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Complete List of Authors:	Michel, Cyril; University of California-Santa Cruz, Institute of Marine Sciences; National Marine Fisheries Service, Southwest Fisheries Science Center Ammann, Arnold; National Marine Fisheries Service, Southwest Fisheries Science Center Lindley, Steven; National Marine Fisheries Service, Southwest Fisheries Science Center Sandstrom, Philip; University of California - Davis, Department of Wildlife, Fish, & Conservation Biology Chapman, Eric; University of California - Davis, Department of Wildlife, Fish, & Conservation Biology Thomas, Michael; University of California - Davis, Department of Wildlife, Fish, & Conservation Biology Singer, Gabriel; University of California - Davis, Department of Wildlife, Fish, & Conservation Biology Klimley, A.; University of California - Davis, Department of Wildlife, Fish, & Conservation Biology MacFarlane, R. Bruce; National Marine Fisheries Service, Southwest Fisheries Science Center
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Chinook salmon outmigration survival in wet and dry years in California's Sacramento River

Cyril J. Michel[1], Arnold J. Ammann[2], Steven T. Lindley[2], Philip T. Sandstrom[3,4], Eric D. Chapman[3], Michael J. Thomas[3], Gabriel P. Singer[3], A. Peter Klimley[3], R. Bruce MacFarlane[2]

Corresponding author:
C. J. Michel
Fisheries Ecology Division
Southwest Fisheries Science Center
NOAA National Marine Fisheries Service
110 Shaffer Rd
Santa Cruz, CA 95060
cyril.michel@noaa.gov
Voice: 831- 420-3986
Fax: 831-420-3977

[1] affiliation:
University of California, Santa Cruz
Under contract to Southwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
110 Shaffer Rd., Santa Cruz, California 95060
USA

[2] affiliation:
arnold.ammann@noaa.gov
steve.lindley@noaa.gov
bruce.macfarlane@noaa.gov
Southwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
110 Shaffer Rd., Santa Cruz, California 95060
USA

[3] affiliation:
edchapman@ucdavis.edu
mjthomas@ucdavis.edu
gsinger@ucdavis.edu
apklimley@ucdavis.edu
Biotelemetry Lab
Department of Wildlife, Fish, & Conservation Biology

University of California, Davis
1334 Academic Surge Building, Davis, California 95616
USA

[4] current affiliation
psandstrom@usgs.gov
Institute on Ecosystems: Montana State University
2327 University Way, Suite 2
Bozeman, Montana 59715
USA

ABSTRACT

Outmigration survival of acoustic tagged hatchery-origin Sacramento River late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts was estimated for five years (2007-2011) using a receiver array spanning the entire outmigration corridor, from the upper river, through the estuary, and into the coastal ocean. The first four years of releases occurred during below-average river flows, while the fifth year (2011) occurred during above-average flows. In 2011, overall outmigration survival was two to five times higher than survival in the other four years. Regional survival estimates indicate that most of the improved survival seen in 2011 occurred in the riverine reaches of the outmigration corridor, while survival in the brackish portions of the estuary did not significantly differ among the five years. For the four low flow years combined, survival rate in the river was lower in the more anthropogenically-modified upper reaches; however, across all regions, survival rate was lowest in the brackish portion of the estuary. Even in the high flow year, outmigration survival was substantially lower than yearling Chinook salmon populations in other large rivers. Potential drivers of these patterns are discussed, including channelization, water flow, and predation. Finally, management strategies are suggested to best exploit survival advantages described in this study.

INTRODUCTION

Knowing where excessive mortality is occurring is crucial to designing effective conservation measures for salmon populations. Salmon utilize many different habitats during the different stages of their life cycle, but it is the degradation of freshwater or estuarine habitats that is commonly cited as the cause of population declines (Nehlsen et al. 1991). Of particular concern is the high mortality often experienced in these habitats during one of the most vulnerable stages in the salmon life cycle: the downstream migration of juveniles ('smolts') heading to the ocean from their riverine birthplace (Healey 1991).

There has been extensive research on juvenile salmonid smolt survival in large rivers of the west coast of North America, most notably in the Columbia and Fraser Rivers (McMichael et al. 2010; Muir et al. 2001; Rechisky et al. 2013; Skalski et al. 1998; Welch et al. 2009; Welch et al. 2008). These studies have indicated that outmigration survival can vary widely from year to year and population to population, and further research in these rivers has shown that survival rates often correlate with environmental variables such as flow, turbidity and temperature (Giorgi et al. 1997; Gregory and Levings 1998; Smith et al. 2003). This information has proved crucial for improving salmon survival in the Columbia River, through improvements in fish passage structures and changes in dam operations (Connor et al. 2003).

California's Sacramento River, in contrast, is critically lacking in smolt outmigration survival information. The Sacramento River, compared to the Columbia and Fraser Rivers, has an order of magnitude lower discharge, exists in a warm and dry Mediterranean climate, and yet is the primary source of water to the state's industrial, domestic and agricultural sectors. The Sacramento River and its estuary are currently the objects of intense conservation concern due to the poor status of some of its salmon and steelhead populations (among other native species) and habitats. In spite of these problems, the Sacramento River is still an important contributor to west coast Chinook salmon (*Oncorhynchus tshawytscha*) fisheries, largely due to extensive hatchery propagation efforts (O'Farrell et al. 2013). Several very large water and habitat management projects are under consideration that are expected by their proponents to contribute to the restoration of Chinook salmon populations, yet survival rates across the life cycle of these populations are poorly known. Several coded-wire and acoustic tagging studies have assessed Chinook salmon smolt survival in the Sacramento-San Joaquin Delta (the freshwater portion of the estuary), which is the hub of water infrastructure for the majority of southern California and a location where anthropogenic modifications are extensive and salmonid losses are great (Baker and Morhardt 2001; Brandes and McLain 2001; Perry et al. 2010). However, no study has assessed smolt survival through the entirety of the outmigration corridor, from the upper limit of anadromy to the Pacific Ocean.

In this study, we quantify the spatial and temporal patterns of hatchery late-fall run Chinook salmon smolt survival in the Sacramento River system. Utilizing an extensive network of acoustic receivers, we estimated survival through the river and estuary over 5 years at a fine-scale spatial resolution previously not possible. This resolution allowed us to discern regional and temporal differences in survival that cannot be obtained using traditional tagging methods.

