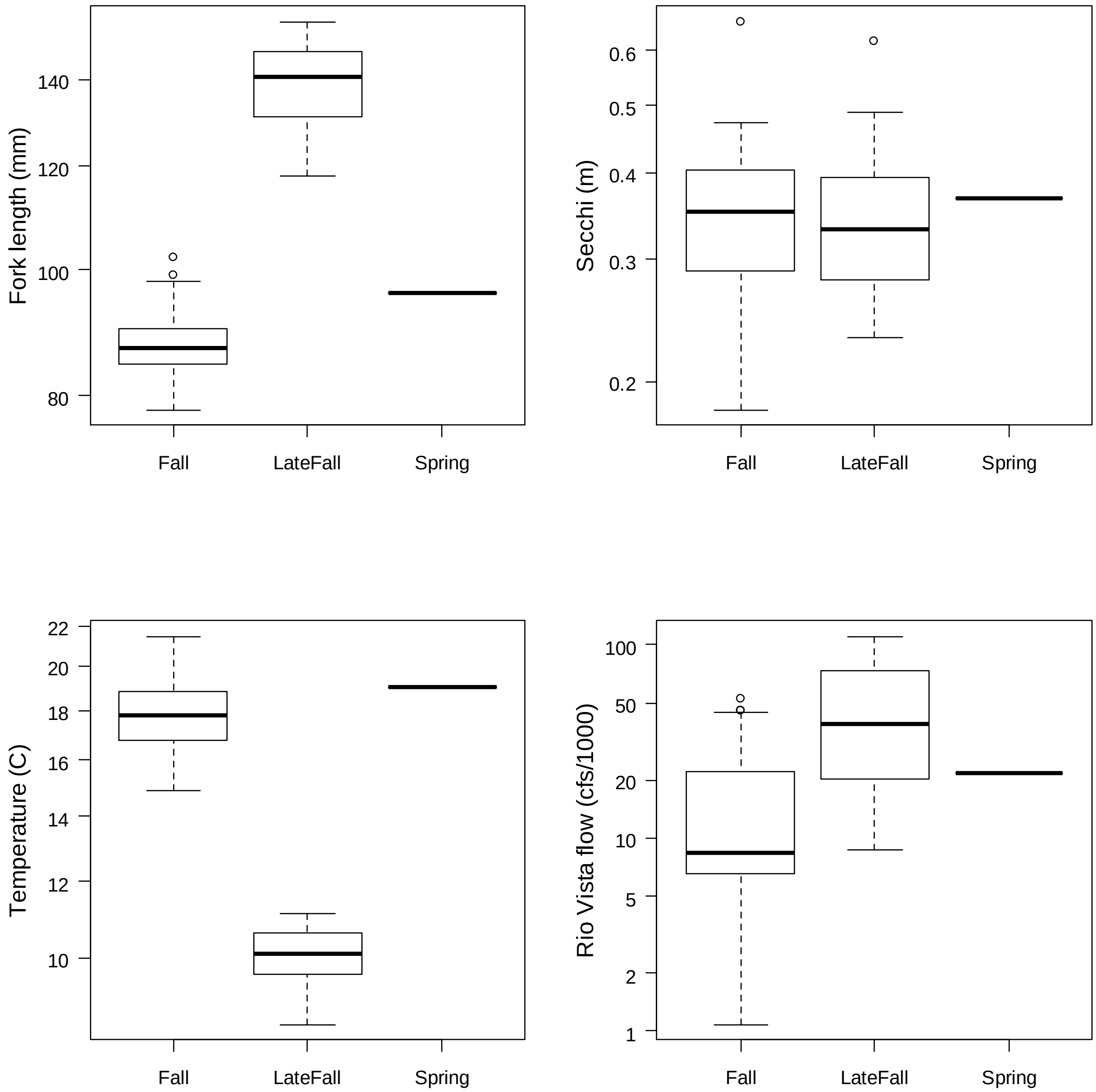


Figure 9. Boxplots by fish race of variables for upstream releases across the 36 baseline control-group pairings (Table 3).

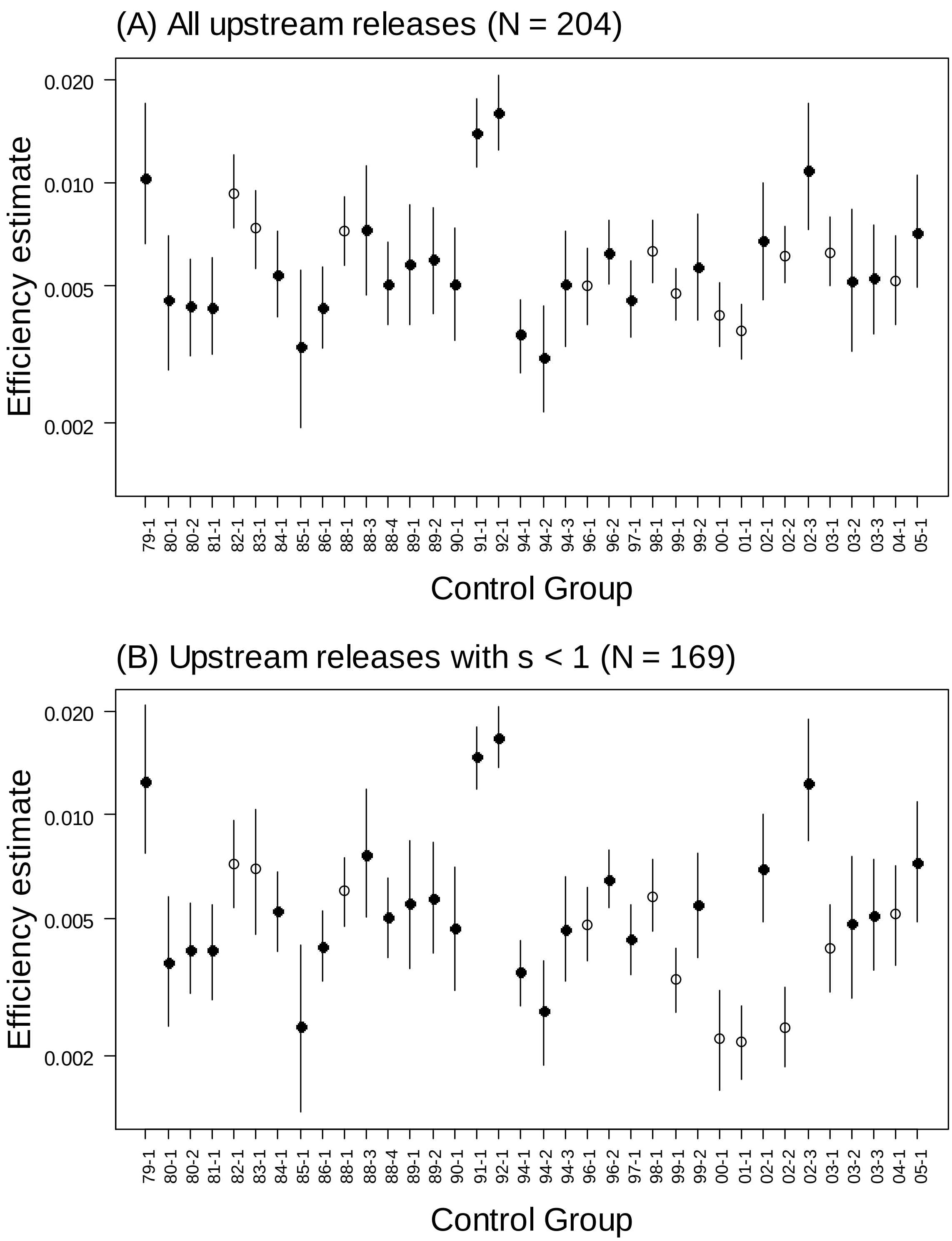


Figure 10. Efficiency estimates (posterior medians) by control group for (A) the "all-upstream" dataset (Table 3, base pairing), and (B) the "s < 1" dataset (Table 4, base pairing). Open circles denote control groups for which some upstream survival estimates exceeded 1.0. Error bars denote 80% intervals.

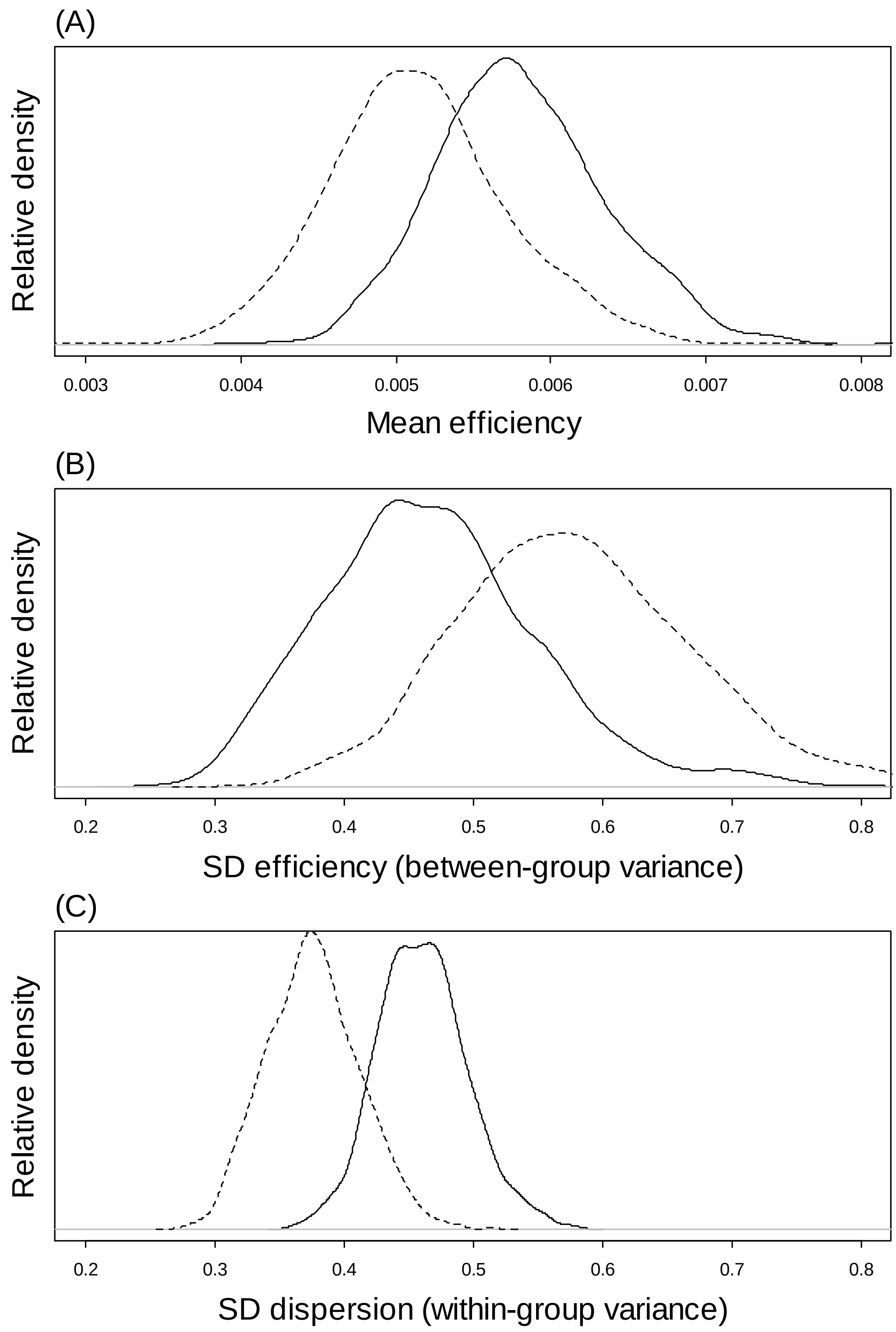


Figure 11. Posterior probability distributions (characterized by density functions) of mean efficiency (A), SD efficiency (B), and SD dispersion (C) for the mean-only model fit to the "all-upstream" dataset (solid lines; Table 3, base pairing) and the "s < 1" dataset (dashed lines; Table 4, base pairing).

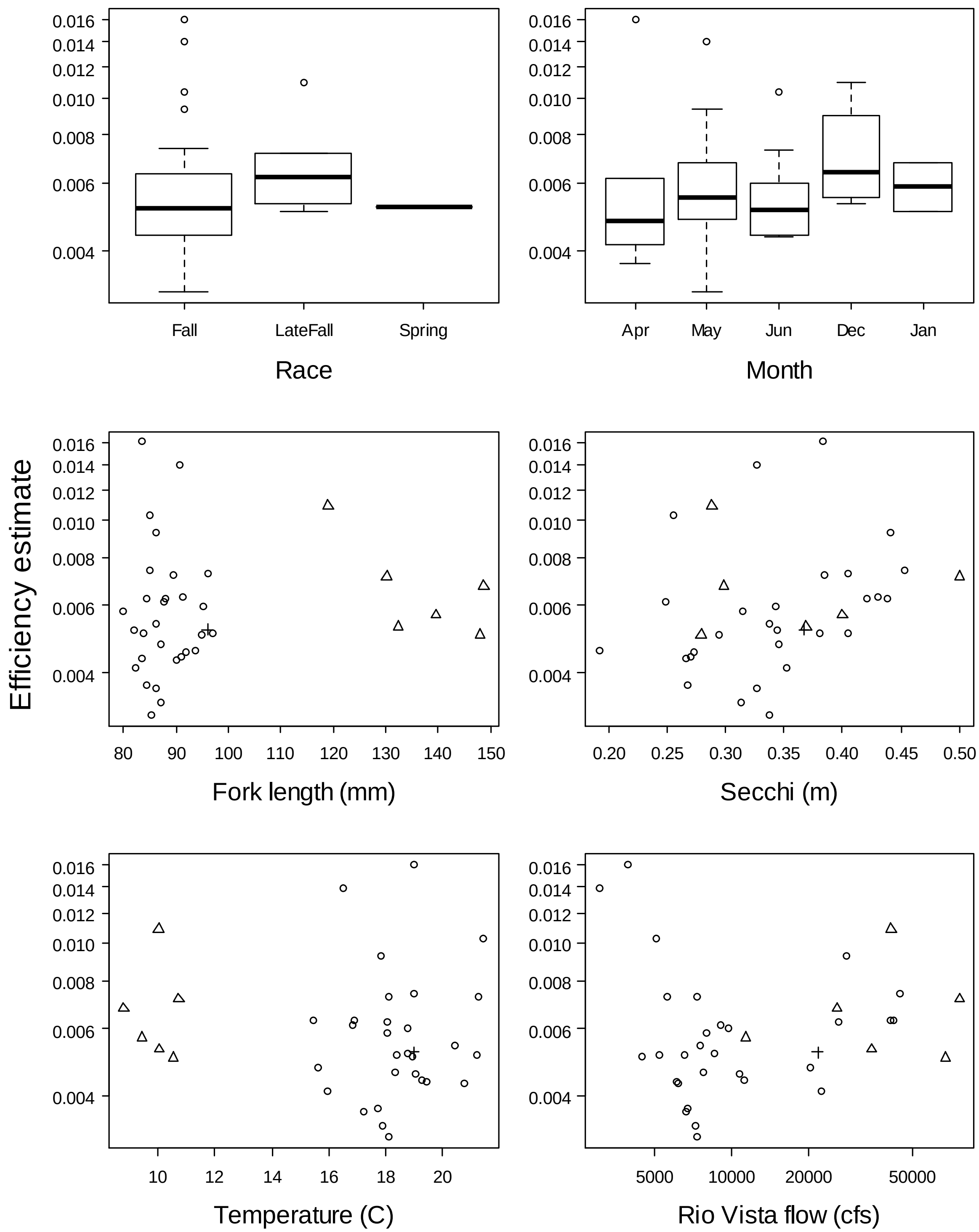


Figure 12. Efficiency estimates by control group ("all-upstream" dataset; Figure 10A) as a function of race, month, and control-specific measures of fork length, secchi, temperature, and flow. Open circles denote fall releases; triangles = late fall; "+" = spring run.

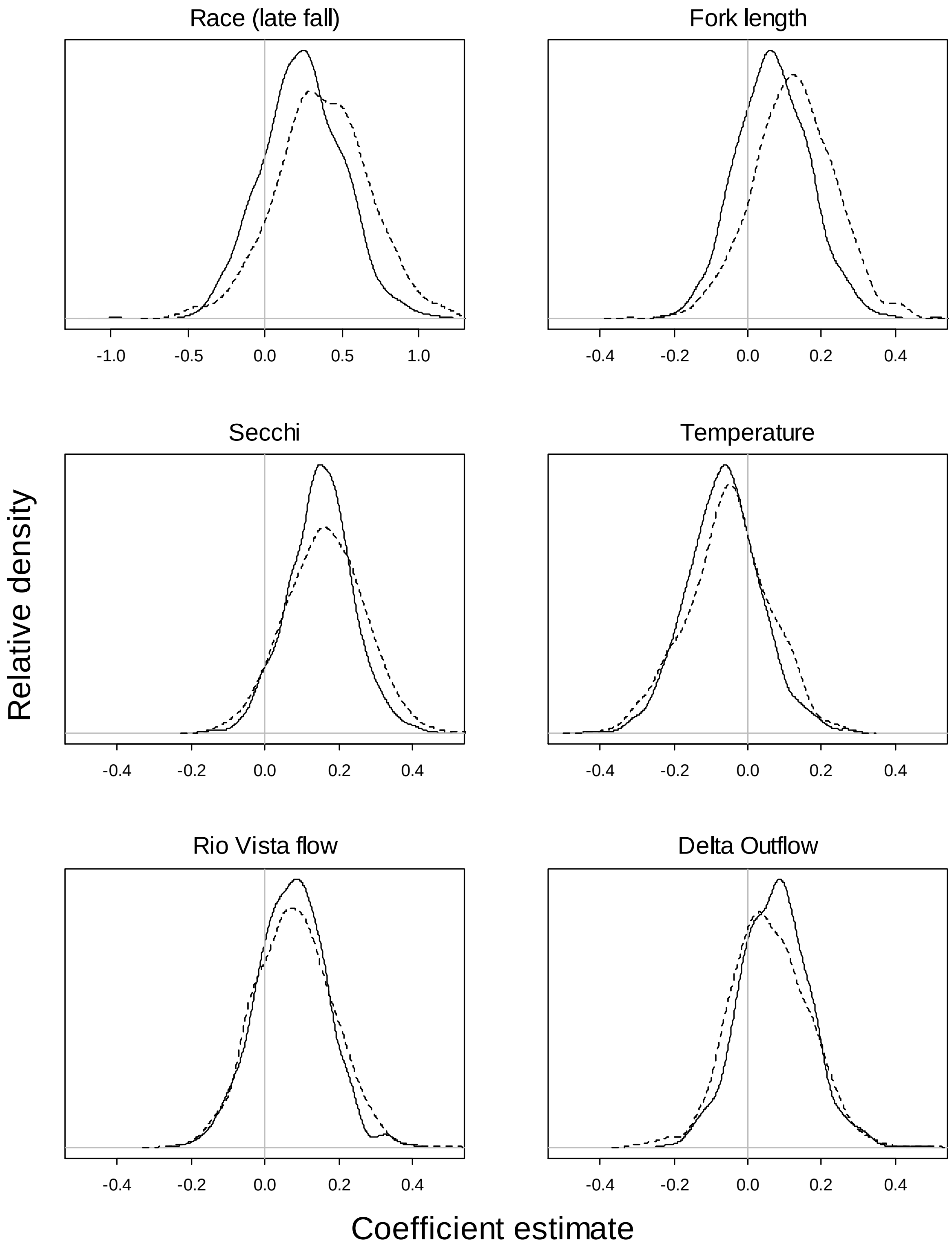


Figure 13. Posterior probability distributions (characterized by density functions) of coefficients in single-covariate models of efficiency fit to the “all-upstream” dataset (solid lines; Table 3, base pairing) and the “s < 1” dataset (dashed lines; Table 4, base pairing).

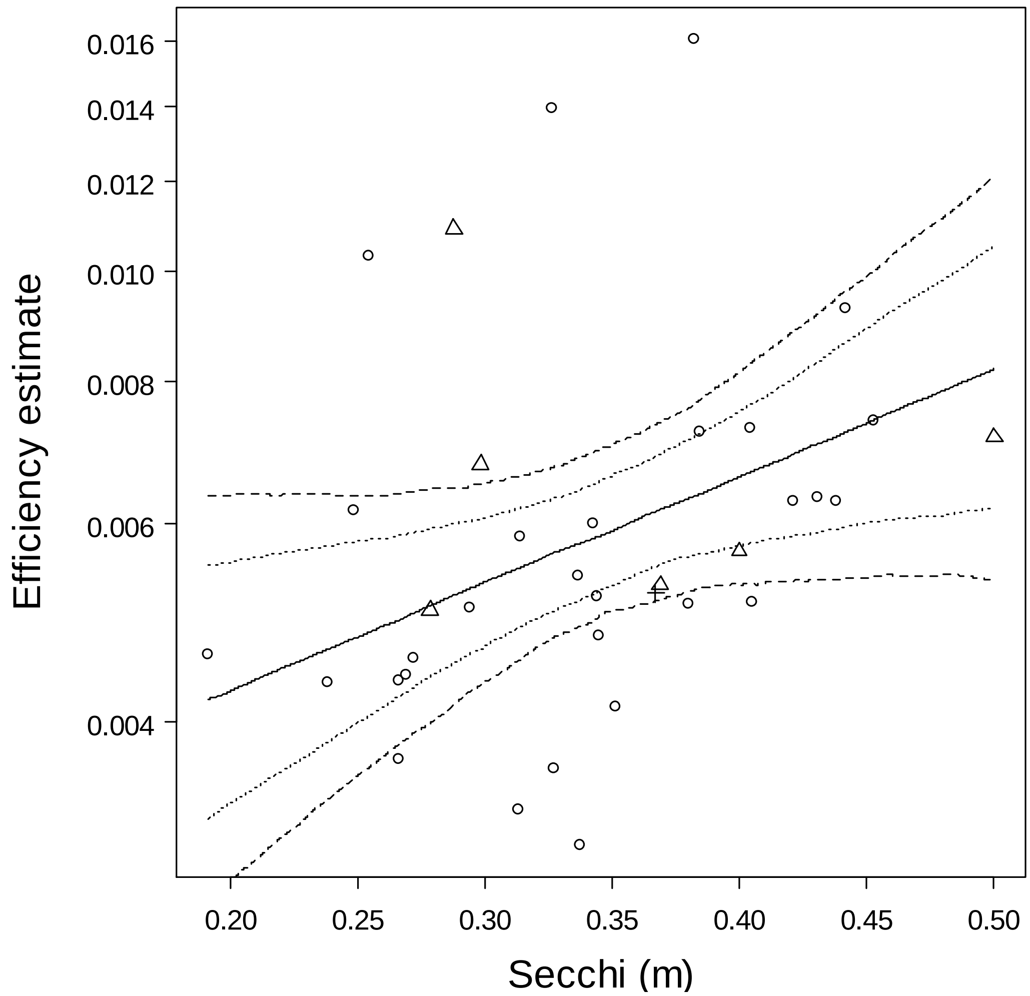


Figure 14. Model predictions (solid line) of efficiency as a function of secchi for the base pairing "all-upstream" dataset. Dotted and dashed lines respectively denote 80% and 95% posterior probability intervals for the fitted regression. Efficiency estimates by control group are shown for the mean-only model, where open circles denote fall releases, triangles = late fall, and "+" = spring run.

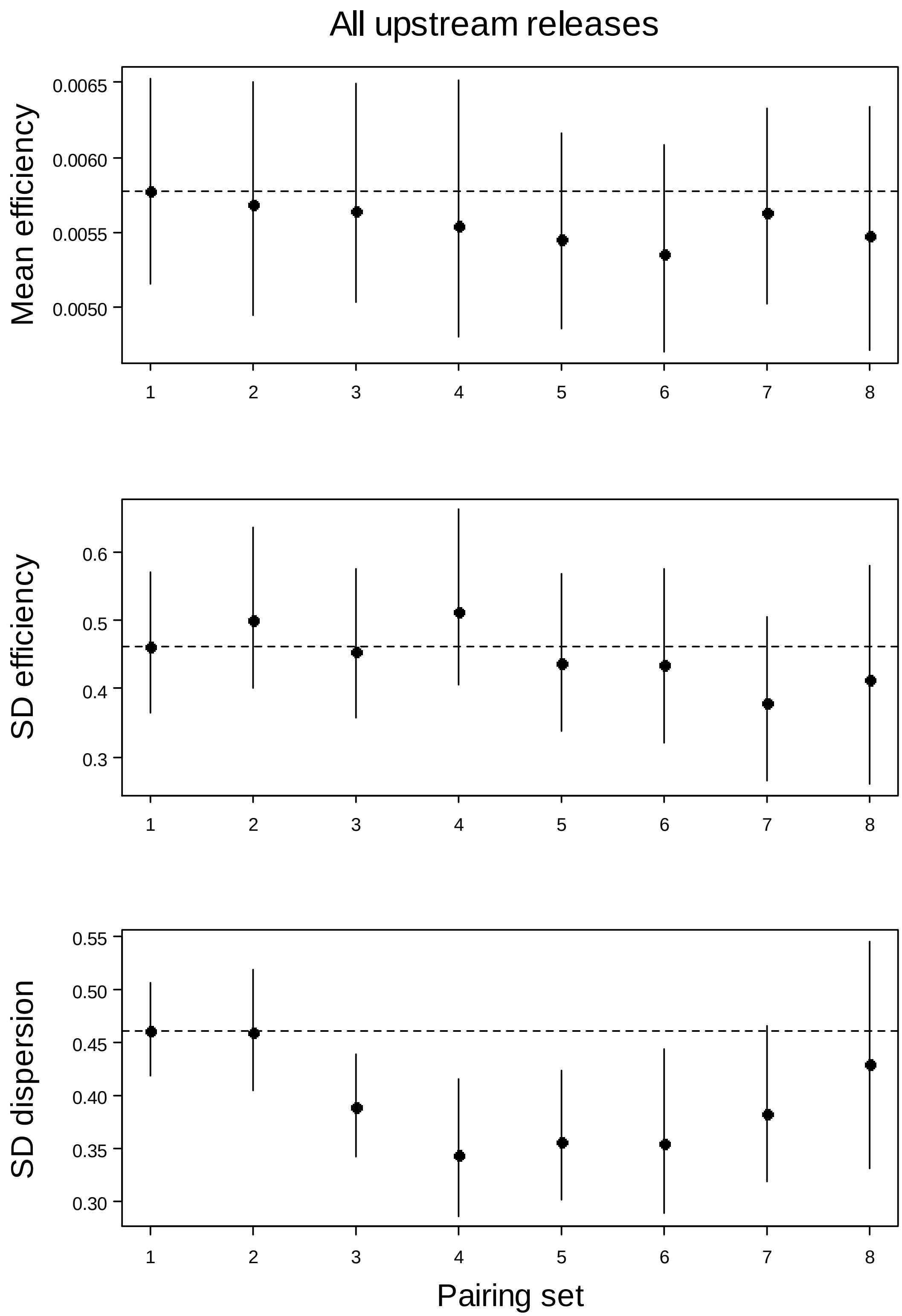


Figure 15. Mean-only model estimates (posterior medians) by pairing set for the "all-upstream" dataset (Table 3). Error bars denote 80% intervals; dashed lines denote base (set 1) estimates.

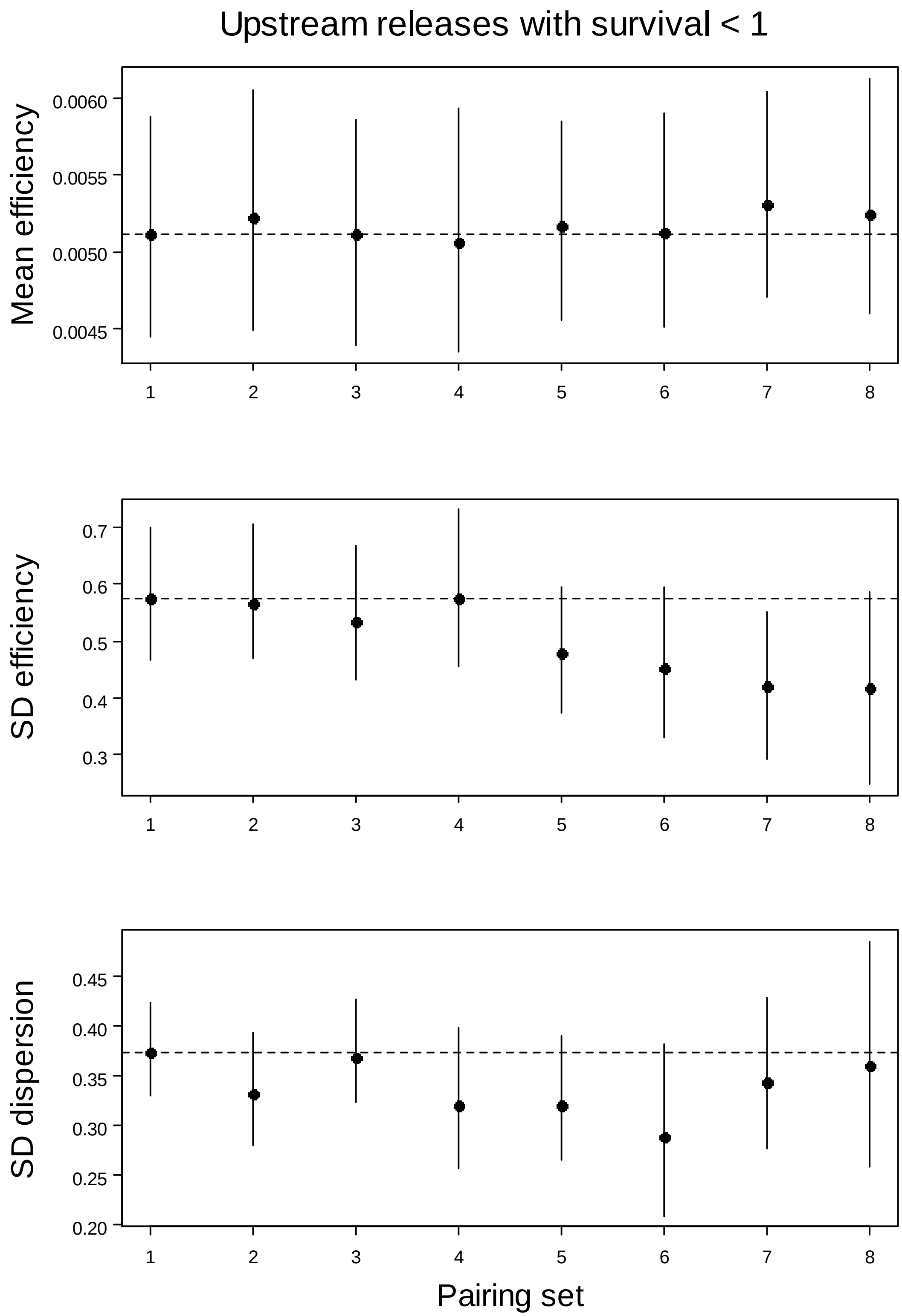


Figure 16. Mean-only model estimates (posterior medians) by pairing set for the "s < 1" dataset (Table 4). Error bars denote 80% intervals; dashed lines denote base (set 1) estimates.

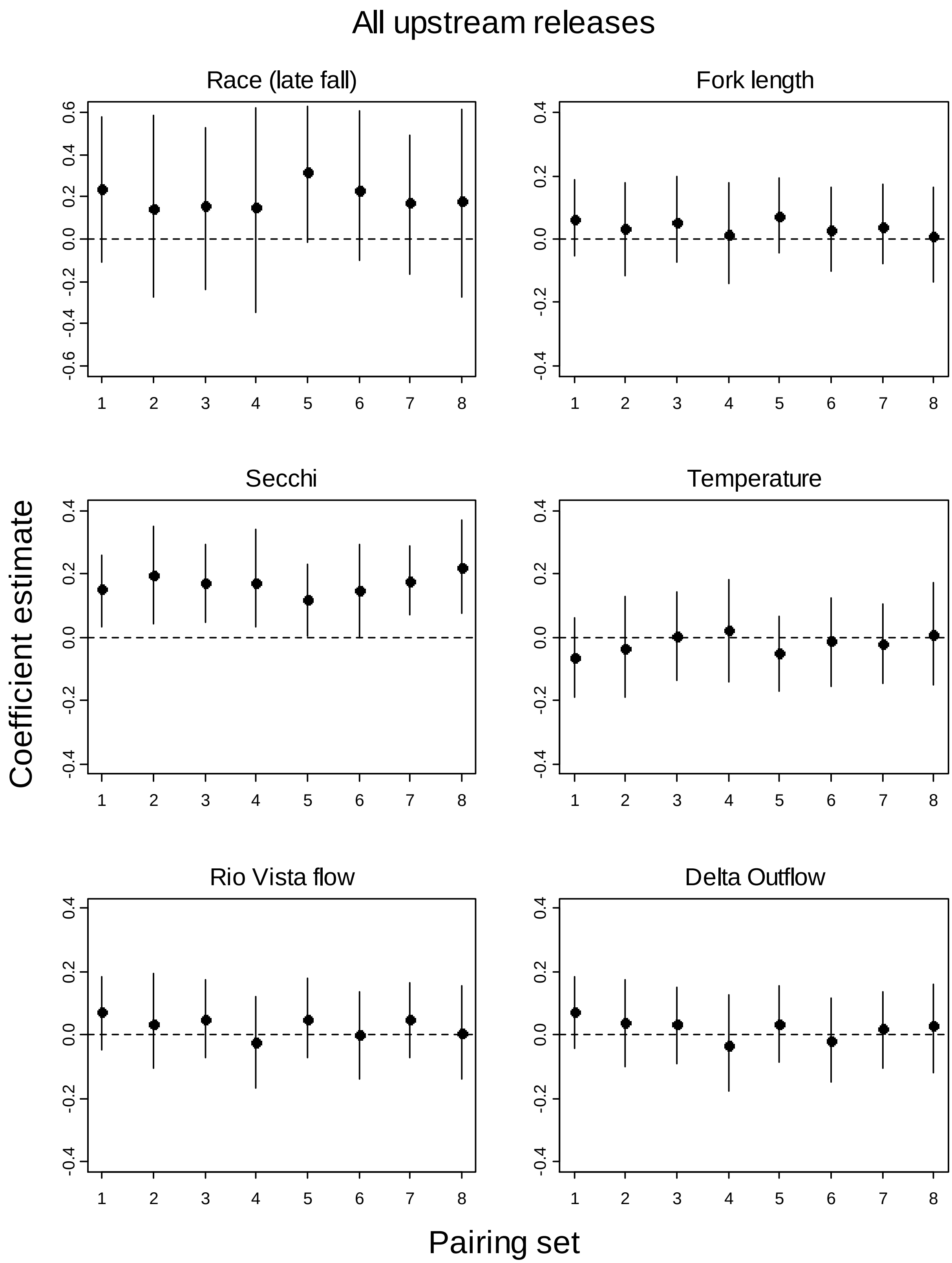


Figure 17. Estimates of coefficients for single-covariate models by pairing set for the "all-upstream" dataset (Table 3). Error bars denote 80% intervals; dashed lines denote no-effect (zero) values.

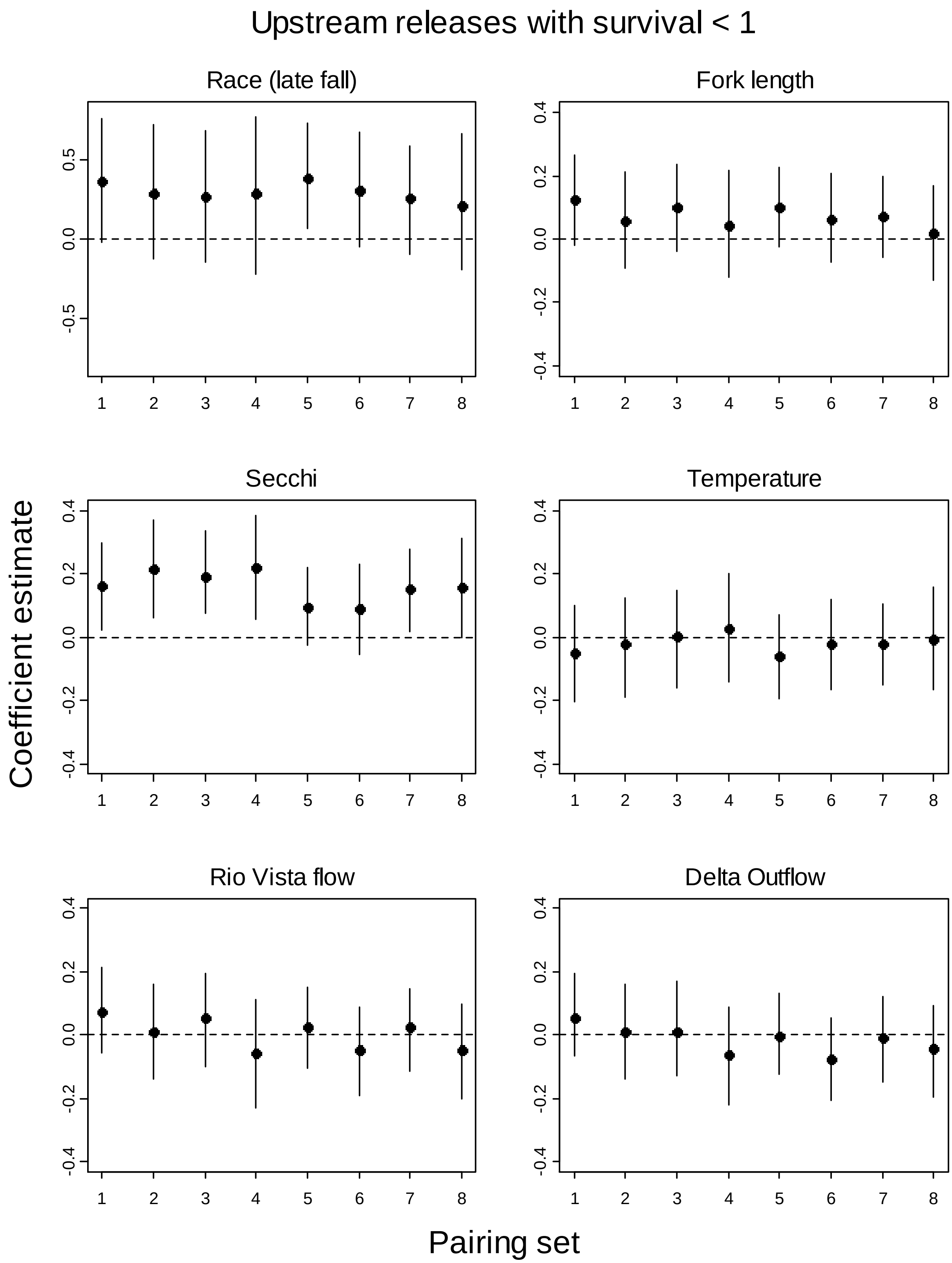


Figure 18. Estimates of coefficients for single-covariate models by pairing set for the “s < 1” dataset (Table 4). Error bars denote 80% intervals; dashed lines denote no-effect (zero) values.