METHODS

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river that is fully contained within the state of California, and is the third largest river that flows into the Pacific Ocean in the contiguous United States (Fig. 1). The headwaters are located just south of Mount Shasta in the lower Cascade Range and the river enters the ocean through the San Francisco Estuary at the Golden Gate. The total catchment area spans approximately 70,000 km^2. The Sacramento River and its tributaries have been heavily dammed and otherwise impacted by human activities; it is estimated that 47% of the historic spawning, migration and/or rearing area is no longer accessible to Chinook salmon (Yoshiyama et al. 2001).

The Sacramento River watershed includes diverse habitats, from relatively pristine run-riffle reaches in the north, to a heavily channelized and impacted waterway further south, and finally to the San Francisco Estuary, the largest and most modified estuary on the west coast of North America (Nichols et al. 1986). The San Francisco Estuary is comprised of an expansive tidally-influenced freshwater delta upstream of its confluence with the San Joaquin River and a series of increasingly saline bays. The sheer size and physical differences between these two sections of the estuary merit separate consideration with respects to their influence on salmon survival, therefore, we use the terms “delta” and “bays” to differentiate between the two.

The annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 m^3s^{-1} (Interagency Ecological Program, 2004). However, this water does not continue downstream unimpeded; due to one of the world’s largest water storage and water transportation infrastructures, replete with abundant dams, reservoirs, diversions and aqueducts, it is estimated that current discharge of the Sacramento and San Joaquin Rivers combined is less than 40% of the pre-development discharge (Nichols et al. 1986). The damming and water diversions of the Sacramento River and its tributaries have also homogenized river flows throughout the year, reducing winter high flows and flooding while increasing flows in the summer and fall (Buer et al. 1989).

The study area included approximately 92% of the current outmigration corridor of late-fall run Chinook salmon, from release to ocean entry. Specifically, the study area’s furthest upstream release site at Jelly’s Ferry (518 km upstream from the Golden Gate Bridge) is only 47 km downstream from Keswick Dam, the first impassable barrier to adult salmon returning to spawn on the Sacramento River.

Central Valley late-fall run Chinook salmon

The late-fall run is one of the four Chinook salmon runs occurring in the Sacramento River drainage, and is the only run to exhibit a predominately yearling migrant life history (Moyle 2002). Following emergence from the gravel, wild late-fall run juveniles exhibit a river residency of 7 to 13 months, after which smolts (juvenile salmon that are actively migrating to the ocean) will migrate to the ocean between the months of October and May at a fork length of 90 to 170 mm (Fisher 1994; Snider and Titus 2000a, b). In contrast, the subyearling life history demonstrated by a 4 to 7 months freshwater residency is the more common life history strategy used by the other salmon populations in the Sacramento River. Moyle et al. (1995) outlined six major threats to the late-fall run Chinook salmon population, one of which was mortality during outmigration, potentially due to water diversions and increased predation in bank-altered areas. In 2004, the fall/late-fall run Chinook salmon Evolutionarily Significant Unit (ESU) was designated a “species of concern” by the United States Endangered Species Act.

The United States Fish and Wildlife Service’s (USFWS) Coleman National Fish Hatchery (Anderson, CA) is the only hatchery to produce late-fall run Chinook salmon, releasing approximately one million smolts a year between mid-December and mid-January. Annual escapement for this population can vary from just several hundred to 42,000; the average annual escapement from the winter of 1973/1974 to the winter of 2007/2008 is 12,386 individuals (Azat 2015). Little information exists regarding what proportion of the late-fall run adult population is of hatchery origin versus wild origin. Palmer-Zwahlen and Kormos (2013) estimated that in 2011, 100% of late-fall run adults returning to Coleman National Fish Hatchery were hatchery fish while 44% of late-fall adults recovered during carcass surveys on the Sacramento River were hatchery origin.

Fish Tagging and Releases

For five consecutive winters, from January 2007 to December 2010/January 2011 (henceforth referred to as 2007, 2008, 2009, 2010 and 2011 seasons, based on the year during which January tagging occurred), 200 to 304 late-fall run Chinook salmon smolts from Coleman National Fish Hatchery were implanted with acoustic tags and released into the Sacramento River. Release times were scheduled to be within a few days of the release times of the general production of hatchery fish. Only smolts 140 mm or larger were tagged to keep the tag weight to less than 6% of the fish weight. Therefore, tagged smolts were representative of the larger hatchery individuals; specifically, from 2007 to 2011, smolts at or above the 140 mm cutoff represented 23.5%, 38.4%, 50.2%, 29.6, and 50.9% of the total hatchery production. In the rare instance that a smolt had severe descaling, fin erosion, or other obvious injuries, the smolt was discarded and not tagged.

Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized fish. The tag was inserted through a 12 mm incision anterior to the pelvic girdle and 3 mm to the side of the *linea alba*. The incision was then closed with two simple interrupted stitches tied with square knots of non-absorbable nylon cable-type suture. All fish were allowed to recover for a minimum of 24 hours before release. Additional surgery details can be found in Ammann et al. (2013). In study years 2008 and 2009, an additional group of smolts from the same hatchery were tagged with dummy acoustic transmitters to monitor tag effects and tag retention in laboratory trials. No fish shed their tags over 221 and 160 days (the entire length of the trial in both years respectively) and tagged fish growth and survival was not significantly different than untagged fish (Ammann et al. 2013). Since fish in the field and captive studies had similar tag burdens (1.6 to 6.3% for field study, 2.6 to 5.6% for captive study), we assumed that mortality in the field study was not tag related.