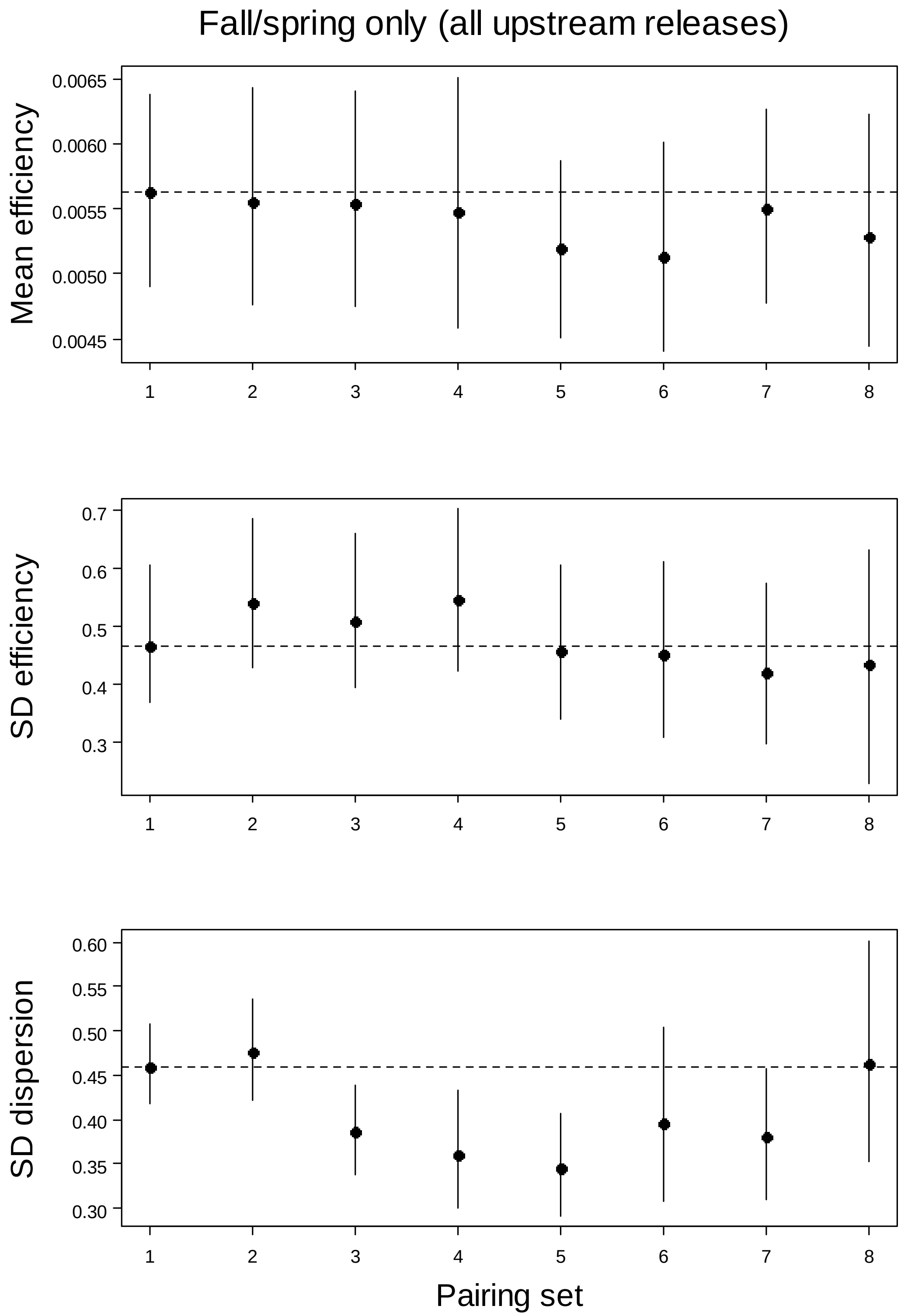


Figure 19. Fall/spring releases: mean-only model estimates (posterior medians) by pairing set for the "all-upstream" dataset (Table 3). Error bars denote 80% intervals; dashed lines denote base (set 1) estimates.

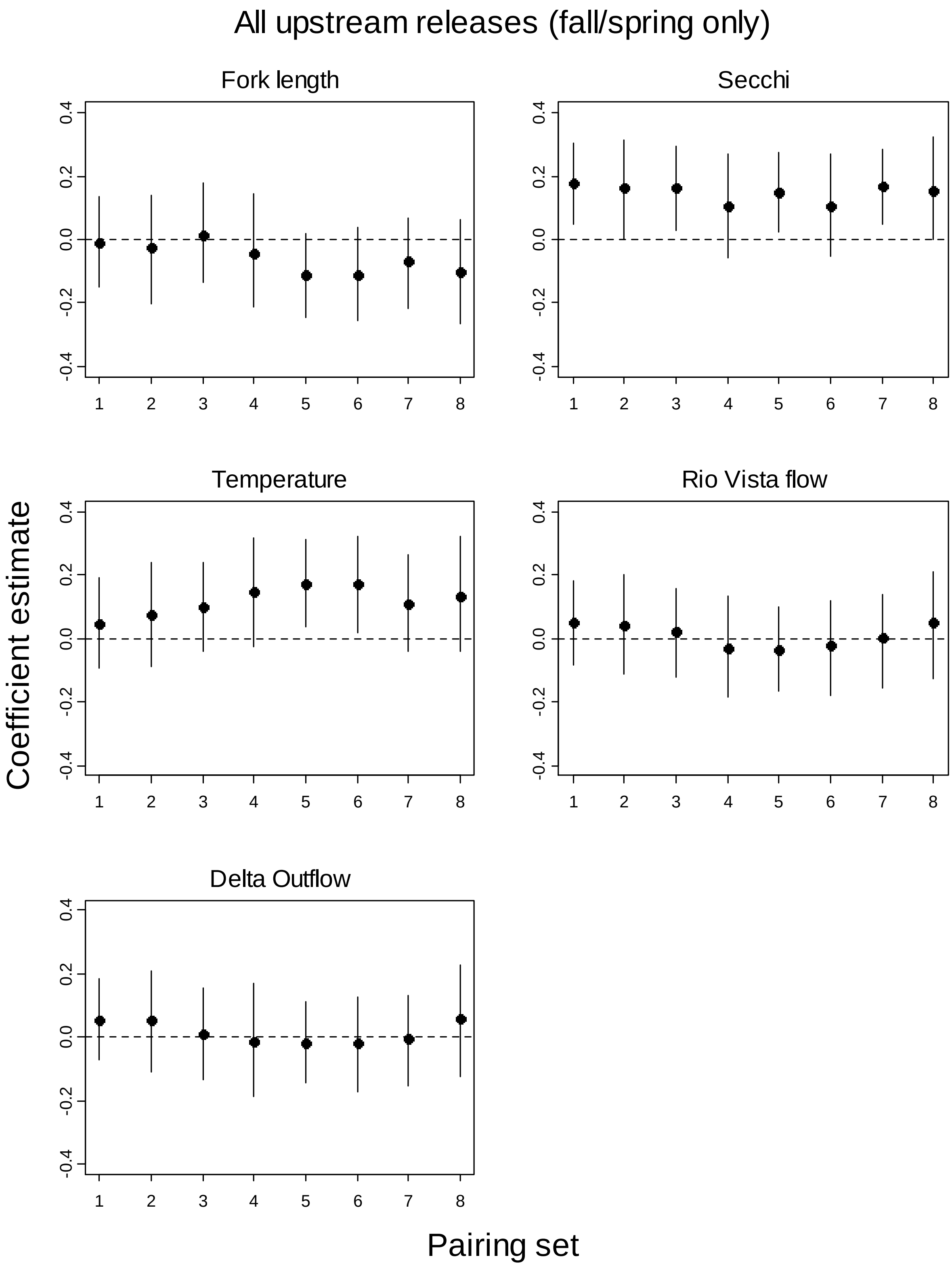


Figure 20. Fall/spring releases: estimates of coefficients for single-covariate models by pairing set for the "all-upstream" dataset (Table 3). Error bars denote 80% intervals; dashed lines denote no-effect (zero) values.

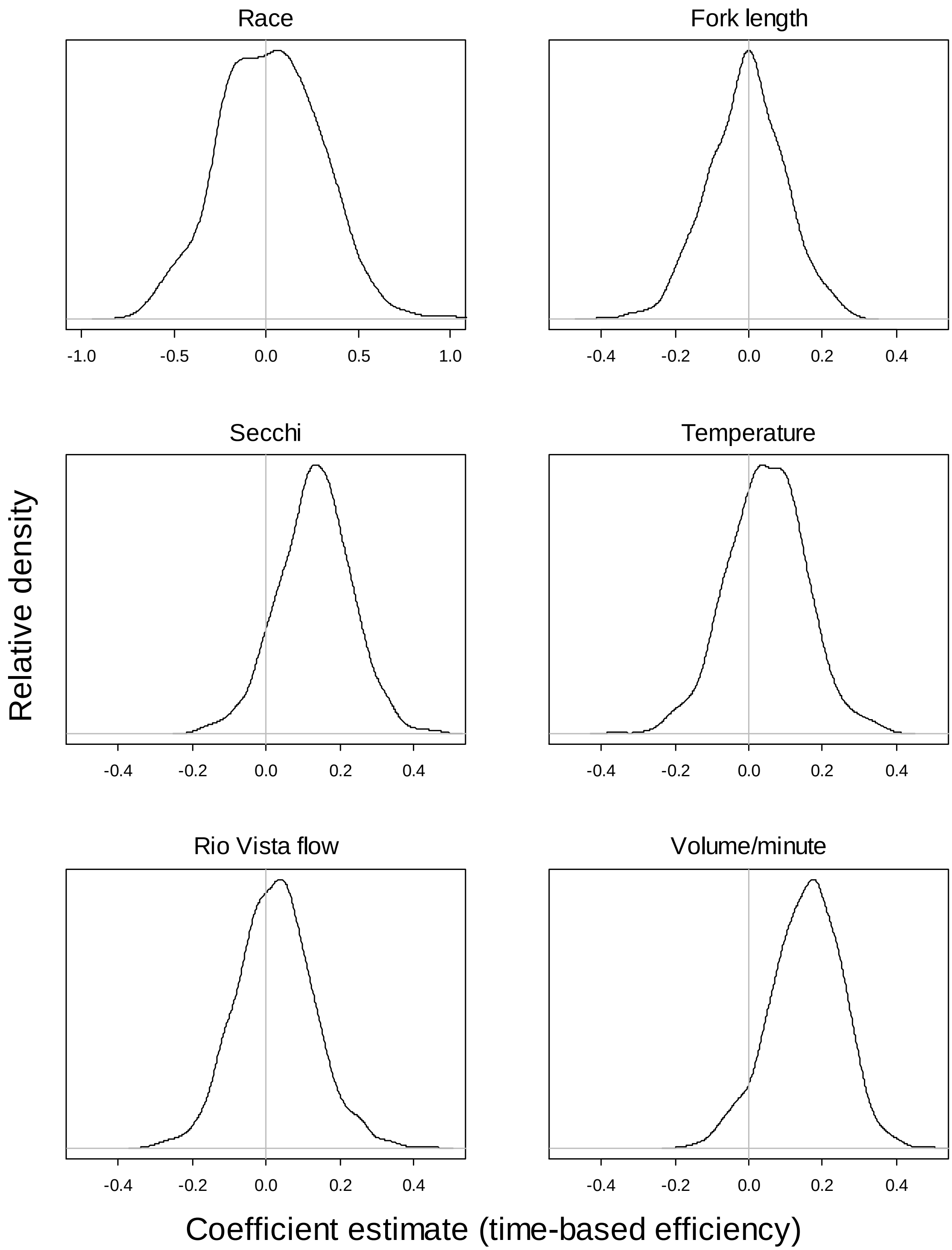


Figure 21. Posterior probability distributions (characterized by density functions) of coefficients in single-covariate models of efficiency fit to the base pairing "all-upstream" dataset (Table 3) using time-based *p* (instead of volume-based *p*) to standardize efficiency estimates.

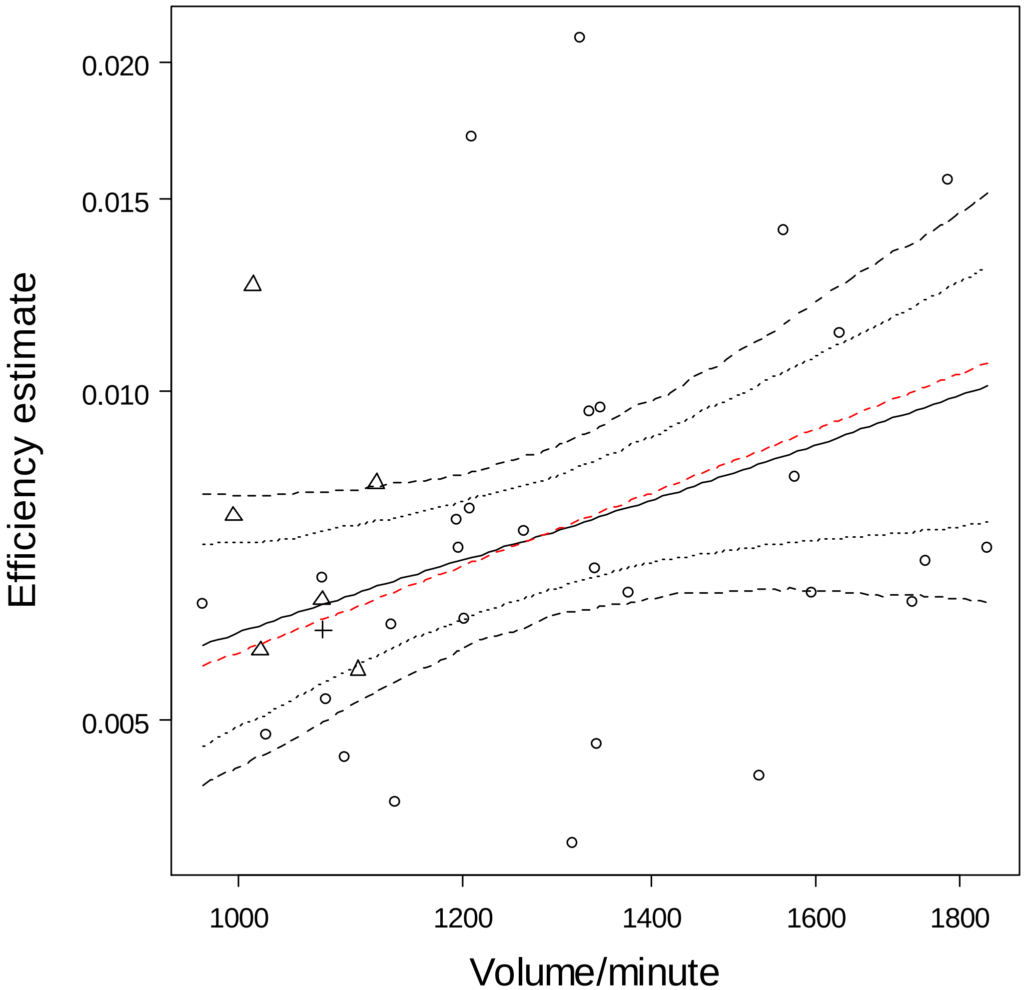


Figure 22. Model predictions (solid line) of efficiency as a function of volume/minute for the base pairing “all-upstream” dataset (Table 3) using time-based *p* to standardize efficiency estimates. Dotted and dashed lines respectively denote 80% and 95% posterior probability intervals for the fitted regression. The dashed red line depicts the hypothetical 1:1 relationship between efficiency and volume/minute sampled. Efficiency estimates by control group are shown for the mean-only model, where open circles = fall releases, triangles = late fall, and “+” = spring run.

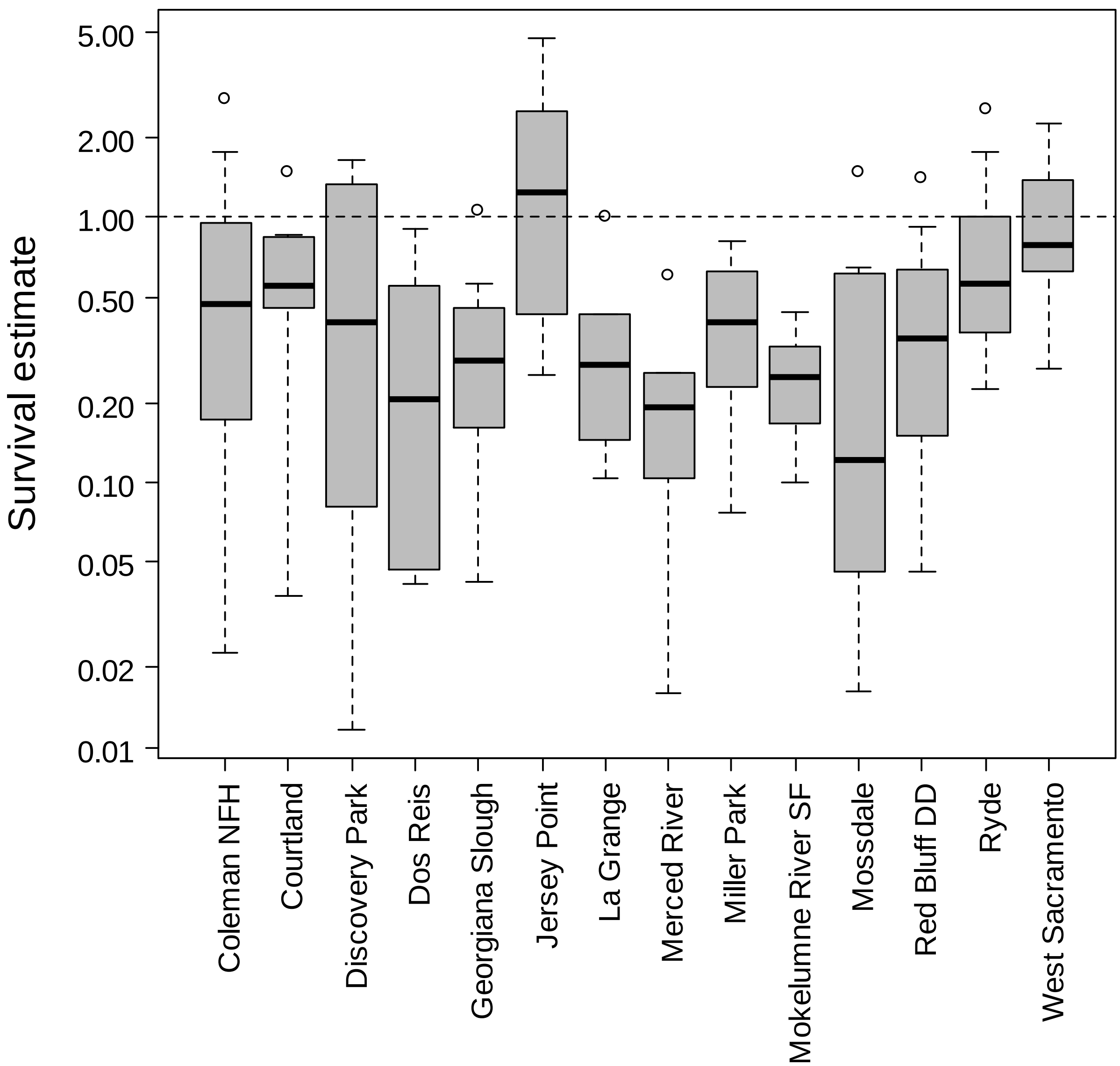


Figure 23. Boxplots of (ML) survival estimates for releases locations with five or more upstream releases. See Appendix B for map of Delta locations.

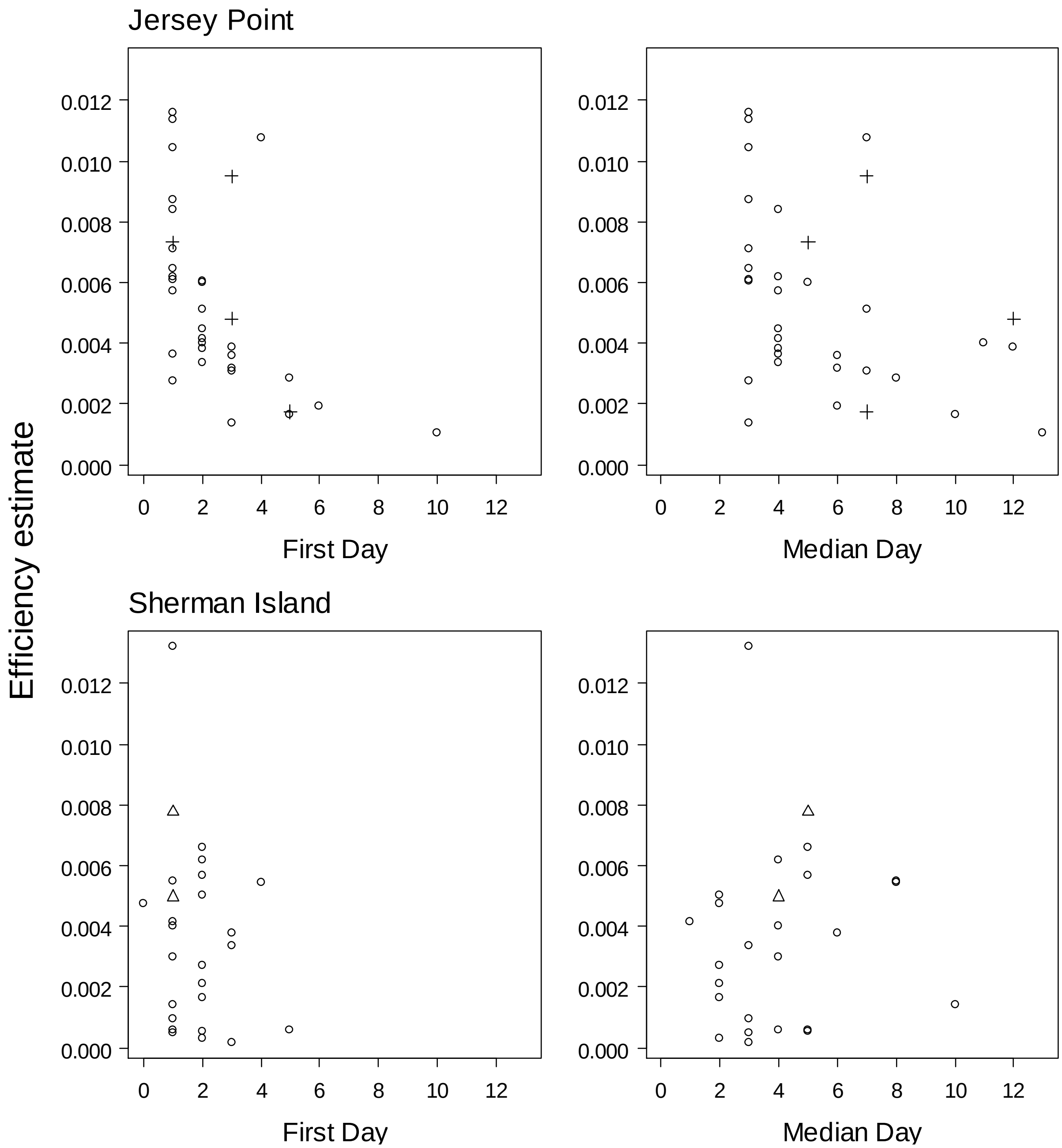


Figure 24. Efficiency estimates for Jersey Point (top row) and Sherman Island (bottom row) releases as a function of the first day (left column) and median day (right column) of capture at Chipps trawl. "+" denotes Jersey Point fall releases with high fork lengths at release; triangles denotes late-fall releases at Sherman Island.

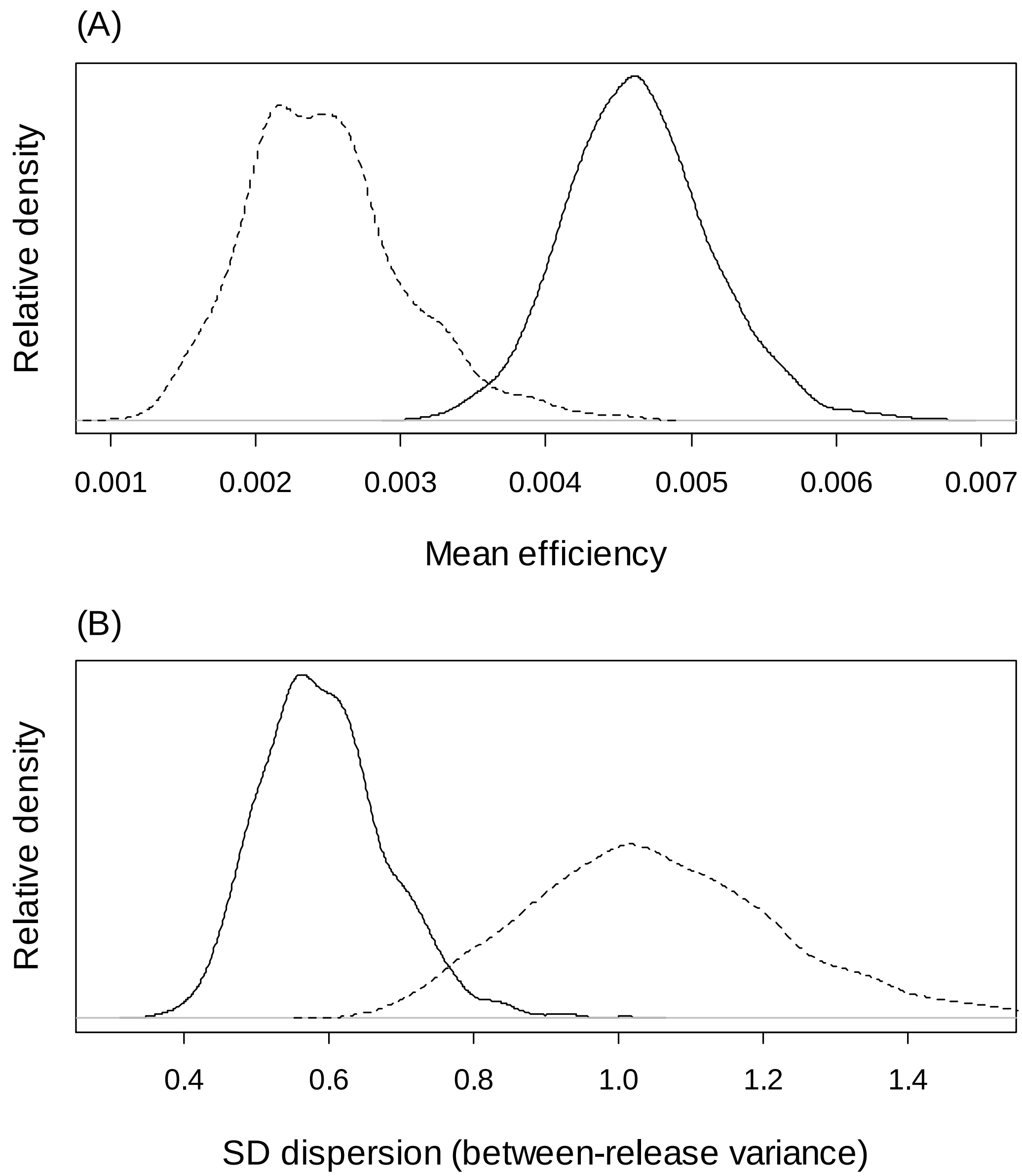


Figure 25. Posterior probability distributions (characterized by density functions) of mean efficiency (A) and SD dispersion (B) for the mean-only model fit to Jersey Point releases (solid lines) and Sherman Island releases (dashed lines).

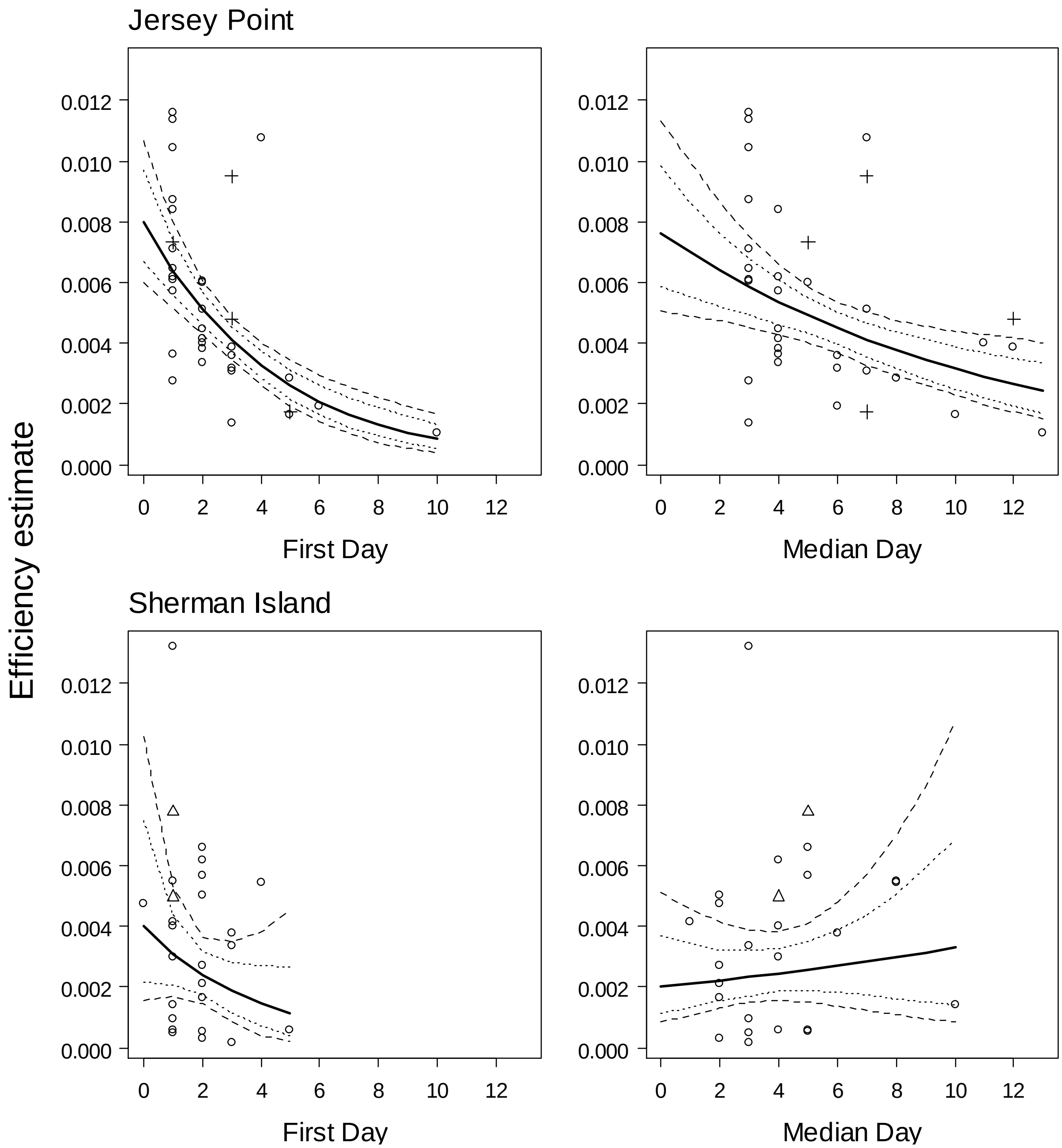


Figure 26. Model predictions (bold lines) of efficiency for Jersey Point (top row) and Sherman Island (bottom row) releases as a function of the first day (left column) and median day (right column) of capture at Chipps trawl. Dotted and dashed lines respectively denote 80% and 95% posterior probability intervals for the fitted regressions; "+" symbols denote four Jersey Point fall releases with high fork lengths at release; triangles denote late-fall releases at Sherman Island.

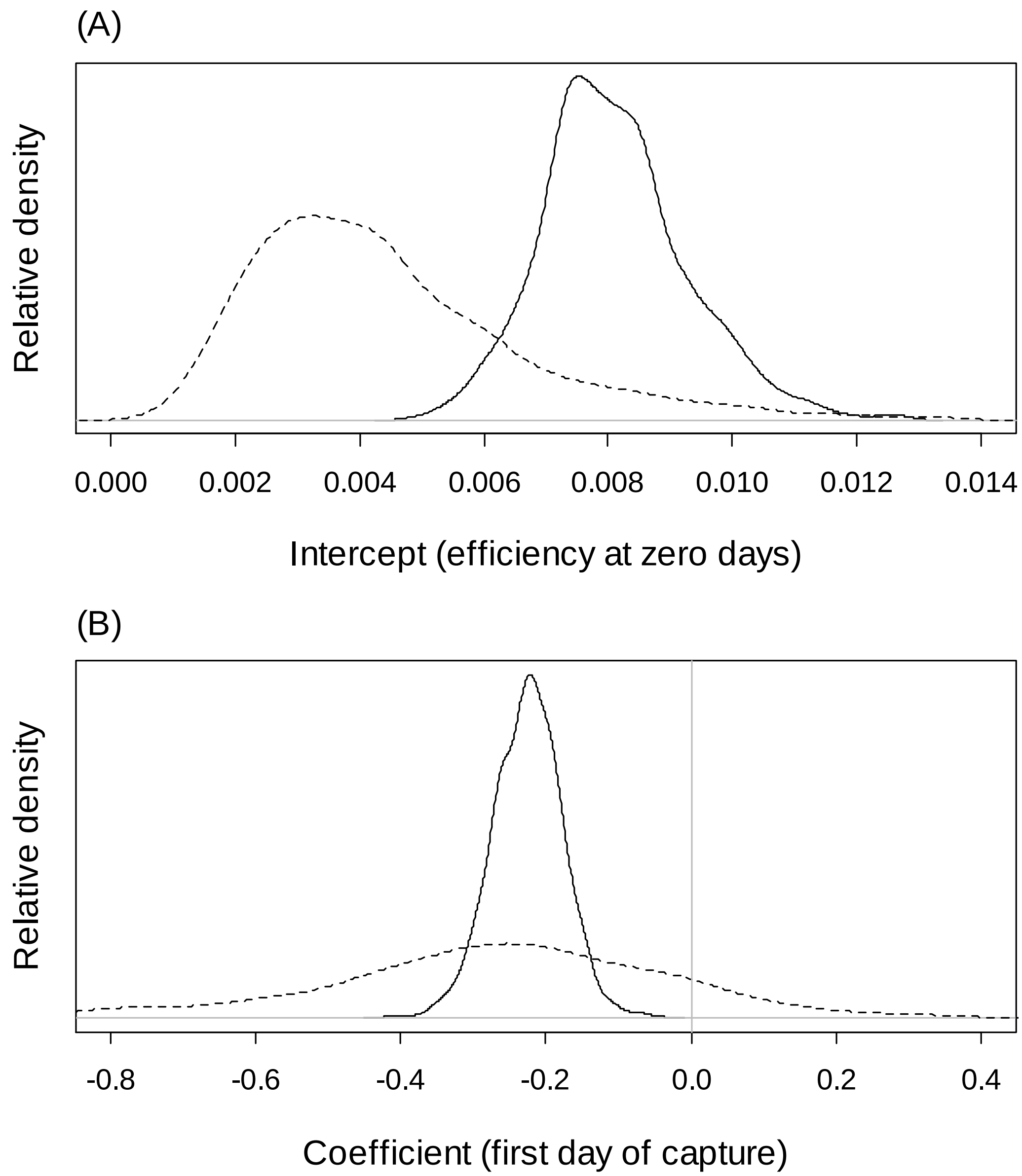


Figure 27. Posterior probability distributions (characterized by density functions) of the intercept (A) and slope coefficient (B) for first-day covariate models fit to Jersey Point releases (solid lines) and Sherman Island releases (dashed lines).

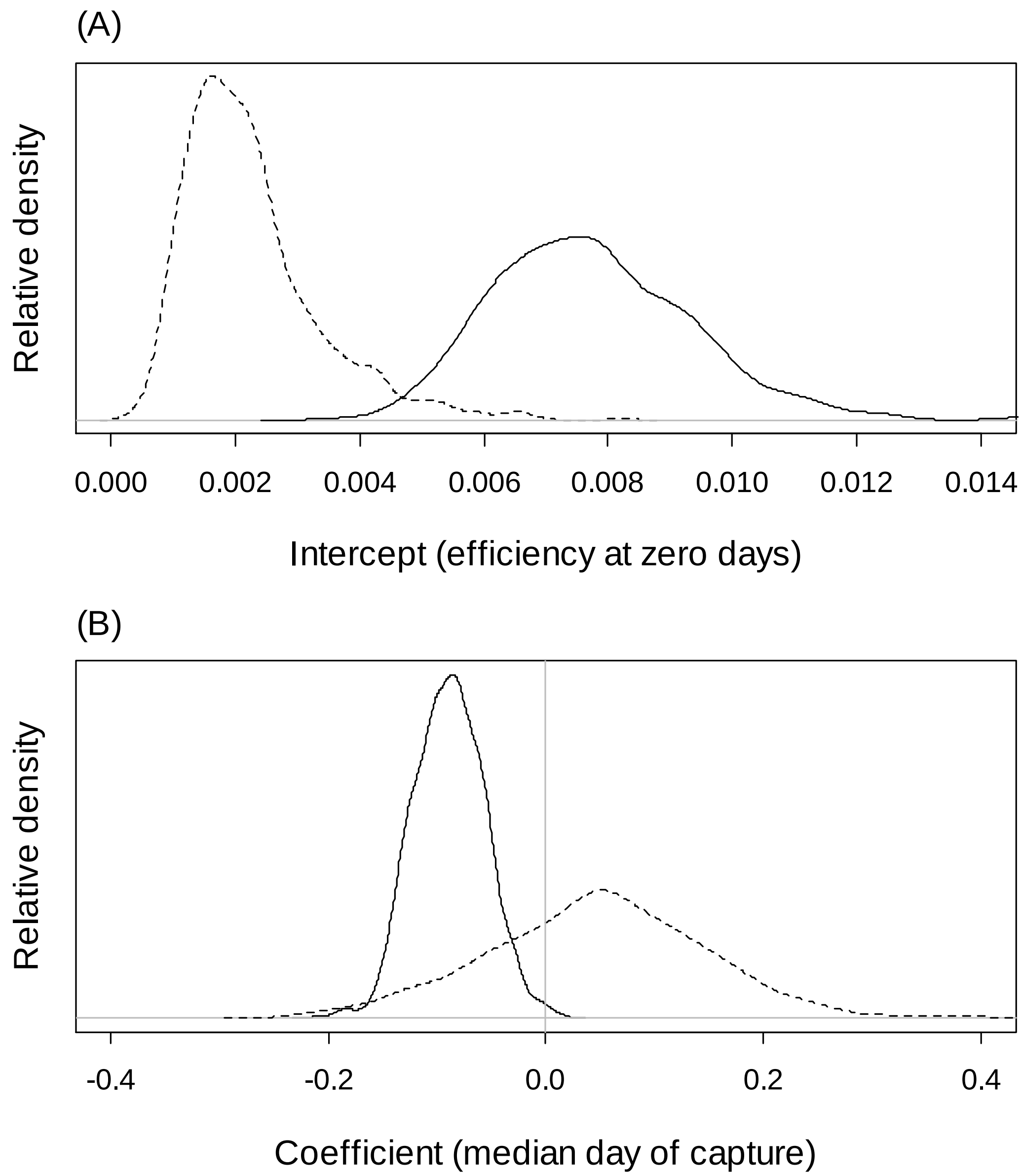


Figure 28. Posterior probability distributions (characterized by density functions) of the intercept (A) and slope coefficient (B) for median-day covariate models fit to Jersey Point releases (solid lines) and Sherman Island releases (dashed lines).