In the first year (2007), a total of 200 fish were released in small batches (13-14 fish each) every weekday afternoon for the third, fourth and fifth weeks of January 2007 at the Coleman National Fish Hatchery into Battle Creek (river km 534 - "rkm" is distance from ocean), a tributary to the Sacramento River (Table 1). In the following four years, fish were released in two groups. In 2008-2010 a total of approximately 300 fish was released: ~50 fish were simultaneously released at dusk at three release sites in the upper 150 km of the mainstem Sacramento River (rkm 518, 412, 363) in mid-December and early January allowing the lower release groups to reach the lower river and estuary in larger numbers, which improved statistical precision of the survival estimation. In 2011, 240 fish were released: 120 fish were released in mid-December and early January at dusk at Jelly's Ferry (rkm 518), a site on the mainstem Sacramento River, only 7.3 kilometers downstream of the confluence with Battle Creek. Fish were transported to the release sites by truck at low densities (~ 10 $g•l^{-1}$) in coolers with aerators. In years with multiple release sites, transport times were extended for closer sites to keep potential transport stress equal among all release groups.

Acoustic Telemetry

Acoustic tagging technology was used to acquire high-resolution movement data and survival estimates. Uniquely coded Vemco 69 kHz V7-2L acoustic tags (1.58g ± 0.03 S.D. in air, 7mm diameter by 20mm long; Amirix Systems, Inc., Halifax, Nova Scotia, Canada) and Vemco

VR2/VR2W receivers were used to tag and track fish. The tags transmitted every 30 to 90 seconds (with a mean of 60 seconds) in the first year of the study, then transmitted every 15 to 60 seconds (with a mean of 45 seconds) in the following four years. Battery life tests were conducted in 2007, 2010, and 2011 with a subset of tags from the same batch used for tagging smolts. In 2007, tag life of 11 test tags ranged from 138 to 749 days with a mean of 513; in 2010, tag life of 20 test tags ranged from 127 to 297 days with a mean of 194; in 2011, tag life of 25 test tags ranged from 98 to 214 days, with a mean of 172. For the purposes of verifying that tag life was sufficient to last the entire migration of all smolts, the time elapsed from release to last known detection was calculated for each smolt for all five years of the study. Last known detection for smolts was either last known detection before disappearance, or time of arrival to the Golden Gate receiver location (considered the end of the outmigration in this study). The longest outmigrating individual per year took 32, 89, 67, 97, and 79 days respectively for the years 2007-2011, with 99.2% of smolts successfully outmigrating or disappearing within the first 60 days after release. Therefore, we believe the battery life for our tags were sufficient to last the entire outmigration period of our tagged smolts.

The receiver array spanned 550 km of the Sacramento River watershed from below Keswick Dam to the entrance to the ocean (Golden Gate) and beyond to Point Reyes. This network of approximately 300 receivers at 210 receiver locations was maintained by the California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu), a group of academic, federal and state institutions, and private consulting firms. We selected a subset of these receiver locations for the final survival analyses, as per the selection criteria described in the Data Analysis section of the methods.

The acoustic receivers automatically process all detection data and drop most false detections or incomplete codes from the detection file. All detections were then subject to standardized quality control procedures to remove any remaining false detections (see Michel et al. (2013)).

Data Analysis

Survival in each reach

Juvenile Chinook salmon express obligate anadromy, meaning that they will travel toward the ocean once the emigration has begun with scarce exceptions (Healey 1991). Therefore, in a linear system such as the Sacramento River, if receiver locations were capable of detecting every passing tag, then if a fish is detected at one receiver location but is never detected thereafter, we could assume that the fish has died somewhere in the reach between the receiver location where it was last detected and the next downstream receiver location.

However, receiver locations rarely operate perfectly, necessitating the estimation of detection and survival probabilities at each receiver location. We used the Cormack-Jolly-Seber (CJS) model for live recaptures (Cormack 1964; Jolly 1965; Seber 1965) within Program MARK (White and Burnham 1999) using the RMark package (Laake and Rexstad) within program R (v. 3.0.1; R Development Core Team 2013). The CJS model was originally conceived to calculate survival of tagged animals over time, by re-sampling (recapturing) individuals and estimating survival and recapture probabilities using maximum likelihood. For species that express an obligate migratory behavior, a spatial form of the CJS model can be used, in which recaptures (i.e., tagged fish detected acoustically downstream from release) occur along a migratory corridor (Burnham 1987). The model determines if fish not detected at certain receivers were ever detected at any receiver downstream of that specific receiver, thus enabling calculation of maximum-likelihood estimates for detection probability of all receiver locations (p), survival (Φ), and 95% confidence intervals for both (Lebreton et al. 1992).

An initial run of the model with all possible river receiver locations together with the major estuary receiver locations was performed for each individual year separately, after which a subset of the river receiver locations that had consistently high tag detection probabilities through the years and that were strategically located were chosen to delimit the river reaches that were used in the spatial survival analysis. Additionally, because survival between the Battle Creek release site and Jelly's Ferry receiver location was only estimated in 2007, and because Jelly's Ferry was the furthest upstream release site for all following years, only fish known to have reached the Jelly's Ferry receiver location in 2007 were included in all survival analyses, and Jelly's Ferry was considered to be their release location. In total, 145 of the 200 smolts released in 2007 were known to have reached the Jelly's Ferry release location and were included in survival analyses. A total of 19 receiver locations were chosen, extending from just below the most upstream release site, Jelly's Ferry, to the Golden Gate (Fig. 1; Table 2). Between them, we delineated 17 reaches in which mortality can be accurately estimated (the detection probability and survival of the 18th and last reach can only be estimated jointly as there is no detection information beyond this point in which to assess the final receiver location).

Parallel receiver lines were installed at the Golden Gate approximately 1 km apart in order to estimate detection probability and survival at the inner (East) Golden Gate receiver line by using the western line to assess performance of the eastern line. After the 2008 outmigration season, a coastal ocean receiver line was deployed across the continental shelf at Point Reyes, approximately 60 km north of the Golden Gate. Detections from this receiver line were included in the encounter history for the Golden Gate West line to improve accuracy in the estimation of survival and detection probability to the Golden Gate East line. However, because the Point Reyes receiver location did not exist in the 2007 or 2008 season, and few fish were detected there in subsequent years, it was not formally included as a receiver location in the survival analyses.

Survival per 10 km, regional survival and overall survival

For each year, we used the 18 receiver locations to estimate reach survival ("ϕ_R") for 17 reaches, using the fully time-varying CJS model, which in this case actually varies over space, specifically each reach has a parameter ("reach model"). Detection probabilities were also allowed to vary by reach. These survival estimates were then standardized by reach lengths l (giving survival per 10 km, "ϕ_{10}") to allow inter-reach survival comparisons. This was done by setting the time intervals (in reality, space intervals for this application) in the process.data() function of RMark package to a vector of reach lengths (in units of 10 km). The per 10 km survival estimates are calculated by RMark according to this formula (Eqn 1):

$$(1) \qquad \phi_{10} = \sqrt[l]{\phi_R}$$

To account for the propagation of error, standard errors for *n*th root parameter estimates were calculated by the RMark package using the delta method (Powell 2007; Seber 1982).

Regional (river, delta, and bays) and overall (from the release site to the Golden Gate) survival was then assessed for each year. We did this by taking the product of the reach survival estimates that fall inside the spatial extent of interest, and we present this as percent survival. To account for the propagation of error, standard errors of the cumulative products of survival estimates were also calculated using the RMark package, using the deltamethod.special() function. When using the delta method for estimating the variance of the product of survival estimates, the variance-covariance matrix for the survival estimates must be included in the estimation. Confidence intervals for the product of survival estimates must be calculated on the logit scale, then back-transformed to the real probability scale. Therefore, to estimate 95% confidence intervals, we used our product of survival estimates ($\hat{\Phi}$) along with its respective standard error of the beta estimate ($\widehat{SE}logit(\hat{\Phi})$) by using the formula (Eqn 2):

$$(2) \qquad expit[logit(\hat{\Phi}) \pm 1.96 \times \widehat{SE}logit(\hat{\Phi})]$$

The influences of different spatial and temporal factors on survival rates were assessed by modeling ϕ_R as a function of the factor in question. Specifically, the influence of these factors was assessed by allowing each release group (e.g., five groups for the release year model: 2007, 2008, 2009, 2010 and 2011) within each model to have its own set of survival parameters. Each factor-specific survival model was compared to one another and to a base model (a model with no factor-specific parameters) using Akaike's Information Criterion corrected for small sample sizes (AICc). Goodness-of-fit was assessed by estimating the $\hat{c}$ variance inflator factor of the base model. For this we used two different methods, and adopted the more conservative estimate. Firstly, we simulated $\hat{c}$ and deviance from 100 simulations using the bootstrap procedure. Then, we estimated $\hat{c}$ in two ways, first by dividing the deviance estimate from the original data by the mean of simulated deviances, giving a $\hat{c}$ of 1.309, then by dividing the $\hat{c}$ from the original data by the mean $\hat{c}$ from the bootstraps, giving a $\hat{c}$ of 1.494. We therefore adopted the more conservative $\hat{c}$ of 1.494 and used it to adjust all AIC values for overdispersion (herafter called QAICc). As a rule of thumb, if a test model lowered QAICc relative to the base model by a difference of more than seven, the test model was deemed substantially more parsimonious, and therefore supported over the base model.

The effects of reach (n=17), release year (n=5), release site (n=3), and all interactions of those factors were tested (Table 3 for models). This was done by comparing the QAICc score of each model to the QAICc score of a version of the "reach model" that combines data from all five years, which henceforth will be considering the "*base* model". We used the reach model as our base model under the assumption that survival must vary through space given the spatial heterogeneity of the study system. To test this assumption, a "null model" was also included for comparison. This model only allowed one parameter for survival (representing the null hypothesis: constant survival through space and time). An initial run of several models that allowed for different parameterization of the detection probability terms, while keeping the survival terms the same, indicated that the model allowing for detection probability to vary by reach and year was the best supported. Therefore, all survival models presented in Table 3 allow detection probability to vary by reach and year [*p(*reach*year)].

In order to better understand whether annual fluctuations in survival occurred on a regional scale, we also included three models that allowed survival to vary per reach and per year (reach*year) in only the river, the delta (the delta being the freshwater portion of the estuary) or the bays (Suisun, San Pablo and San Francisco Bays, i.e. the brackish portion of the estuary). These models allowed survival to vary by reach in the remaining regions, and are therefore also comparable with the base model.

Finally, the influence of individual covariates (fork length (mm) and weight (g)) on survival was assessed. The model selected *a priori* to include these covariates was the base model. The individual covariates were added both as an additive factor (different intercept per reach, but common slope), and as factor including the interaction term (different intercept and different slope). These models were then compared using QAICc to the base model without any individual covariates to determine whether fish size and weight affects survival.

For the purpose of considering migration rate as a potential driver for survival rates, mean successful migration movement rate (km/day MSMMR; (Michel et al. 2013)) was calculated per year. Migration movement rate from release site to the West Golden Gate receiver line (i.e., entry to the Pacific Ocean) was calculated for every fish that was detected (i.e., successfully reached the ocean) at either of the Golden Gate receiver lines. These values were then averaged per year and compared to the overall survival for that year in Table 4.

RESULTS

Overall survival of late-fall run Chinook through the entire migration corridor (rkm 518 to rkm 2) per year ranged from 2.8 to 15.7%, with 2011 having the highest survival (Table 4). The MSMMR values indicate that the first four years of the study had relatively similar migration rates, ranging from 17.5 to 23.5 kilometers per day, whereas 2011 had a faster migration rate of 36 kilometers per day.

Survival rate on a reach-by-reach basis was quite variable. During the first four years of the study, the upper river reaches (reaches 1 through 8; rkm 518 to 325) had some of the lowest survival per 10 km and the lower reaches of the river (reaches 9-12; rkm 325-169) had the highest. The delta was comparable to the upper river, and the San Francisco and Suisun Bays (reaches 13-17; rkm 169-2) had the lowest survival rates (Fig. 2). During these same four years, detection probabilities per year and per receiver location throughout the watershed ranged from

4% to 100%, with 90% of all detection probabilities being larger than 50%. In the fifth year, river flows at the time of release were much higher than in the previous four years (Fig. 3), and as a result detection rates were much lower in the river, with only three of the twelve river receiver locations having a detection probability higher than 1%. Therefore 2011 reach-specific survival in the river was not estimable.