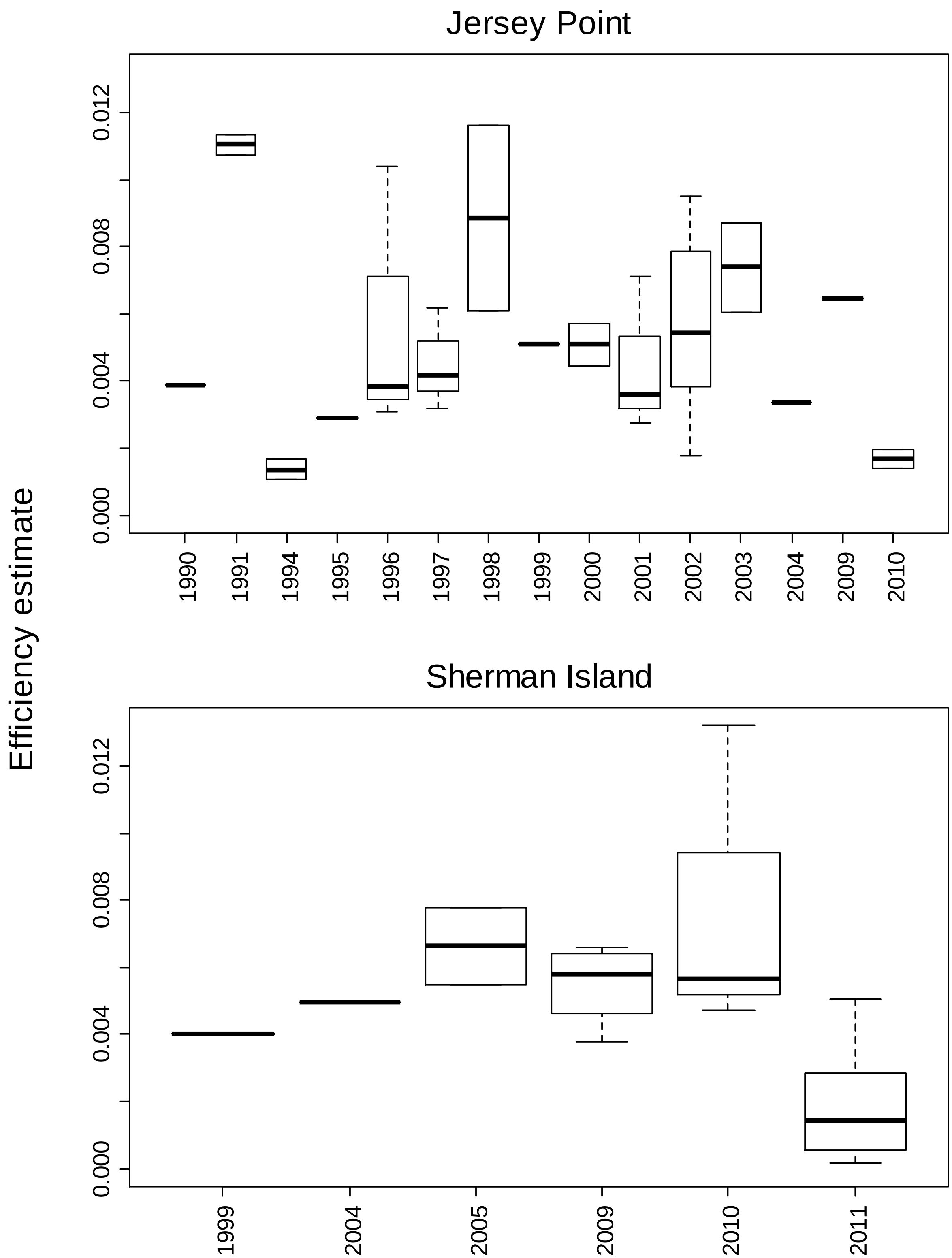


Figure 29. Boxplots of efficiency estimates by year for Jersey Point and Sherman Island releases.

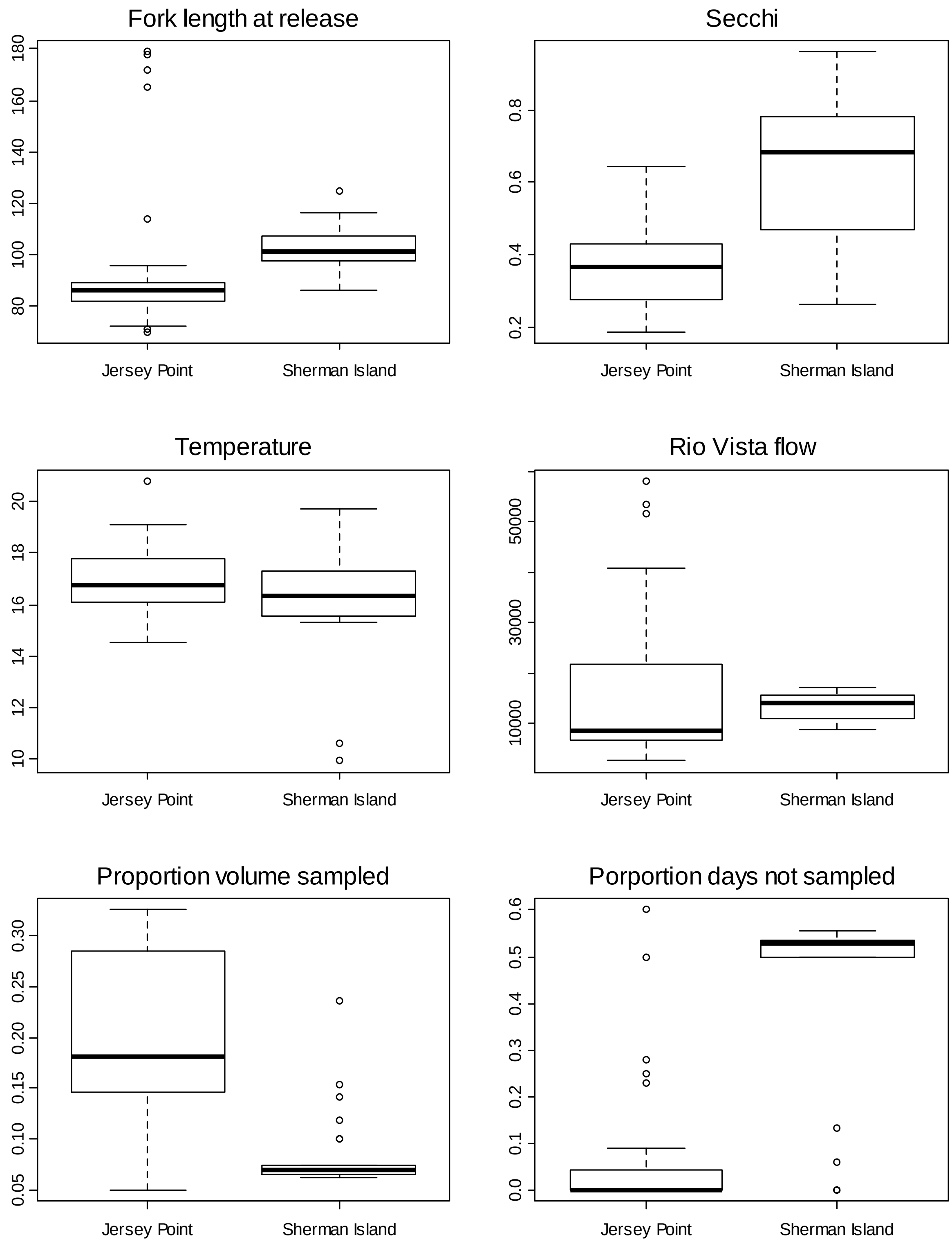


Figure 30. Boxplots of variables for Jersey Point and Sherman Island releases.

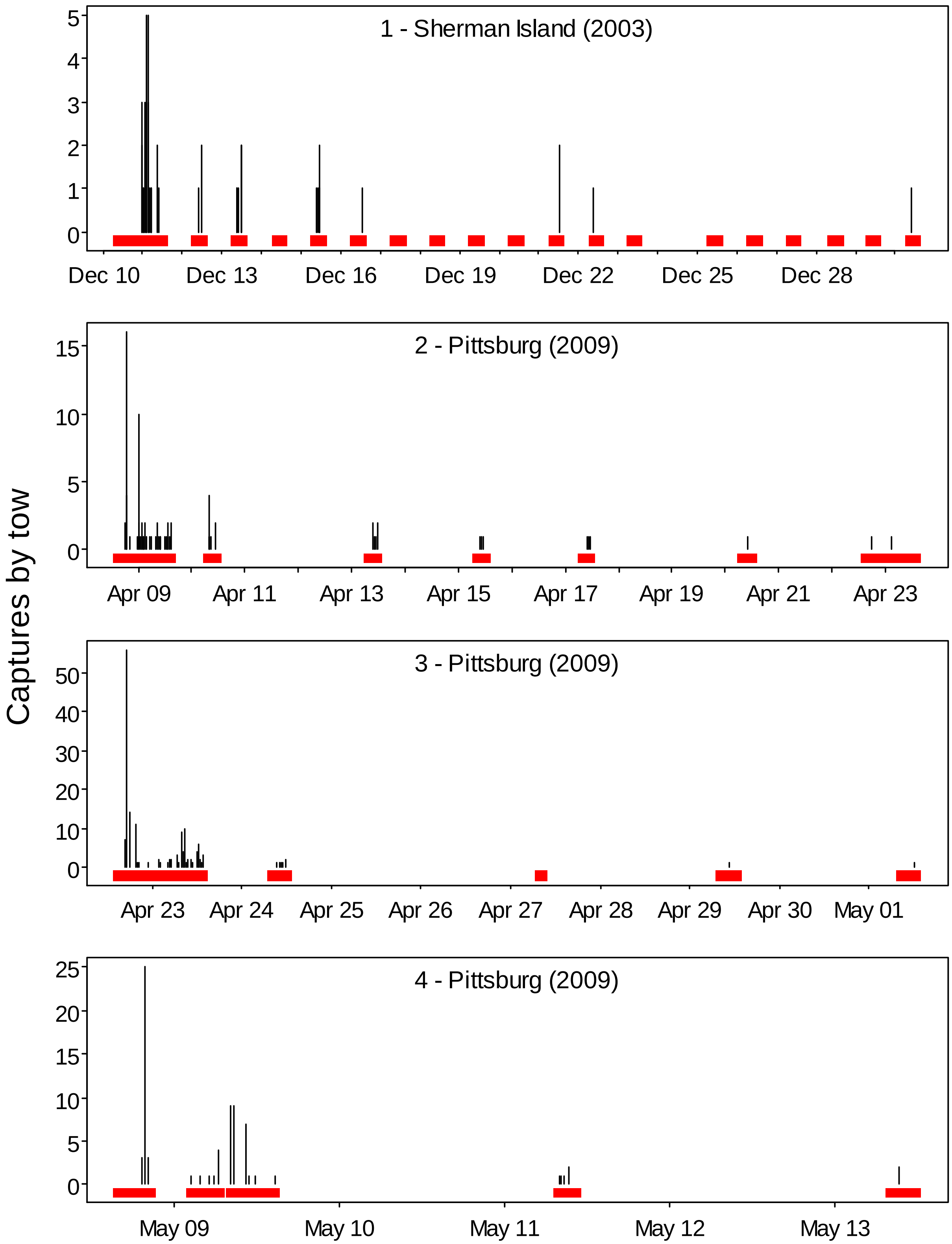


Figure 31. Captures by trawl tow across the full recovery period for the four special releases. Red bars indicate trawl sampling periods.

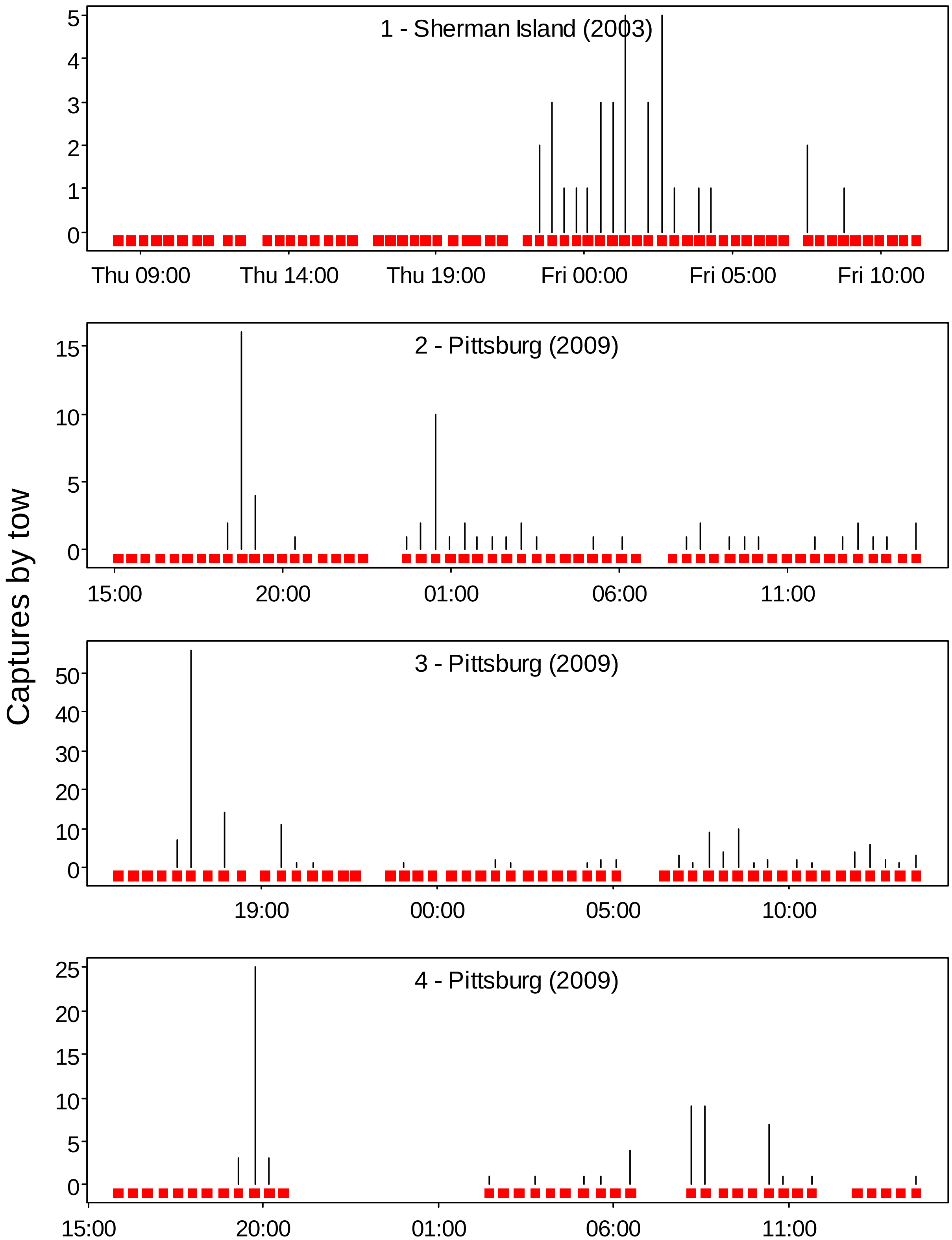


Figure 32. Captures by trawl tow during the initial intensive sampling period for the four special releases. Red squares denote approximate sample times for individual tows.

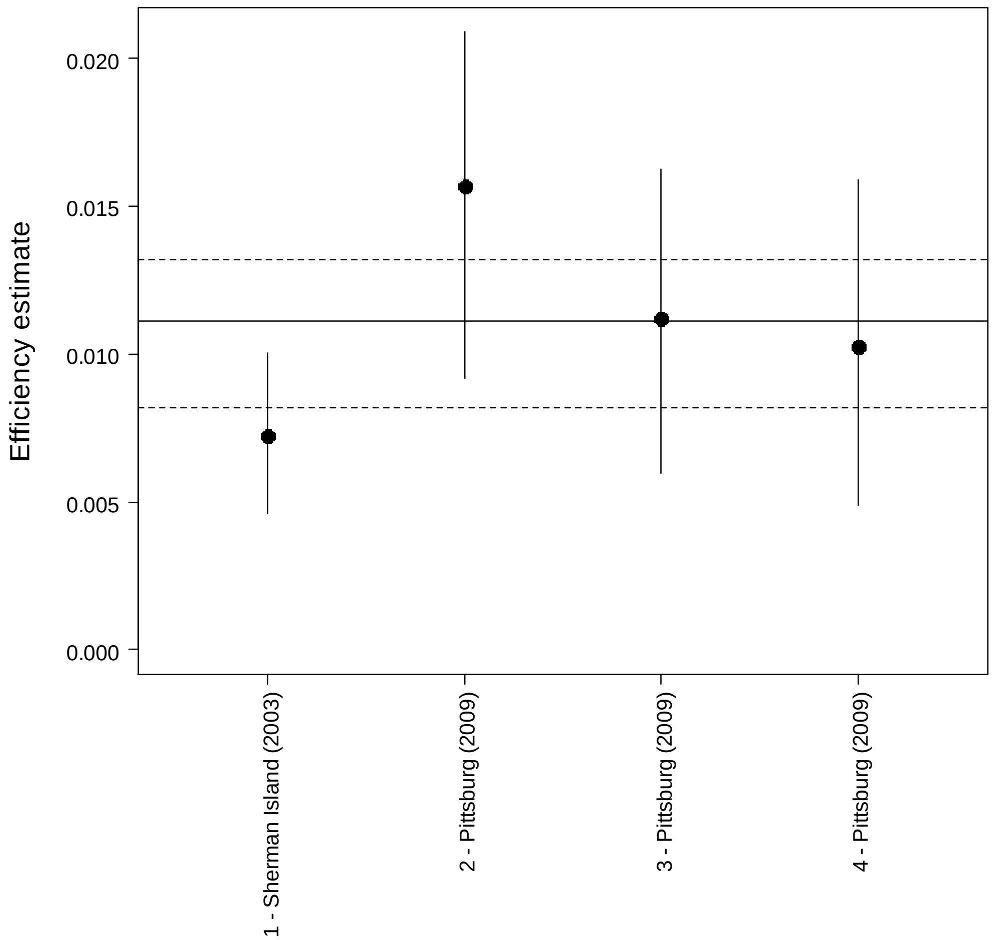


Figure 33. Efficiency estimates (*E*, based on standardized volume) for the four special releases. Error bars denote 95% bootstrap confidence intervals (see Table 21). Horizontal lines depict the mean estimate (solid) and its 95% bootstrap confidence interval (dashed).

Tables

Table 2. Summary of the initial 40 control groups considered for analysis. Shaded rows denote control groups removed in subsequent analysis. FL = average fork length (mm) at release; Base = number of upstream release groups paired with a given control; "$\hat{s}$ > 1" = number of upstream releases with ML estimates of survival rate > 1.0; "% > 1" = percentage of upstream releases with $\hat{s}$ > 1.

Control groups							Upstream releases		
Index	Name	Date	Race	Location	Number	FL	Base	$\hat{s}$ > 1	% > 1
1	79-1	6/6/1979	Fall	Port Chicago	110122	88.0	1	0	0
2	80-1	6/10/1980	Fall	Port Chicago	88700	93.0	1	0	0
3	80-2	6/13/1980	Fall	Port Chicago	79443	92.0	3	0	0
4	81-1	6/8/1981	Fall	Port Chicago	78339	90.0	5	0	0
5	82-1	5/17/1982	Fall	Port Chicago	86877	83.0	5	2	40
6	83-1	5/23/1983	Fall	Port Chicago	43374	82.0	5	3	60
7	84-1	6/29/1984	Fall	Port Chicago	42000	82.1	5	0	0
8	85-1	5/13/1985	Fall	Port Chicago	48252	78.0	1	0	0
9	86-1	6/2/1986	Fall	Port Chicago	47995	75.0	5	0	0
10	88-1	5/11/1988	Fall	Port Chicago	55265	84.0	7	2	29
11	88-2	5/17/1988	Fall	Benicia	51651	88.0	3	3	100
12	88-3	6/20/1988	Fall	Benicia	36325	99.0	1	0	0
13	88-4	6/29/1988	Fall	Port Chicago	54151	91.0	5	0	0
14	89-1	5/15/1989	Fall	Benicia	39379	73.0	2	0	0
15	89-2	6/5/1989	Fall	Port Chicago	51760	90.0	3	0	0
16	90-1	5/22/1990	Fall	Benicia	52446	84.0	4	0	0
17	90-2	6/11/1990	Fall	Benicia	47663	98.0	2	2	100
18	90-3	6/12/1990	Fall	Benicia	46156	95.0	1	1	100
19	91-1	5/13/1991	Fall	Benicia	43750	88.0	10	0	0
20	92-1	4/28/1992	Fall	Benicia	54055	80.0	10	0	0
21	94-1	5/4/1994	Fall	Benicia	102991	88.0	9	0	0
22	94-2	5/10/1994	Fall	Benicia	54297	87.0	5	0	0
23	94-3	5/31/1994	Fall	Benicia	152929	88.0	3	0	0
24	96-1	1/16/1996	LateFall	Port Chicago	34596	145.0	6	1	17
25	96-2	5/7/1996	Fall	Benicia	51288	84.0	13	0	0
26	97-1	5/5/1997	Fall	Port Chicago	48538	99.0	6	0	0
27	98-1	5/7/1998	Fall	Benicia	30558	92.1	15	3	20
28	99-1	4/26/1999	Fall	Port Chicago	51094	89.0	15	5	33
29	99-2	12/29/1999	LateFall	Port Chicago	49208	138.0	3	0	0
30	00-1	4/12/2000	Fall	Port Chicago	46934	79.0	10	6	60
31	01-1	4/27/2001	Fall	Benicia	51520	80.1	14	5	36
32	02-1	1/10/2002	LateFall	Port Chicago	47876	156.0	2	0	0
33	02-2	4/26/2002	Fall	Port Chicago	44789	95.0	12	4	33
34	02-3	12/9/2002	LateFall	Port Chicago	47048	124.0	2	0	0
35	03-1	5/1/2003	Fall	Port Chicago	50475	79.0	6	3	50
36	03-2	5/16/2003	Spring	Benicia	222500	93.2	1	0	0
37	03-3	12/11/2003	LateFall	Benicia	24785	127.0	2	0	0
38	04-1	5/3/2004	Fall	Port Chicago	49568	78.0	4	1	25
39	05-1	12/14/2005	LateFall	Port Chicago	25661	125.5	3	0	0
40	08-1	5/28/2008	Fall	Benicia	50649	85.5	5	4	80
						Total	**215**	**45**	**21**

Table 3. Summary of the eight control-upstream pairing sets for the "all-upstream" dataset (includes upstream releases with ML estimates of survival rate > 1.0). For each set, the number of upstream releases (paired with each control) is shown. Pairing criteria included (a) fish source (rearing hatchery), (b) the maximum number of days between the control-release date and the median capture date of upstream recoveries at Chipps, and (c) the maximum difference in average fork length (mm) between control releases and upstream recoveries at Chipps.