Region-specific survival estimates were calculated using the product of all reach-specific survival estimates within the region of interest (Fig. 4; Table 4). Although reach specific survival parameters could not be estimated for the river region in 2011, detection probability improved downstream as water velocity decreased, allowing the estimation of reach specific and region specific survival estimates downstream of the river region. To estimate river region survival in 2011, and to further investigate differences in survival between 2011 and the previous years, the detection data was simplified for a post-hoc CJS modeling exercise that would allow the inclusion of 2011. We simplified the detection data by only including detections from four receiver locations separating the major watershed regions: Freeport at the downstream end of the river region, Chipps Island at the downstream end of the delta region, and the two parallel Golden Gate receiver lines at the downstream end of the bays region. Additionally, only fish released at the Jelly’s Ferry site were included for all years since the other release locations did not have associated receiver locations. A preliminary model that allowed survival and detection probability to vary by region and by year (region*year) allowed us to estimate survival in the river region in 2011 (Fig. 4; Table 4). This estimate revealed that survival in the river in 2011 was much higher than in all previous years, while survival in the delta and bays was similar among all five years. We also constructed a set of similar models where one year was given its own set of region specific survival parameters, while the remaining four years shared the same region specific survival parameters. These models allowed detection probability to vary by region and by year. Five models were constructed, each one allowing a different year to have its own survival parameters. The model allowing 2011 to have its own region-specific survival parameters while the other four years shared the same region-specific parameters was substantially better supported (ΔQAICc >7) than all the other models of the same type, as well as the preliminary model (permitting all years to have different region-specific survival parameters).

In the analysis of the effect of different spatial and temporal factors on survival, 2011 data was omitted due to the lack of detection data available in the river portions of the watershed. The influence of reach on survival rates (base model) was found to have substantially better support (ΔQAICc >>7) than the null model (constant survival through space and time; Table 3). The reach models that included release site or year ("Reach*release" and "Reach*year", respectively), as well as the interaction model ("Reach*year*release"), did not improve their support over the base model. The year model was better supported than the release model. The only model that had substantially better support than the base model was the model that allowed for river survival to have a year effect, while delta and bays survival was held constant through time. ("(River survival*year)*reach"). The model allowing only the delta reach to have a year effect ("(Delta survival*year)*reach") was marginally better supported than the base model (ΔQAICc <2).

Tagged fish weight and fork length varied significantly among years (P<0.001), and pairwise hypothesis testing using Bonferroni and Tukey's honestly significant difference tests both indicate that fish sizes were statistically different among all years (with the exception of the 2009/2010 pair) (Table 1). However, the addition of individual covariates (weight, length) as factors to the base model did not improve parsimony in any circumstance, although the length model did fit the data better than the weight model. A model adding length as an additive factor had more support than the other covariate models, and had approximately equal support with the base model (ΔQAICc <0.1; Table 3). Therefore the significant differences in weight and fork length among years did not appear to affect survival.

DISCUSSION

This study used high resolution fish tracking and environmental data to provide the first reach-specific survival estimates of Chinook salmon smolts in the Sacramento River over the entire migration corridor. Survival was relatively high in the lower river compared to other areas, a somewhat unexpected finding given that this reach is channelized and rip-rapped. Also, and in contrast with the commonly-held belief that mortality during the Central Valley smolt outmigration is greatest in the delta (Williams 2006), we observed relatively high mortality in the upper river and especially in the bays downstream of the delta. We found that survival over the entire migration route was much lower in four low-discharge years (2.8 – 5.9%) than in one high-discharge year (15.9%; Fig. 3); higher survival in the high-discharge year was due mainly to increased survival in the river region. This suggests that riverine survival dynamics may be playing an underappreciated role in determining annual salmon stock abundance, as shown with Cheakamus River steelhead stock in British Columbia (Melnychuk et al. 2014).

One potential reason why the lower Sacramento River had higher survival than expected may be due to channelization. Levees, riprap, and channelization have been considered detrimental for salmon populations due to their degradation of spawning grounds (reduced input of gravel), the paucity of prey to feed upon, and an absence of cover that results in a greater frequency of predation on juveniles (Buer et al. 1989; Chapman and Knudsen 1980; Garland et al. 2002; Schmetterling et al. 2001)). However, Michel (2010) found a strong positive correlation between channelized reaches and smolt survival. Given limited rearing potential, smolts likely migrate through channelized reaches, reducing the period of exposure to sources of mortality. The majority of potential predator species in the watershed are typically found associated with submerged structure and vegetation, which in the lower Sacramento River are mostly limited to the riprapped littoral zone. A smolt travelling downstream in the lower Sacramento River only needs to avoid the channel margins to minimize exposure to predators. Outmigrating Chinook salmon smolts in the Sacramento River travel disproportionally more in the center of the channel (Sandstrom et al. 2013). Similarly, smolt survival was higher in deep impoundments compared to shallower undammed reaches of the Columbia River (Welch et al. 2008).

Previous studies of salmon survival in the Sacramento River and estuary, based primarily on coded-wire tags, suggested significantly lower mortality in the bays, but higher mortality in the river. Brandes and McLain (2001) found survival of sub-yearling fall-run Chinook salmon smolts from Port Chicago to the Golden Gate (roughly equal to our bays region) during the 1984-1986 years to vary between 76% and 84%, compared to a range of 26% to 43% in this study. California Department of Fish and Wildlife monitored survival rates of late-fall Chinook salmon from Battle Creek to rkm 239 (within the river region) during the 1996-2000 years using coded-wire tag recoveries at rotary screw traps. They estimated survival rates to vary between 1.1% and 2.7% (Snider and Titus 1998, 2000a, b, c; Vincik et al. 2006), compared to a range of 15.5% to

63.2% over a longer distance in this study. Reasons for these discrepancies could lie in the conditions during the years compared, or could have to do with the difference in sampling protocol and survival estimation.

Overall survival of outmigrating late-fall run Chinook salmon smolts in the Sacramento River is low in comparison to the Columbia and Fraser rivers, in spite of those rivers having substantially longer migration corridors. Welch et al. (2008) found that yearling Chinook salmon smolts from the Snake River (a tributary to the Columbia River) had an overall survival of 27.5% (± 6.9% S.E.) to the ocean over a distance of 910 km in 2006. That study also found that overall survival for yearling Chinook salmon smolts from various tributaries of the Fraser River to the ocean over distances ranging from 330.8 to 395.2 km had an overall survival varying from 2.0% (± 3.6 S.E.) to 32.2% (± 20.7 S.E.), with the majority of the tributary and year-specific survival estimates above 15%. Rechisky et al. (2009) found that outmigrating yearling Chinook salmon smolts from the Yakima River (a tributary to the Columbia River) had an overall survival of 28% (± 5 S.E.) to the ocean over a distance of 655 km.

There are also striking differences in the spatial patterns of survival between the Sacramento River and the Columbia and Fraser Rivers. Columbia River tagging studies have found survival for yearling Chinook salmon through the lower river and estuary to vary between 82% and 100% (or between 98.3% and 100% per 10km), depending on the year and population (Harnish et al. 2012; Rechisky et al. 2013). Similarly-sized sockeye salmon (*Oncorhynchus nerka*) smolts experienced little to no mortality during outmigration through the mainstem Fraser River (including the estuary) during the years 2010-2013 (Rechisky et al. 2014). In our study, survival through the estuary (delta and bays region combined) ranged from 15.1% to 23.4% (89.3%-91.7% per 10 km).

There are a number of possible explanations for why the survival of Chinook smolts in the Sacramento River is generally lower than in other west coast rivers. Flows in the Sacramento River are highly regulated by large water storage dams, and peak discharge is typically much reduced in the outmigration period (Buer et al. 1989; Larry and Marissa 2009). In contrast, no dams exist on the mainstem Fraser River, and the dams on the Columbia River are used for hydropower and do not reduce or homogenize flows to the same extent as water storage dams. It is only in wet years such as 2011 that water flows are high enough for water managers to allow significant dam releases in the Sacramento River. We observed much higher in-river survival during 2011, and other studies have shown positive relationships between survival and river flow (Connor et al. 2003; Smith et al. 2003). Higher flows correspond to higher velocities and faster travel times, reducing the time smolts are exposed to predators (Hogasen 1998). High flows may also be correlated to higher turbidities, which can reduce the effectiveness of visual predators (Ferrari et al. 2014; Gregory and Levings 1998).

Differences in the condition of estuaries offer another explanation. Magnusson and Hilborn (2003) found that in comparing the survival of subyearling Chinook salmon smolts in 27 different small to medium sized estuaries in the U.S. Pacific Northwest, there was a significant positive relationship between survival and the percentage of the estuary that was in pristine condition. They also note that according to MacFarlane and Norton (2002), estuary use by subyearling Chinook salmon smolts was less in the brackish portion of San Francisco Estuary than other estuaries in the Pacific Northwest, potentially due to the poor condition of the estuary.

Nichols et al. (1986) posited that the San Francisco estuary is the most modified estuary on the west coast of the United States, which suggests that the low survival estimates seen in this study are consistent with Magnusson and Hilborn's findings. Cohen and Carlton (1998) suggested that the extensive modification of the San Francisco Estuary contributes to it being perhaps the most invaded estuary in the world. Invaders include a number of piscivorous fish species that likely prey on migrating juvenile salmon. The role of predation clearly warrants study.

Survival rates during drought years observed in this study, if applicable to natural populations, suggest that populations are likely contracting. Bradford's (1995) review of Pacific salmon mortality rates suggested that typical fished Chinook salmon populations have a total mortality rate of 6.76 (based on fecundity) and an average observed egg-to-smolt mortality rate of 2.56. Average smolt mortality rate ($-\log_e(survival)$) during the first four years of our study was 3.23. A stable population subject to these mortality rates would require total mortality to be no more than 0.97 (or no less than 38% survival) for the period between ocean entry and reproduction, a period of two to four years for late-fall Chinook subject to significant ocean harvest rates.

Our results have implications for the management of Central Valley salmon hatcheries. Much of the hatchery production in the Central Valley is transported by tanker truck to the bays in order to avoid mortality incurred during the migration through the river and delta. Offsite release leads to undesirable levels of straying, and a recent independent review of California salmon hatchery practices recommends on-site release of hatchery production (CHSRG 2012). Salmon smolts have long been known to migrate during peak flows (Healey 1991; Hogasen 1998; Kjelson et al. 1981). Our study has shown that fish migrating during high flows have higher survival. Hatcheries could employ a “release window” strategy during which they wait for a peak flow, or coordinate their operations with releases from upstream reservoirs that could create artificial pulse flows. Reservoir releases have been shown to improve subyearling Chinook salmon smolt survival (Zeug et al. 2014), although evidence for improved yearling survival is not as clear (Giorgi et al. 1997; Young et al. 2011). The efficacy of reservoir release will depend on the degree to which survival benefits of migrating during freshets are due to decreased travel time versus higher turbidity, which may not be easily manipulated through reservoir operations.

Our study has demonstrated remarkably low survival rates for late-fall run Chinook salmon smolts in the Sacramento River. The Sacramento River is also home to three other runs of Chinook salmon that migrate at smaller sizes and later in the season (Fisher 1994), when water temperatures are higher and predators may be more active. These other runs may therefore be experiencing even lower survival. Furthermore, most mortality in this study occurred in a 1-2 week period for hatchery fish. This has disconcerting implications for wild fish that must spend several months to a year rearing in the watershed. As tags become smaller, the study design utilized here can be applied to document spatial and temporal patterns of survival in these other runs that are of significant conservation and fishery concerns, providing resource managers with valuable information on where and when survival problems are occurring - information necessary to effective mitigation of survival problems.

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Table 1. Means and standard deviations for weight and fork length of acoustically-tagged smolts by year and for all years combined

Year	Sample size	Fork length ± SD (mm)	Weight ± SD (g)
ALL	1350	158.8 ± 12.4	43.9 ± 11.2
2007	200	164.6 ± 10.7[a]	46.6 ± 9.8[a]
2008	304	168.7 ± 13.3[b]	52.6 ± 13.8[b]
2009	300	152.1 ± 8.5[c]	38.9 ± 7.9[c]
2010	306	152.5 ± 10.2[c]	39.3 ± 8.8[c]
2011	240	158.1 ± 7.8[d]	42.9 ± 6.8[d]

[abcd] Size distributions with different superscripts are significantly different ($P < 0.05$)

Table 2. Locations of acoustic receivers and tagged smolt release locations. Positive river km values indicate distance upstream from the Golden Gate Bridge, negative values indicate distance seaward from the Golden Gate Bridge.