		Source:	Any				Same			
		Days:	±14		±7		±14		±7	
		FL:	±10	±5	±10	±5	±10	±5	±10	±5
Index	Control	Race	Base 1	Set 2	Set 3	Set 4	Set 5	Set 6	Set 7	Set 8
1	79-1	Fall	1	1	1	1	1	1	1	1
2	80-1	Fall	1	1	1	1	1	1	1	1
3	80-2	Fall	3	3	3	3	3	3	3	3
4	81-1	Fall	5	5	2	2	2	2	2	2
5	82-1	Fall	5	5	5	5	4	4	4	4
6	83-1	Fall	5	5	4	4	4	4	4	4
7	84-1	Fall	5	3	0	0	5	3	0	0
8	85-1	Fall	1	0	1	0	0	0	0	0
9	86-1	Fall	5	0	5	0	5	0	5	0
10	88-1	Fall	7	2	7	2	5	0	5	0
11	88-3	Fall	1	1	1	1	0	0	0	0
12	88-4	Fall	5	2	5	2	5	2	5	2
13	89-1	Fall	2	0	1	0	1	0	1	0
14	89-2	Fall	3	2	3	2	3	2	3	2
15	90-1	Fall	4	4	2	2	2	2	2	2
16	91-1	Fall	10	8	7	5	3	2	3	2
17	92-1	Fall	10	9	5	4	3	3	2	2
18	94-1	Fall	9	8	6	5	5	5	2	2
19	94-2	Fall	5	4	5	4	4	3	4	3
20	94-3	Fall	3	1	1	0	1	1	0	0
21	96-1	LateFall	6	4	4	3	6	4	4	3
22	96-2	Fall	13	9	10	7	8	5	5	3
23	97-1	Fall	6	3	5	3	5	3	4	3
24	98-1	Fall	15	10	7	2	4	2	3	1
25	99-1	Fall	15	14	11	11	3	3	3	3
26	99-2	LateFall	3	3	1	1	3	3	1	1
27	00-1	Fall	10	7	2	2	3	3	1	1
28	01-1	Fall	14	7	7	4	6	3	6	3
29	02-1	LateFall	2	0	2	0	2	0	2	0
30	02-2	Fall	12	4	8	3	1	0	0	0
31	02-3	LateFall	2	1	0	0	2	1	0	0
32	03-1	Fall	6	4	5	3	4	4	3	3
33	03-2	Spring	1	1	0	0	1	1	0	0
34	03-3	LateFall	2	1	2	1	2	1	2	1
35	04-1	Fall	4	3	4	3	2	2	2	2
36	05-1	LateFall	3	1	2	1	3	1	2	1
		Controls	**36**	**32**	**33**	**28**	**34**	**29**	**29**	**25**
		Upstream	**204**	**136**	**135**	**87**	**112**	**74**	**85**	**55**

Table 4. Summary of the eight control-upstream pairing sets for the "s < 1" dataset (excludes upstream releases with ML estimates of survival rate > 1.0). For each set, the number of upstream releases (paired with each control) is shown. Pairing criteria included (a) fish source (rearing hatchery), (b) the maximum number of days between the control-release date and the median capture date of upstream recoveries at Chipps, and (c) the maximum difference in average fork length (mm) between control releases and upstream recoveries at Chipps.

		Source:	Any				Same			
		Days:	±14		±7		±14		±7	
		FL:	±10	±5	±10	±5	±10	±5	±10	±5
Index	Control	Race	Base 1	Set 2	Set 3	Set 4	Set 5	Set 6	Set 7	Set 8
1	79-1	Fall	1	1	1	1	1	1	1	1
2	80-1	Fall	1	1	1	1	1	1	1	1
3	80-2	Fall	3	3	3	3	3	3	3	3
4	81-1	Fall	5	5	2	2	2	2	2	2
5	82-1	Fall	3	3	3	3	3	3	3	3
6	83-1	Fall	2	2	1	1	1	1	1	1
7	84-1	Fall	5	3	0	0	5	3	0	0
8	85-1	Fall	1	0	1	0	0	0	0	0
9	86-1	Fall	5	0	5	0	5	0	5	0
10	88-1	Fall	5	2	5	2	3	0	3	0
11	88-3	Fall	1	1	1	1	0	0	0	0
12	88-4	Fall	5	2	5	2	5	2	5	2
13	89-1	Fall	2	0	1	0	1	0	1	0
14	89-2	Fall	3	2	3	2	3	2	3	2
15	90-1	Fall	4	4	2	2	2	2	2	2
16	91-1	Fall	10	8	7	5	3	2	3	2
17	92-1	Fall	10	9	5	4	3	3	2	2
18	94-1	Fall	9	8	6	5	5	5	2	2
19	94-2	Fall	5	4	5	4	4	3	4	3
20	94-3	Fall	3	1	1	0	1	1	0	0
21	96-1	LateFall	5	3	3	2	5	3	3	2
22	96-2	Fall	13	9	10	7	8	5	5	3
23	97-1	Fall	6	3	5	3	5	3	4	3
24	98-1	Fall	12	8	6	2	4	2	3	1
25	99-1	Fall	10	10	9	9	2	2	2	2
26	99-2	LateFall	3	3	1	1	3	3	1	1
27	00-1	Fall	4	2	1	1	2	2	1	1
28	01-1	Fall	9	4	4	2	3	1	3	1
29	02-1	LateFall	2	0	2	0	2	0	2	0
30	02-2	Fall	8	3	5	2	1	0	0	0
31	02-3	LateFall	2	1	0	0	2	1	0	0
32	03-1	Fall	3	3	2	2	3	3	2	2
33	03-2	Spring	1	1	0	0	1	1	0	0
34	03-3	LateFall	2	1	2	1	2	1	2	1
35	04-1	Fall	3	3	3	3	2	2	2	2
36	05-1	LateFall	3	1	2	1	3	1	2	1
		Controls	**36**	**32**	**33**	**28**	**34**	**29**	**29**	**25**
		Upstream	**169**	**114**	**113**	**74**	**99**	**64**	**73**	**46**

Table 5. Total controls and upstream releases by pairing set and fish race for the "all-upstream" dataset (includes upstream releases with ML estimates of survival rate > 1.0) and "s ≤ 1" dataset (excludes upstream releases with survival estimates > 1.0). Pairing criteria included (a) fish source (rearing hatchery), (b) the maximum number of days between the control-release date and the median capture date of upstream recoveries at Chipps, and (c) the maximum difference in average fork length (mm) between control releases and upstream recoveries at Chipps.

	Pairing criteria			Control groups				Upstream releases (all $\hat{s}$)				Upstream releases ($\hat{s} \leq 1$)			
Set	Source	Days ±	FL ±	Fall	LateFall	Spring	Total	Fall	LateFall	Spring	Total	Fall	LateFall	Spring	Total
Base (1)	Any	14	10	29	6	1	**36**	185	18	1	**204**	151	17	1	**169**
2	Any	14	5	26	5	1	**32**	125	10	1	**136**	104	9	1	**114**
3	Any	7	10	28	5	0	**33**	124	11	0	**135**	103	10	0	**113**
4	Any	7	5	24	4	0	**28**	81	6	0	**87**	69	5	0	**74**
5	Same	14	10	27	6	1	**34**	93	18	1	**112**	81	17	1	**99**
6	Same	14	5	23	5	1	**29**	63	10	1	**74**	54	9	1	**64**
7	Same	7	10	24	5	0	**29**	74	11	0	**85**	63	10	0	**73**
8	Same	7	5	21	4	0	**25**	49	6	0	**55**	41	5	0	**46**

Table 6. Estimates of mean efficiency (β_0), SD efficiency (σ_E), and SD dispersion (σ_δ) for mean-only models by pairing set for (1) all races using "all-upstream" datasets (Table 3); (2) all races using the "s < 1" datasets (Table 4); and (3) fall/spring releases using all-upstream datasets. Med = posterior median; SD = standard deviation of the posterior probability distribution; e^{Med} = exp[posterior median] for mean efficiency, which gives efficiency in units of the proportion of migrating fish captured (continuous 24-hour trawling at a volume rate of 1000 m^3/minute).

	Pair	Mean efficiency			SD efficiency		SD dispersion	
Data	Set	Med	SD	e^{Med} (95% interval)	Med	SD	Med	SD
All	1	-5.16	0.09	0.0058 (0.0048, 0.0069)	0.46	0.08	0.46	0.03
	2	-5.17	0.11	0.0057 (0.0045, 0.0070)	0.50	0.09	0.46	0.04
	3	-5.18	0.10	0.0056 (0.0046, 0.0070)	0.45	0.09	0.39	0.04
	4	-5.20	0.12	0.0055 (0.0044, 0.0072)	0.51	0.10	0.34	0.05
	5	-5.21	0.10	0.0055 (0.0045, 0.0066)	0.44	0.09	0.36	0.05
	6	-5.23	0.10	0.0054 (0.0044, 0.0066)	0.44	0.10	0.35	0.06
	7	-5.18	0.09	0.0056 (0.0047, 0.0068)	0.38	0.10	0.38	0.06
	8	-5.21	0.12	0.0055 (0.0043, 0.0069)	0.41	0.13	0.43	0.09
s < 1	1	-5.28	0.11	0.0051 (0.0041, 0.0063)	0.57	0.09	0.37	0.04
	2	-5.26	0.12	0.0052 (0.0042, 0.0066)	0.57	0.10	0.33	0.04
	3	-5.28	0.11	0.0051 (0.0041, 0.0063)	0.53	0.09	0.37	0.04
	4	-5.29	0.13	0.0051 (0.0039, 0.0065)	0.58	0.11	0.32	0.06
	5	-5.27	0.10	0.0052 (0.0042, 0.0062)	0.48	0.09	0.32	0.05
	6	-5.27	0.11	0.0051 (0.0042, 0.0064)	0.45	0.10	0.29	0.07
	7	-5.24	0.10	0.0053 (0.0044, 0.0065)	0.42	0.11	0.34	0.06
	8	-5.25	0.11	0.0052 (0.0042, 0.0066)	0.42	0.14	0.36	0.09
Fall/	1	-5.18	0.10	0.0056 (0.0046, 0.0069)	0.47	0.09	0.46	0.04
spring	2	-5.19	0.12	0.0056 (0.0044, 0.0070)	0.54	0.10	0.48	0.05
	3	-5.20	0.11	0.0055 (0.0044, 0.0070)	0.51	0.11	0.39	0.04
	4	-5.21	0.14	0.0055 (0.0042, 0.0072)	0.55	0.11	0.36	0.05
	5	-5.26	0.11	0.0052 (0.0042, 0.0064)	0.46	0.11	0.35	0.05
	6	-5.27	0.12	0.0051 (0.0041, 0.0065)	0.45	0.12	0.40	0.08
	7	-5.20	0.11	0.0055 (0.0044, 0.0068)	0.42	0.11	0.38	0.06
	8	-5.24	0.14	0.0053 (0.0040, 0.0069)	0.44	0.16	0.46	0.10

Table 7. Estimates of coefficients (β_1) and SD efficiency (σ_E) for single-covariate models by pairing set for "all-upstream" datasets (Table 3). Med = posterior median; SD = standard deviation of the posterior probability distribution. Shaded cells denote lower percentiles that exceed zero (no effect). The coefficient for "race" reflects the difference between late-fall releases compared to fall/spring releases (proportional difference = exp[β_1]); all other covariates were standardized to have a mean of zero and a standard deviation of one.

Pair	Covariate	Coefficient β_1		Lower percentiles (β_1)			Upper percentiles (β_1)			SD efficiency	
set	model	Med	SD	2.5	5.0	10.0	90.0	95.0	97.5	Med	SD
1	Race	0.24	0.27	-0.27	-0.19	-0.11	0.58	0.65	0.77	0.46	0.08
	Length	0.06	0.10	-0.12	-0.09	-0.05	0.19	0.23	0.27	0.46	0.09
	Secchi	0.15	0.09	-0.03	0.00	0.03	0.26	0.29	0.32	0.43	0.08
	Temperature	-0.06	0.10	-0.26	-0.23	-0.19	0.06	0.10	0.14	0.46	0.09
	Flow (Rio)	0.07	0.09	-0.12	-0.09	-0.05	0.19	0.22	0.24	0.46	0.09
2	Race	0.15	0.34	-0.52	-0.40	-0.27	0.58	0.70	0.84	0.52	0.09
	Length	0.03	0.12	-0.20	-0.16	-0.12	0.18	0.22	0.26	0.52	0.10
	Secchi	0.19	0.12	-0.03	0.00	0.04	0.35	0.39	0.42	0.48	0.09
	Temperature	-0.03	0.13	-0.29	-0.24	-0.19	0.13	0.18	0.23	0.52	0.09
	Flow (Rio)	0.04	0.11	-0.19	-0.14	-0.10	0.19	0.23	0.27	0.52	0.10
3	Race	0.16	0.30	-0.45	-0.38	-0.24	0.53	0.62	0.71	0.46	0.09
	Length	0.05	0.10	-0.15	-0.11	-0.07	0.20	0.23	0.26	0.47	0.09
	Secchi	0.17	0.10	-0.02	0.01	0.05	0.29	0.34	0.36	0.43	0.09
	Temperature	0.00	0.11	-0.22	-0.17	-0.14	0.14	0.19	0.21	0.47	0.09
	Flow (Rio)	0.05	0.10	-0.15	-0.11	-0.07	0.18	0.22	0.27	0.46	0.09
4	Race	0.15	0.39	-0.62	-0.47	-0.34	0.62	0.74	0.91	0.54	0.10
	Length	0.01	0.13	-0.24	-0.19	-0.14	0.18	0.22	0.27	0.53	0.11
	Secchi	0.17	0.13	-0.07	-0.03	0.03	0.34	0.39	0.44	0.50	0.10
	Temperature	0.02	0.13	-0.24	-0.19	-0.14	0.18	0.24	0.27	0.53	0.11
	Flow (Rio)	-0.02	0.12	-0.25	-0.21	-0.17	0.12	0.18	0.22	0.53	0.10
5	Race	0.32	0.25	-0.18	-0.11	-0.01	0.63	0.72	0.80	0.44	0.09
	Length	0.07	0.10	-0.11	-0.08	-0.05	0.19	0.23	0.27	0.44	0.09
	Secchi	0.12	0.09	-0.06	-0.04	0.00	0.23	0.26	0.29	0.41	0.10
	Temperature	-0.05	0.09	-0.23	-0.21	-0.17	0.06	0.10	0.14	0.45	0.09
	Flow (Rio)	0.05	0.10	-0.13	-0.10	-0.07	0.18	0.21	0.24	0.45	0.09
6	Race	0.23	0.28	-0.32	-0.20	-0.10	0.61	0.71	0.82	0.45	0.10
	Length	0.03	0.11	-0.19	-0.15	-0.10	0.17	0.21	0.26	0.44	0.10
	Secchi	0.15	0.12	-0.08	-0.04	0.00	0.29	0.32	0.37	0.42	0.11
	Temperature	-0.01	0.11	-0.23	-0.20	-0.16	0.12	0.17	0.20	0.45	0.12
	Flow (Rio)	0.00	0.11	-0.22	-0.18	-0.14	0.14	0.18	0.21	0.45	0.10
7	Race	0.18	0.26	-0.34	-0.25	-0.16	0.49	0.59	0.68	0.38	0.10
	Length	0.04	0.10	-0.15	-0.12	-0.08	0.18	0.22	0.24	0.39	0.11
	Secchi	0.18	0.09	-0.01	0.03	0.07	0.29	0.32	0.34	0.32	0.10
	Temperature	-0.02	0.10	-0.21	-0.18	-0.14	0.11	0.15	0.18	0.38	0.10
	Flow (Rio)	0.05	0.10	-0.16	-0.12	-0.07	0.17	0.20	0.22	0.38	0.10
8	Race	0.18	0.35	-0.54	-0.41	-0.27	0.62	0.76	0.87	0.43	0.13
	Length	0.01	0.12	-0.23	-0.19	-0.14	0.16	0.20	0.24	0.43	0.14
	Secchi	0.22	0.12	-0.01	0.04	0.07	0.37	0.41	0.45	0.34	0.15
	Temperature	0.01	0.13	-0.24	-0.20	-0.15	0.17	0.22	0.27	0.43	0.15
	Flow (Rio)	0.01	0.12	-0.25	-0.18	-0.14	0.16	0.21	0.26	0.43	0.15

Table 8. Estimates of coefficients (β_1) and SD efficiency (σ_E) for single-covariate models by pairing set for "s < 1" datasets (Table 4). Med = posterior median; SD = standard deviation of the posterior probability distribution. Shaded cells highlight lower percentiles that exceed zero (no effect). The coefficient for "race" reflects the difference between late-fall releases compared to fall/spring releases (proportional difference = exp[β_1]); all other covariates were standardized to have a mean of zero and a standard deviation of one.

Pair	Covariate	Coefficient β_1		Lower percentiles (β_1)			Upper percentiles (β_1)			SD efficiency	
Set	Model	Med	SD	2.5	5.0	10.0	90.0	95.0	97.5	Med	SD
1	Race	0.37	0.31	-0.23	-0.13	-0.02	0.77	0.86	0.99	0.57	0.09
	Length	0.12	0.11	-0.10	-0.06	-0.02	0.26	0.30	0.33	0.56	0.09
	Secchi	0.16	0.11	-0.04	-0.01	0.02	0.30	0.33	0.37	0.53	0.09
	Temperature	-0.05	0.11	-0.29	-0.24	-0.21	0.10	0.13	0.16	0.58	0.09
	Flow (Rio)	0.08	0.11	-0.12	-0.08	-0.06	0.21	0.25	0.28	0.57	0.09
2	Race	0.29	0.33	-0.35	-0.27	-0.13	0.73	0.83	0.91	0.58	0.10
	Length	0.06	0.12	-0.17	-0.13	-0.09	0.21	0.25	0.28	0.58	0.10
	Secchi	0.22	0.12	-0.03	0.01	0.06	0.37	0.41	0.46	0.54	0.10
	Temperature	-0.02	0.13	-0.28	-0.24	-0.19	0.12	0.18	0.21	0.58	0.10
	Flow (Rio)	0.01	0.12	-0.24	-0.19	-0.14	0.16	0.21	0.24	0.58	0.10
3	Race	0.27	0.33	-0.38	-0.28	-0.15	0.69	0.79	0.87	0.54	0.10
	Length	0.10	0.11	-0.13	-0.07	-0.04	0.23	0.28	0.31	0.54	0.10
	Secchi	0.19	0.11	0.00	0.04	0.08	0.34	0.39	0.42	0.50	0.10
	Temperature	0.01	0.12	-0.24	-0.21	-0.16	0.15	0.20	0.25	0.55	0.10
	Flow (Rio)	0.06	0.11	-0.17	-0.13	-0.10	0.19	0.23	0.28	0.56	0.10
4	Race	0.29	0.38	-0.48	-0.37	-0.22	0.77	0.90	0.99	0.59	0.11
	Length	0.04	0.14	-0.22	-0.17	-0.12	0.21	0.28	0.32	0.59	0.11
	Secchi	0.22	0.13	-0.03	0.01	0.06	0.39	0.45	0.50	0.55	0.10
	Temperature	0.03	0.14	-0.25	-0.20	-0.14	0.20	0.25	0.30	0.59	0.11
	Flow (Rio)	-0.06	0.13	-0.32	-0.28	-0.23	0.11	0.18	0.21	0.59	0.11
5	Race	0.39	0.26	-0.08	-0.02	0.07	0.73	0.80	0.89	0.47	0.10
	Length	0.10	0.10	-0.09	-0.06	-0.02	0.23	0.26	0.29	0.47	0.10
	Secchi	0.10	0.10	-0.10	-0.07	-0.03	0.22	0.27	0.30	0.46	0.10
	Temperature	-0.06	0.10	-0.26	-0.23	-0.19	0.07	0.10	0.14	0.48	0.10
	Flow (Rio)	0.03	0.10	-0.17	-0.15	-0.10	0.15	0.19	0.23	0.48	0.10
6	Race	0.30	0.29	-0.24	-0.16	-0.05	0.67	0.78	0.93	0.46	0.10
	Length	0.06	0.11	-0.14	-0.12	-0.07	0.21	0.25	0.28	0.46	0.10
	Secchi	0.09	0.12	-0.14	-0.09	-0.06	0.23	0.27	0.32	0.45	0.11
	Temperature	-0.02	0.11	-0.25	-0.21	-0.17	0.12	0.16	0.20	0.46	0.11
	Flow (Rio)	-0.05	0.11	-0.27	-0.24	-0.19	0.09	0.12	0.15	0.46	0.10
7	Race	0.26	0.27	-0.30	-0.21	-0.09	0.58	0.68	0.76	0.41	0.10
	Length	0.07	0.10	-0.13	-0.09	-0.06	0.20	0.23	0.25	0.42	0.11
	Secchi	0.16	0.10	-0.05	-0.02	0.02	0.28	0.31	0.34	0.39	0.11
	Temperature	-0.02	0.10	-0.22	-0.18	-0.15	0.11	0.15	0.19	0.42	0.11
	Flow (Rio)	0.02	0.10	-0.19	-0.16	-0.12	0.15	0.18	0.21	0.41	0.11
8	Race	0.21	0.35	-0.47	-0.34	-0.19	0.67	0.78	0.90	0.43	0.16
	Length	0.02	0.12	-0.20	-0.17	-0.13	0.17	0.22	0.30	0.40	0.17
	Secchi	0.16	0.13	-0.08	-0.05	0.00	0.31	0.36	0.40	0.37	0.16
	Temperature	-0.01	0.12	-0.26	-0.21	-0.17	0.16	0.20	0.23	0.42	0.15
	Flow (Rio)	-0.05	0.12	-0.28	-0.25	-0.20	0.10	0.14	0.19	0.43	0.13

Table 9. Estimates of coefficients (β_1) and SD efficiency (σ_E) for single-covariate models fit to only fall/spring releases (all-upstream datasets; Table 4). Med = posterior median; SD = standard deviation of the posterior probability distribution. Shaded cells highlight lower percentiles that exceed zero (no effect).

Pair	Covariate	Coefficient β_1		Lower percentiles (β_1)			Upper percentiles (β_1)			SD efficiency	
Set	Model	Med	SD	2.5	5.0	10.0	90.0	95.0	97.5	Med	SD
1	Length	-0.01	0.12	-0.24	-0.19	-0.15	0.14	0.18	0.22	0.49	0.10
	Secchi	0.18	0.10	-0.01	0.02	0.05	0.30	0.34	0.37	0.43	0.09
	Temperature	0.05	0.11	-0.15	-0.13	-0.09	0.19	0.23	0.26	0.49	0.09
	Flow (Rio)	0.05	0.11	-0.15	-0.12	-0.08	0.18	0.23	0.27	0.48	0.09
2	Length	-0.02	0.13	-0.29	-0.25	-0.20	0.14	0.20	0.23	0.56	0.11
	Secchi	0.17	0.13	-0.08	-0.04	0.00	0.32	0.36	0.41	0.51	0.11
	Temperature	0.08	0.13	-0.18	-0.14	-0.09	0.24	0.29	0.33	0.55	0.11
	Flow (Rio)	0.04	0.13	-0.22	-0.17	-0.11	0.20	0.25	0.28	0.56	0.11
3	Length	0.02	0.12	-0.22	-0.18	-0.13	0.18	0.23	0.27	0.52	0.11
	Secchi	0.16	0.11	-0.06	-0.01	0.03	0.30	0.34	0.36	0.47	0.11
	Temperature	0.10	0.11	-0.12	-0.08	-0.04	0.24	0.29	0.34	0.51	0.11
	Flow (Rio)	0.02	0.11	-0.21	-0.16	-0.12	0.16	0.20	0.23	0.52	0.11
4	Length	-0.04	0.14	-0.31	-0.26	-0.21	0.14	0.19	0.23	0.55	0.12
	Secchi	0.11	0.13	-0.15	-0.11	-0.06	0.27	0.32	0.36	0.54	0.13
	Temperature	0.15	0.14	-0.12	-0.08	-0.03	0.31	0.37	0.42	0.54	0.12
	Flow (Rio)	-0.03	0.13	-0.26	-0.23	-0.18	0.13	0.18	0.25	0.57	0.12
5	Length	-0.11	0.11	-0.33	-0.29	-0.25	0.02	0.06	0.10	0.46	0.10
	Secchi	0.15	0.10	-0.08	-0.01	0.02	0.27	0.31	0.34	0.42	0.11
	Temperature	0.17	0.11	-0.05	-0.01	0.04	0.31	0.36	0.41	0.45	0.10
	Flow (Rio)	-0.04	0.10	-0.23	-0.20	-0.16	0.10	0.14	0.17	0.47	0.10
6	Length	-0.11	0.12	-0.35	-0.31	-0.26	0.04	0.08	0.13	0.45	0.12
	Secchi	0.11	0.13	-0.13	-0.10	-0.05	0.27	0.31	0.35	0.45	0.13
	Temperature	0.17	0.12	-0.07	-0.02	0.02	0.32	0.37	0.42	0.44	0.12
	Flow (Rio)	-0.02	0.12	-0.27	-0.24	-0.18	0.12	0.16	0.20	0.47	0.13
7	Length	-0.07	0.11	-0.30	-0.26	-0.22	0.07	0.11	0.16	0.43	0.11
	Secchi	0.17	0.10	-0.04	0.01	0.05	0.28	0.32	0.36	0.37	0.12
	Temperature	0.11	0.12	-0.12	-0.08	-0.04	0.27	0.31	0.36	0.44	0.12
	Flow (Rio)	0.00	0.12	-0.24	-0.20	-0.15	0.14	0.18	0.23	0.45	0.11
8	Length	-0.10	0.13	-0.36	-0.32	-0.26	0.06	0.13	0.17	0.42	0.17
	Secchi	0.16	0.13	-0.09	-0.05	0.00	0.32	0.36	0.40	0.40	0.18
	Temperature	0.13	0.15	-0.12	-0.09	-0.04	0.32	0.38	0.43	0.44	0.15
	Flow (Rio)	0.05	0.14	-0.25	-0.20	-0.13	0.21	0.26	0.32	0.43	0.17

Table 10. Estimates of coefficients (β_1) and SD efficiency (σ_E) for single-covariate models fit to the base pairing "all-upstream" dataset (Table 3) when using time-based *p* instead volume-based *p* to standardize efficiency estimates across paired-release tests. Med = posterior median; SD = standard deviation of the posterior probability distribution. Shaded cells highlight lower percentiles that exceed zero (no effect). The coefficient for "race" reflects the difference between late-fall releases compared to fall/spring releases (proportional difference = exp[β_1]); all other covariates were standardized to have a mean of zero and a standard deviation of one.

Covariate	Coefficient β_1		Lower percentiles (β_1)			Upper percentiles (β_1)			SD efficiency	
Model	Med	SD	2.5	5.0	10.0	90.0	95.0	97.5	Med	SD
Race	0.02	0.27	-0.51	-0.43	-0.31	0.38	0.45	0.55	0.50	0.09
Length	0.00	0.10	-0.21	-0.18	-0.15	0.12	0.17	0.20	0.49	0.09
Secchi	0.13	0.10	-0.07	-0.03	0.00	0.26	0.29	0.32	0.47	0.08
Temperature	0.05	0.11	-0.16	-0.12	-0.08	0.18	0.21	0.26	0.49	0.09
Flow (Rio)	0.02	0.10	-0.17	-0.14	-0.11	0.15	0.20	0.25	0.50	0.09
Volume/min.	0.16	0.10	-0.05	-0.02	0.03	0.27	0.30	0.33	0.46	0.08

Table 11. Summary of Jersey Point releases (all fall-run) used in the proximal-release analysis. FL = fork length (mm); First day = number of days from release to first capture at Chipps; Median day = number of days from release to median day of capture at Chipps; Duration = number of days from first to last capture at Chipps (capture period); NS = number of days not sampled within the capture period; *p* = estimate of the proportion volume sampled across the capture period (standardized to a volume rate of 1000 m^3/minute); *E* = efficiency estimate.

Release	Release date	Number released	FL	First day	Median day	Duration	NS	Catch	*p*	*E*
1	4/18/1990	52962	71	3	12	24	1	32	0.156	0.0039
2	4/19/1991	52139	82	4	7	25	0	94	0.168	0.0107
3	5/13/1991	49184	86	1	3	10	0	89	0.159	0.0114
4	4/13/1994	50689	72	10	13	11	0	10	0.187	0.0011
5	4/27/1994	53810	78	5	10	21	0	16	0.180	0.0017
6	4/19/1995	50779	70	5	8	18	0	26	0.178	0.0029
7	4/18/1996	50041	78	3	7	44	2	25	0.161	0.0031
8	5/3/1996	97010	82	2	4	18	0	63	0.169	0.0038
9	5/20/1996	103221	93	1	3	10	0	195	0.181	0.0104
10	4/30/1997	104000	73	2	4	10	0	63	0.146	0.0042
11	5/2/1997	101437	87	1	4	17	0	82	0.130	0.0062
12	5/12/1997	47534	74	3	6	11	1	18	0.119	0.0032
13	4/20/1998	50271	89	1	3	13	0	184	0.315	0.0116
14	4/28/1998	134597	83	1	3	16	0	253	0.309	0.0061
15	4/21/1999	49460	81	2	7	17	0	59	0.234	0.0051
16	4/20/2000	51351	82	2	4	11	0	65	0.284	0.0045
17	5/1/2000	151845	83	1	4	16	0	247	0.285	0.0057
18	4/24/2001	102953	86	3	6	14	1	88	0.237	0.0036
19	5/4/2001	49437	88	1	3	7	0	111	0.316	0.0071
20	5/11/2001	51376	88	1	3	11	0	44	0.309	0.0028
21	4/9/2002	51261	87	2	11	23	0	59	0.286	0.0040
22	4/22/2002	48930	84	2	5	20	0	83	0.282	0.0060
23	4/23/2002	50745	96	1	4	13	0	125	0.293	0.0084
24	4/30/2002	46912	82	1	4	19	0	46	0.270	0.0036
25	10/7/2002	25981	165	3	7	61	14	27	0.109	0.0095
26	10/15/2002	25811	172	1	5	19	0	28	0.148	0.0073
27	10/23/2002	25240	179	3	12	54	15	12	0.099	0.0048
28	10/30/2002	25912	178	5	7	6	0	6	0.133	0.0017
29	4/25/2003	24650	89	1	3	12	0	57	0.265	0.0087
30	5/2/2003	25951	88	2	3	9	0	39	0.249	0.0060
31	4/26/2004	22911	85	2	4	6	0	25	0.325	0.0034
32	5/12/2009	32978	87	1	3	8	4	16	0.075	0.0065
33	5/25/2010	115922	114	3	3	5	3	8	0.050	0.0014
34	5/26/2010	49291	89	6	6	4	1	11	0.114	0.0020

Table 12. Summary of Sherman Island releases used in the proximal-release analysis. FL = fork length (mm); First day = number of days from release to first capture at Chipps; Median day = number of days from release to median day of capture at Chipps; Duration = number of days from first to last capture at Chipps (capture period); NS = number of days not sampled within the capture period; *p* = estimate of the proportion volume sampled across the capture period (standardized to a volume rate of 1000 m^3/minute); *E* = efficiency estimate.

Release	Release date	Race	Number released	FL	First day	Median day	Duration	NS	Catch	*p*	*E*
1	5/21/1999	Fall	202168	86	1	4	15	2	115	0.142	0.0040
2	12/10/2004	LateFall	25558	116	1	4	17	1	15	0.118	0.0050
3	4/22/2005	Fall	52483	94	1	8	25	0	68	0.236	0.0055
4	12/12/2005	LateFall	24986	125	1	5	11	0	30	0.154	0.0078
5	5/13/2009	Fall	53369	110	2	5	18	10	23	0.065	0.0066
6	5/14/2009	Fall	100433	111	4	8	15	8	37	0.068	0.0054
7	5/26/2009	Fall	71587	110	3	6	8	4	17	0.063	0.0038
8	6/8/2009	Fall	24911	105	2	4	17	9	11	0.071	0.0062
9	4/21/2010	Fall	385466	98	2	5	27	15	146	0.067	0.0057
10	4/26/2010	Fall	295317	92	0	2	29	16	94	0.067	0.0047
11	6/1/2010	Fall	1113944	114	1	3	15	8	963	0.065	0.0132
12	4/21/2011	Fall	98081	103	1	4	13	7	19	0.065	0.0030
13	4/22/2011	Fall	99610	100	3	3	15	8	22	0.066	0.0033
14	4/26/2011	Fall	211296	98	1	3	13	7	7	0.066	0.0005
15	4/27/2011	Fall	98227	98	5	5	8	4	4	0.071	0.0006
16	5/7/2011	Fall	100585	100	2	2	15	8	35	0.069	0.0050
17	5/8/2011	Fall	100898	99	1	1	10	5	30	0.072	0.0041
18	5/9/2011	Fall	111036	98	2	2	10	5	22	0.073	0.0027
19	5/10/2011	Fall	98545	108	1	3	15	8	6	0.065	0.0009
20	5/11/2011	Fall	101186	107	2	5	6	3	4	0.075	0.0005
21	5/12/2011	Fall	98175	100	1	4	11	6	4	0.070	0.0006
22	5/21/2011	Fall	141940	98	2	2	15	8	19	0.064	0.0021
23	5/22/2011	Fall	95800	98	1	10	19	10	9	0.066	0.0014
24	5/24/2011	Fall	105389	107	3	3	1	0	2	0.100	0.0002
25	5/25/2011	Fall	30912	107	2	2	1	0	1	0.100	0.0003
26	6/8/2011	Fall	108396	107	2	2	6	3	13	0.073	0.0017

Table 13. Estimates of the intercept (exp[β_0]) and SD dispersion (σ_δ) for proximal-release models by dataset (Jersey Point and Sherman Island). Med = posterior median; SD = standard deviation of the posterior probability distribution.

		$e^{\beta 0}$	Lower percentiles ($e^{\beta 0}$)			Upper percentiles ($e^{\beta 0}$)			SD dispersion	
Dataset	Model	Med	2.5%	5.0%	10.0%	90.0%	95.0%	97.5%	Med	SD
Jersey Point	Mean	0.0046	0.0037	0.0038	0.0040	0.0053	0.0055	0.0057	0.59	0.09
	First day	0.0080	0.0060	0.0063	0.0067	0.0097	0.0102	0.0107	0.43	0.07
	Median day	0.0076	0.0051	0.0054	0.0059	0.0098	0.0107	0.0113	0.52	0.08
Sherman Island	Mean	0.0024	0.0015	0.0017	0.0018	0.0032	0.0034	0.0038	1.04	0.18
	First day	0.0040	0.0016	0.0018	0.0021	0.0075	0.0089	0.0103	1.05	0.20
	Median day	0.0020	0.0009	0.0010	0.0011	0.0037	0.0043	0.0051	1.07	0.19

Table 14. Estimates of the slope coefficient (β_1) for proximal-release models by dataset (Jersey Point and Sherman Island). Med = posterior median; SD = standard deviation of the posterior probability distribution.

				Lower percentiles			Upper percentiles		
Data	Model	Med	SD	2.5%	5.0%	10.0%	90.0%	95.0%	97.5%
Jersey Point	First day	-0.22	0.05	-0.32	-0.30	-0.29	-0.17	-0.15	-0.13
	Median day	-0.09	0.03	-0.15	-0.14	-0.13	-0.05	-0.03	-0.03
Sherman Island	First day	-0.25	0.23	-0.78	-0.69	-0.57	0.02	0.10	0.18
	Median day	0.05	0.10	-0.16	-0.12	-0.08	0.17	0.21	0.24

Table 15. Summary of special releases. NS = number of days not sampled within the capture period.

Release	Date	Location	Number released	Intensive sampling period: First tow	Last tow	Tows	Capture period: Days	NS
1	12/11/2003	Sherman Is.	25956	08:16 12/11	11:11 12/12	61	21	1
2	4/8/2009	Pittsburg	29830	15:07 4/8	14:48 4/9	54	16	7
3	4/22/2009	Pittsburg	34339	14:56 4/22	13:37 4/23	50	10	4
4	5/8/2009	Pittsburg	32055	15:52 5/8	14:37 5/9	36	6	2

Table 16. Trawl data for the first special release (Sherman Island, 12/11/2003). CPUE = catch per minute at a standardized volume-sampled rate of 1000 m^3/min. Estimated Catch (= Period Minutes x CPUE) is an estimate of catch under continuous trawling. For days with no trawl sampling (shaded rows), CPUE was estimated by linear interpolation.

Day	Period Minutes	Tows	Minutes Fished	Volume (m^3)	V/Min	Observed Catch	CPUE	Estimated Catch
12/11/2003	543[a]	21	420	478648	1140	30	0.063	34.0
12/12/2003	927[b]	10	200	197580	988	3	0.015	14.1
12/13/2003	1440	10	200	220643	1103	3	0.014	19.6
12/14/2003	1440	10	200	200108	1001	7	0.035	50.4
12/15/2003	1440	10	200	224328	1122	0	0.000	0.0
12/16/2003	1440	10	200	203965	1020	5	0.025	35.3
12/17/2003	1440	10	200	179380	897	1	0.006	8.0
12/18/2003	1440	10	200	199220	996	0	0.000	0.0
12/19/2003	1440	10	200	198004	990	0	0.000	0.0
12/20/2003	1440	10	200	223222	1116	0	0.000	0.0
12/21/2003	1440	10	200	207933	1040	0	0.000	0.0
12/22/2003	1440	10	200	214502	1073	2	0.009	13.4
12/23/2003	1440	10	200	223734	1119	1	0.004	6.4
12/24/2003	1440	10	190	176191	927	0	0.000	0.0
12/25/2003	1440	0					0.000	0.0
12/26/2003	1440	10	200	190932	955	0	0.000	0.0
12/27/2003	1440	10	200	201318	1007	0	0.000	0.0
12/28/2003	1440	10	200	204961	1025	0	0.000	0.0
12/29/2003	1440	10	200	215427	1077	0	0.000	0.0
12/30/2003	1440	10	200	190167	951	0	0.000	0.0
12/31/2003	1440	10	200	206539	1033	1	0.005	7.0
Total						**53**		**188.2**

[a] Time from tow with first capture to end of "Tows" (intensive sampling; includes tows in next day)
[b] Time from start of final 10 tows in intensive-sampling period to end of day.