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Receiver location & release site 2008-2011
Bend Bridge	504	Receiver location
China Rapids	492	Receiver location
Above Thomes	456	Receiver location
Below GCID	421	Receiver location
Irvine Finch	412	Receiver location & release site 2008-2010
Above Ord	389	Receiver location
Butte City Bridge	363	Receiver location & release site 2008-2010
Above Colusa Bridge	325	Receiver location
Meridian Bridge	309	Receiver location
Above Feather River	226	Receiver location
City of Sacramento	189	Receiver location
Freeport	169	Receiver location
Chipps Island	70	Receiver location
Benicia Bridge	52	Receiver location
Carquinez Bridge	41	Receiver location
Richmond Bridge	15	Receiver location
Golden Gate East	2	Receiver location
Golden Gate West	1	Receiver location
Point Reyes	-58	Receiver location

Table 3. Survival models for different spatial and temporal factors, as well as individual covariates, ordered from lowest to highest QAICc, omitting 2011 data. The ΔQAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities (reach and year-specific).

Survival (φ) treatment	**ΔQAICc**	**# Parameters**
(River survival * year) * reach	0.0	126
(Delta survival * year) * reach	25.3	93
BASE MODEL (Reach)	26.6	90
Reach + length	26.6	91
Reach * year	27.9	144
Reach * length	40.0	108
(Bays survival * year) * reach	49.0	105
Reach * weight	50.0	108
Reach * release	53.8	126
Reach * year * release	270.8	288
NULL MODEL (constant survival)	308.4	73

Table 4. Percent overall survival to Golden Gate East receiver line (rkm 2) per year, including standard error (SE), and mean successful migration movement rate (MSMMR) with standard error.

Release Group	% Survival	SE	MSMMR (km/day) ± SE
2007-ALL	**2.8**	**1.4**	**23.5 ± 3.6**
2007-River	15.5	3.6	
2007-Delta	63.0	14.5	
2007-Bays	28.3	12.4	
2008-ALL	**3.8**	**0.9**	**17.5 ± 1.5**
2008-River	24.5	3.0	
2008-Delta	59.1	4.4	
2008-Bays	26.1	4.9	
2009-ALL	**5.9**	**1.2**	**17.5 ± 1.1**
2009-River	31.9	3.2	
2009-Delta	43.1	4.3	
2009-Bays	43.0	6.5	
2010-ALL	**3.4**	**0.9**	**21.9 ± 2.1**
2010-River	22.7	2.5	
2010-Delta	53.6	5.6	
2010-Bays	28.1	6.4	
2011-ALL	**15.7**	**2.5**	**36.0 ± 3.0**
2011-River*	63.2*	8.5*	
2011-Delta	70.6	4.8	
2011-Bays	33.1	4.7	