Table 17. Trawl data for the second special release (Pittsburg, 4/8/2009). CPUE = catch per minute at a standardized volume-sampled rate of 1000 m^3/min. Estimated Catch (= Period Minutes x CPUE) is an estimate of catch under continuous trawling. For days with no trawl sampling (shaded rows), CPUE was estimated by linear interpolation.

Day	Period Minutes	Tows	Minutes Fished	Volume (m^3)	V/Min	Observed Catch	CPUE	Estimated Catch
4/8/2009	997[a]	36	720	685977	953	53	0.077	77.0
4/9/2009	782[b]	10	200	204025	1020	8	0.039	30.7
4/10/2009	1440	13	200	192726	964	9	0.047	67.2
4/11/2009	1440	0					0.041	59.1
4/12/2009	1440	0					0.035	51.0
4/13/2009	1440	13	200	201329	1007	6	0.030	42.9
4/14/2009	1440	0					0.021	30.6
4/15/2009	1440	13	200	235930	1180	3	0.013	18.3
4/16/2009	1440	0					0.014	20.2
4/17/2009	1440	13	200	195994	980	3	0.015	22.0
4/18/2009	1440	0					0.012	17.1
4/19/2009	1440	0					0.008	12.2
4/20/2009	1440	13	200	197400	987	1	0.005	7.3
4/21/2009	1440	0					0.004	5.5
4/22/2009	1440	20	390	395875	1015	1	0.003	3.6
4/23/2009	1440	30	600	581538	969	1	0.002	2.5
Total						**85**		**467.4**

[a] Time from tow with first capture to end of “Tows” (intensive sampling; includes tows in next day)
[b] Time from start of final 10 tows in intensive-sampling period to end of day.

Table 18. Trawl data for the third special release (Pittsburg, 4/22/2009). CPUE = catch per minute at a standardized volume-sampled rate of 1000 m^3/min. Estimated Catch (= Period Minutes x CPUE) is an estimate of catch under continuous trawling. For days with no trawl sampling (shaded rows), CPUE was estimated by linear interpolation.

Day	Period Minutes	Tows	Minutes Fished	Volume (m^3)	V/Min	Observed Catch	CPUE	Estimated Catch
4/22/2009	1033[a]	36	710	700869	987	129	0.184	190.1
4/23/2009	851[b]	10	200	193572	968	19	0.098	83.5
4/24/2009	1440	13	200	202827	1014	6	0.030	42.6
4/25/2009	1440	0					0.020	28.4
4/26/2009	1440	0					0.010	14.2
4/27/2009	1440	3	40	40460	1011	0	0.000	0.0
4/28/2009	1440	0					0.003	3.6
4/29/2009	1440	13	200	199375	997	1	0.005	7.2
4/30/2009	1440	0					0.005	7.3
5/1/2009	1440	13	200	196531	983	1	0.005	7.3
Total						**156**		**384.3**

[a] Time from tow with first capture to end of “Tows” (intensive sampling; includes tows in next day)
[b] Time from start of final 10 tows in intensive-sampling period to end of day.

Table 19. Trawl data for the fourth special release (Pittsburg, 5/8/2009). CPUE = catch per minute at a standardized volume-sampled rate of 1000 m^3/min. Estimated Catch (= Period Minutes x CPUE) is an estimate of catch under continuous trawling. For days with no trawl sampling (shaded rows), CPUE was estimated by linear interpolation.

Day	Period Minutes	Tows	Minutes Fished	Volume (m^3)	V/Min	Observed Catch	CPUE	Estimated Catch
5/8/2009	880[a]	18	360	344713	958	57	0.165	145.5
5/9/2009	843[b]	10	200	220766	1104	10	0.045	38.2
5/10/2009	1440	0					0.039	56.0
5/11/2009	1440	10	140	153900	1099	5	0.032	46.8
5/12/2009	1440	0					0.021	29.8
5/13/2009	1440	10	200	223770	1119	2	0.009	12.9
Total						**74**		**329.2**

[a] Time from tow with first capture to end of "Tows" (intensive sampling; includes tows in next day)
[b] Time from start of final 10 tows in intensive-sampling period to end of day.

Table 20. Estimates of catch (Est. C; for continuous trawling), proportion of migration sampled (*p*), and trawl efficiency (*E*) for the special release. Estimates are provided for two approaches, either assuming catch is proportional to volume fished (standardized to a volume rate of 1000 m^3/minute) or trawl time (minutes fished).

					Estimates using volume			Estimates using time		
Rel.	Date	Location	Number	Catch	Est. C	*p*	*E*	Est. C	*p*	*E*
1	12/11/03	Sherman	25956	53	188.2	0.282	0.0073	196.7	0.269	0.0076
2	4/8/09	Pittsburg	29830	85	467.4	0.182	0.0157	465.4	0.183	0.0156
3	4/22/09	Pittsburg	34339	156	384.3	0.406	0.0112	380.1	0.410	0.0111
4	5/8/09	Pittsburg	32055	74	329.2	0.225	0.0103	341.9	0.216	0.0107
Mean		**All**					**0.0111**			**0.0112**
		Pittsburg					**0.0124**			**0.0124**

Table 21. Summary of bootstrap distributions (*b*) for estimates of efficiency (*E*, based on standardized volume) for each special release and mean estimates across releases (all releases or Pittsburg only).

				Lower percentiles (*b*)			Upper percentiles (*b*)		
Release	*E*	Mean(*b*)	SD(*b*)	2.5	5.0	10.0	90.0	95.0	97.5
1-Sherman	0.0073	0.0072	0.0014	0.0046	0.0051	0.0055	0.0090	0.0095	0.0100
2-Pittsburg	0.0157	0.0147	0.0030	0.0092	0.0101	0.0110	0.0184	0.0197	0.0209
3-Pittsburg	0.0112	0.0104	0.0027	0.0060	0.0065	0.0072	0.0139	0.0152	0.0163
4-Pittsburg	0.0103	0.0098	0.0029	0.0049	0.0055	0.0062	0.0136	0.0149	0.0159
Mean-All	0.0111	0.0105	0.0013	0.0082	0.0085	0.0089	0.0122	0.0127	0.0132
Mean-Pitt.	0.0124	0.0116	0.0016	0.0087	0.0090	0.0095	0.0116	0.0137	0.0144

Appendix A: Statistical derivation of efficiency estimates

In this section, we outline the assumptions and derivations for estimators of trawl efficiency based on a single paired-release test in which one control (downstream release) is paired with one upstream release. The control release provides the basis for estimating the survival rate of the upstream group from point of release to passage at Chipps trawl, which in turn allows estimation of trawl efficiency. Throughout this report, we define trawl efficiency as the proportion of available fish (i.e., potentially vulnerable fish that are occupying the channel trawl zone when sampling occurs) that are captured when the trawl is operating, which is consistent with previous analyses (e.g., USFWS 2006). Given assumptions of randomness, this is equivalent to defining efficiency as the proportion of all fish surviving to and migrating past Chipps Island trawl that would be captured if the trawl operated continuously.

For our purposes, it was sufficient to develop approximate estimators for efficiency and variance, which were used primarily in exploratory analyses. We note instances where additional complexity could be considered, though these comments are by no means exhaustive.

Define as follows:

R = number of CWT fish released (subscript 1 = upstream, 2 = control)
r = number of actual ocean recoveries of R
x = number of observed ocean recoveries of R
q = probability of a fish (either an upstream release that passes Chipps Island or a control release) being captured in ocean fisheries (function of marine survival, ocean distribution, harvest rates)
f = overall fraction of catch sampled for CWTs in ocean fisheries
s = survival rate of upstream fish from point of release to Chipps Island trawl
N = total number of upstream fish passing Chipps Island trawl
n = number of upstream fish captured by Chipps Island trawl
E = trawl efficiency (proportion of available fish captured when the trawl is operating)
p = proportion of time (or standardized volume) trawled

Note that we use subscripts (1 = upstream, 2 = control) for variables that apply to both groups (R, r, x, q, f), but we do not subscript those that apply only to the upstream release (s, N, n).

In this paired-release design, the observed variables are the upstream captures at Chipps trawl (n) and observed ocean recoveries (x_1, x_2). Quantities that are known (or assumed known) include release numbers (R_1, R_2), sampling fractions for ocean fisheries (f_1, f_2), and the proportion (p) of time or volume trawled during the period in which upstream releases migrate past Chipps trawl (computational details for p are discussed in the Methods section). The unknown quantities of primary interest are the upstream survival rate (s) and trawl efficiency (E).

In past applications (e.g., USFWS 2006), equations for efficiency estimation have used expanded ocean recoveries ($\hat{r} = \sum x_k/f_k$ across fishery strata k). Here, we define equations in terms of total observed ocean recoveries (x) rather than expanded recoveries to make explicit that uncertainty accrues from the actual observations (x). In reality, observed CWT recoveries occur in numerous ocean fisheries (area and time strata k) with differing sampling fractions, and such complexity could be incorporated. However, as a reasonable approximation, we treated the ocean fisheries as a collective unit, with an overall "known" sampling fraction (f) equal to the ratio of reported totals of observed and expanded recoveries across fisheries (i.e., $f = x/\hat{r}$). Differences in sampling fractions between upstream (f_1) and control (f_2) groups are assumed real but incidental, that is, they do not affect the validity of the assumption (discussed below) that ocean capture probabilities are equal ($q_1 = q_2$).

We adopt the standard assumptions that all fish of a given release (upstream or control) are independent and have equal probabilities of survival and capture (at Chipps trawl or in the ocean). Given these assumptions, we could specify the following binomial distributions for variables of upstream releases (with theoretical expectations and variances denoted by E[ ] and V[ ]):

$$
\begin{array}{lll}
N \sim \text{binomial}(R_1, s) & \text{E}[N] = R_1 s & \text{V}[N] = R_1 s(1 - s) \\
n \sim \text{binomial}(N, Ep) & \text{E}[n] = NEp & \text{V}[n] = NEp(1 - Ep) \\
r_1 \sim \text{binomial}(N - n, q_1) & \text{E}[r_1] = (N - n)q_1 & \text{V}[r_1] = (N - n)q_1(1 - q_1) \\
x_1 \sim \text{binomial}(r_1, f_1) & \text{E}[x_1] = r_1 f_1 & \text{V}[x_1] = r_1 f_1(1 - f_1);
\end{array}
$$

and similarly, for control releases:

$$
\begin{array}{lll}
r_2 \sim \text{binomial}(R_2, q_2) & \text{E}[r_1] = R_2 q_2 & \text{V}[r_2] = R_2 q_2(1 - q_2) \\
x_2 \sim \text{binomial}(r_2, f_2) & \text{E}[x_2] = r_2 f_2 & \text{V}[x_2] = r_2 f_2(1 - f_2)
\end{array}
$$

We do not discuss these distributions further because we can obtain adequate estimators by further simplification. Specifically, because trawl capture rates (Ep) and ocean recovery rates (qf) are very low, such that $(n, x_1) << (N, R_1)$ and $x_2 << R_2$, we can ignore the "binomial" nature of processes leading to the observations (n, x_1, x_2) and assume instead that they follow Poisson distributions (this simplification has trivial consequences for estimators):

$$
\text{(A1)} \qquad
\begin{array}{lll}
n \sim \text{Poisson}(R_1 sEp) & \text{E}[n] = R_1 sEp & \text{V}[n] = R_1 sEp \\
x_1 \sim \text{Poisson}(R_1 sq_1 f_1) & \text{E}[x_1] = R_1 sq_1 f_1 & \text{V}[x_1] = R_1 sq_1 f_1 \\
x_2 \sim \text{Poisson}(R_2 q_2 f_2) & \text{E}[x_2] = R_2 q_2 f_2 & \text{V}[x_2] = R_2 q_2 f_2
\end{array}
$$

The key assumption of paired-release design is that control fish (R_2) and upstream fish that migrate past Chipps Island trawl ($N = R_1 s$) have the same probability of being captured in ocean fisheries (i.e., $q_1 = q_2$). That is, they have identical marine survival rates, ocean distributions, and harvest rates, or some combination of these processes that yields a ratio of expanded ocean recoveries (r_1/r_2) equal to the ratio of their initial abundances (N/R_2). This assumption ($q_1 = q_2$) allows estimation of the upstream survival rate, s. For example, using the "method of moments" (Mood et al. 1974, p. 274), we can solve for, and equate, q_1 and q_2 from the definitions of $\text{E}[x_1]$ and $\text{E}[x_2]$ in Equation (A1):

$$
\text{(A2)} \qquad \frac{\text{E}[x_1]}{R_1 s f_1} = \frac{\text{E}[x_2]}{R_2 f_2} \ .
$$

Solving for s in Equation (A2) and substituting the observed recoveries (x_1, x_2) for (E[x_1], E[x_2]) gives the following estimate for s:

(A3) $$\hat{s} = \frac{x_1 f_2 R_2}{x_2 f_1 R_1} \;.$$

Given this estimate of s, we can similarly derive an estimate for trawl efficiency (E) based on the definition of E[n] in Equation (A1):

(A4) $$\hat{E} = \frac{n}{R_1 \hat{s} p} = \frac{n x_2 f_1}{x_1 f_2 R_2 p} \;.$$

These estimators for s and E are equivalent to the maximum-likelihood (ML) estimators that would be derived via the likelihood functions of the Poisson distributions in Equation (A1).

The estimator for s is based on a ratio of two random variables (x_1/x_2), while the estimator for E is both a product and ratio of random variables (nx_2/x_1). Accordingly, the following variance estimators for estimates of s and E can be derived based on approximate (Delta method) variance formulas for ratios and products of independent random variables (e.g., Mood et al. 1974, p. 180):

(A5) $$\hat{\sigma}^2_{\hat{s}} \cong \hat{s}^2\left(\frac{1}{x_1} + \frac{1}{x_2}\right),$$

(A6) $$\hat{\sigma}^2_{\hat{E}} \cong \hat{E}^2\left(\frac{1}{n} + \frac{1}{x_2} + \frac{1}{x_1}\right).$$

In addition, because estimates of s and E are based on ratios, they may be biased, in particular when expected numbers of observed ocean recoveries (x) are low. Specifically, the Delta method provides the approximate expectation of a ratio of two independent random variables X and Y (Mood et al. 1974, p. 181):

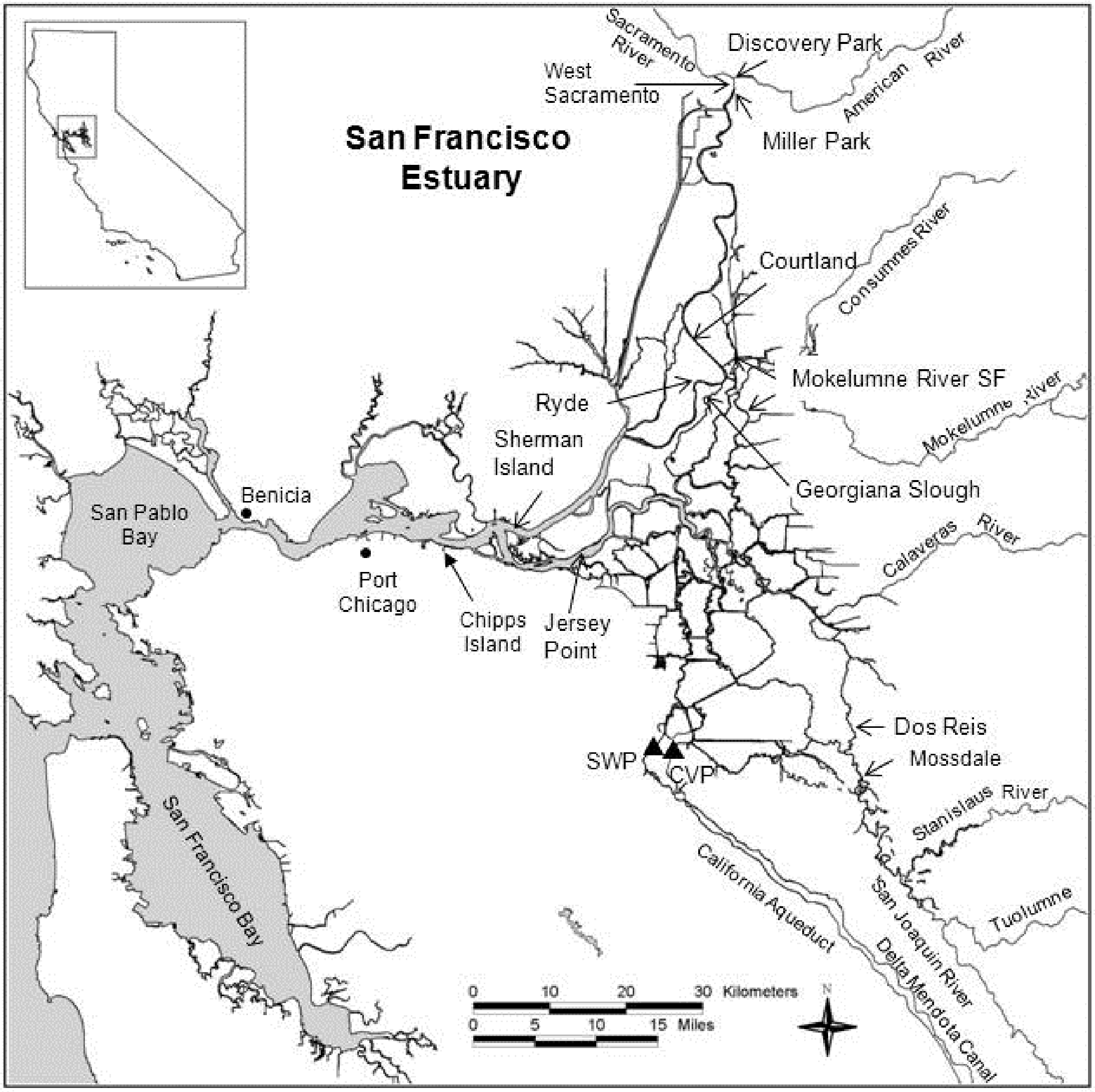
(A7) $$E\left[\frac{X}{Y}\right] \cong \frac{E[X]}{E[Y]}\left(1 + \frac{\mathrm{V}[Y]}{E[Y]^2}\right) \;.$$

We are interested in estimating the ratio of true means, E[X]/E[Y], but the expected value of our estimators will be biased high with approximate bias equal to the right-hand term in Equation (A7). Thus, to obtain approximately unbiased estimators, referred to here as “bias-corrected” estimates, we subtract the relevant right-hand terms instead. For example, in the case of s (Equation A3), the denominator variable (Y) is x_2, and V[x_2]/E[x_2]^2 is equal to 1/E[x_2] based on the definitions in Equation (A1). We substitute the observation x_2 for E[x_2], and multiply our original estimator for s by ($1 - 1/x_2$). This process leads to the following bias-corrected estimates for s and E:

(A8) $$\hat{s}' = \hat{s}\left(1 - \frac{1}{x_2}\right) = \frac{x_1 f_2 R_2}{x_2 f_1 R_1}\left(1 - \frac{1}{x_2}\right) = \frac{x_1 (x_2 - 1) f_2 R_2}{x_2^2 f_1 R_1} \ ,$$

(A9) $$\hat{E}' = \hat{E}\left(1 - \frac{1}{x_1}\right) = \frac{n x_2 f_1}{x_1 f_2 R_2 p}\left(1 - \frac{1}{x_1}\right) = \frac{n x_2 (x_1 - 1) f_1}{x_1^2 f_2 R_2 p} \ .$$

These bias-corrected estimates were validated using simulations, but as we report in the Results section, differences between the ML and bias-corrected estimates were typically minimal. In addition, simulations confirmed that the approximate variance estimators (Equations A5 and A6) were very accurate for conditions typical of the data we examined (including when all processes were modeled using the binomial distributions presented above). However, as discussed in the main text, there are several potential shortcomings of the estimators described here.



Appendix B: Map of coded-wire-tag release sites in the San Francisco Estuary, California.