*Estimated from post-hoc survival model

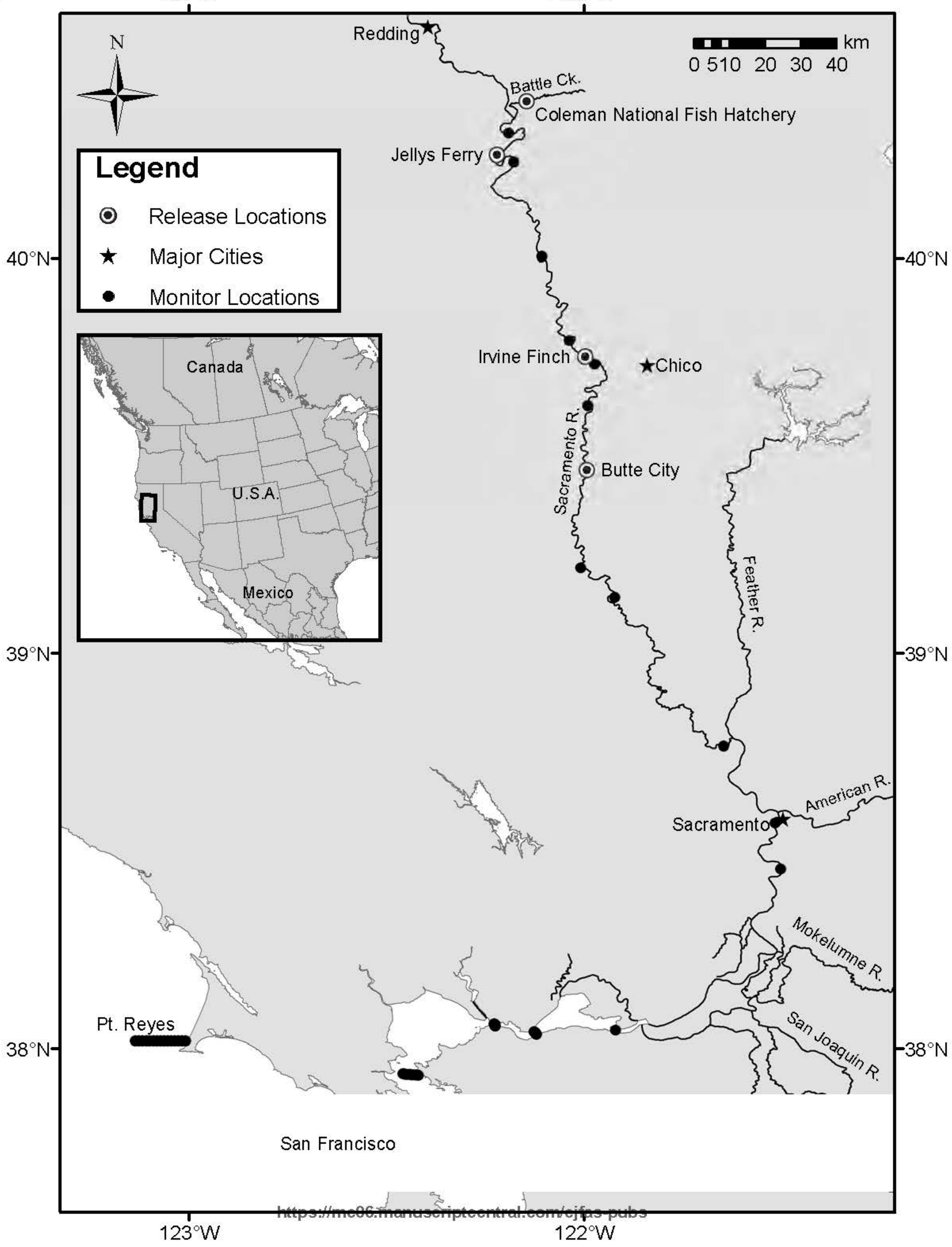
Figure Captions

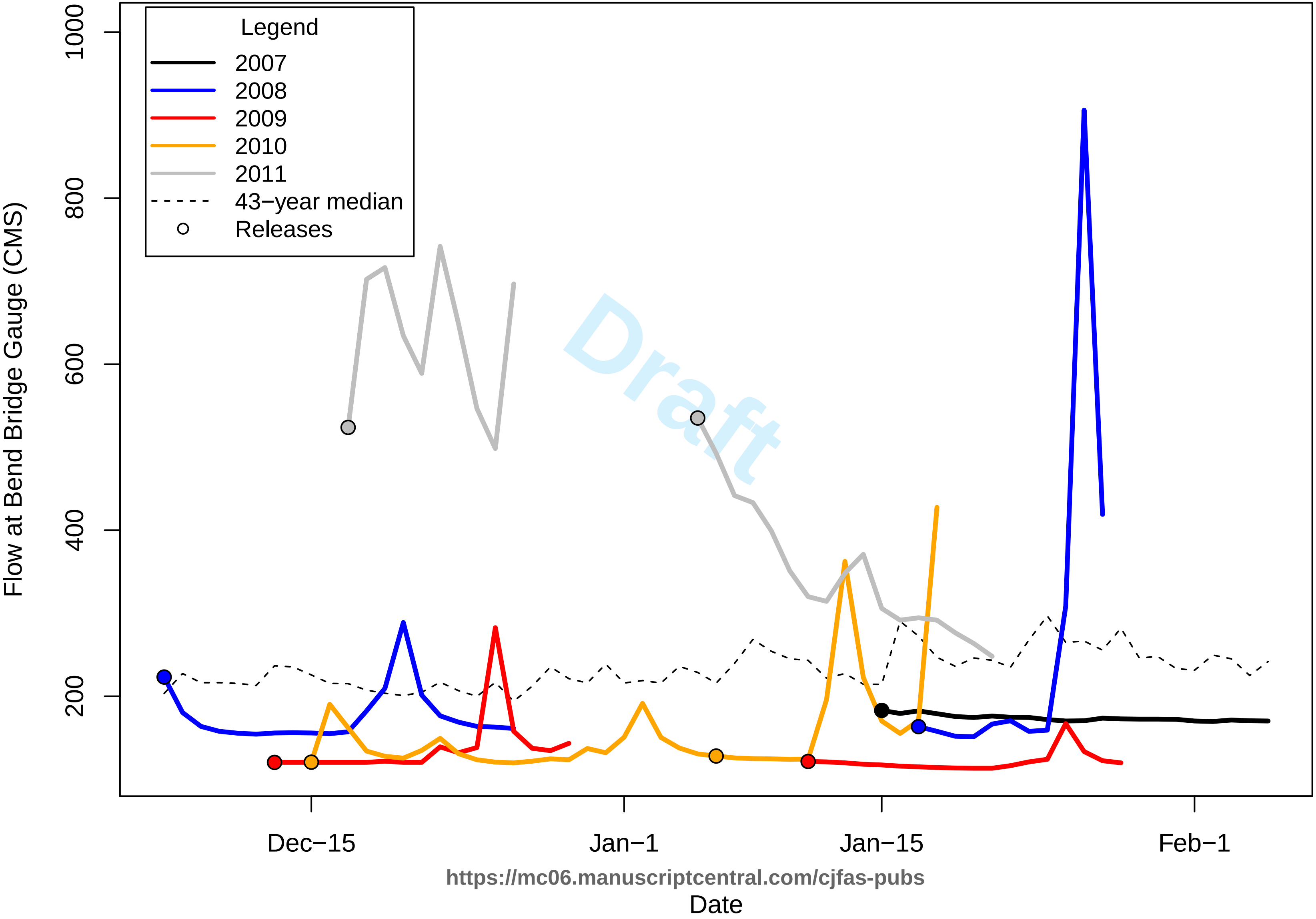
Fig. 1. Study area map including the Sacramento River, Sacramento – San Joaquin River Delta, Suisun/San Pablo/San Francisco Bays and Pacific Ocean. Bull's-eye icons signify a release location, star symbolizes a major city, and black dot symbolizes a receiver location.

Fig. 2. Percent survival per 10 km per reach for the 2007-2010 study years combined. Figure and map are delimited based on the regions (from upstream to downstream): upper Sacramento River, lower Sacramento River, Sacramento – San Joaquin River Delta, and Suisun/San Pablo/San Francisco Bays. The Sacramento River was delimited into an upper and lower section to highlight the shift in survival rates. Error bars represent 95% confidence intervals. 2011 data was omitted due to poor detection probabilities.

Fig 3. Hydrograph at the Bend Bridge gauging station, 14 rkm downstream from furthest upstream release site (Jelly's Ferry), for each of the five years of the study. The median daily flow values over a 43 year period (including the study years) are represented with a dotted line. Black dots represent release date for tagged smolts in relation to the respective year's hydrograph. Hydrographs are only depicted as long as 90% of released smolts are still actively migrating in the river region; in some years December released fish have all died or outmigrated before January release, and therefore some yearly hydrographs are not continuous.

Fig. 4. Percent survival per major region for all five study years. Regions include river, delta, bays, and the percent survival for the entire watershed "All". Error bars represent 95% confidence intervals.


123°W
122°W
N
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
km
0 5 10 20 30 40
Legend
◉ Release Locations
★ Major Cities
● Monitor Locations
40°N
Canada
U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
39°N
American R.
Sacramento
Mokelumne R.
San Joaquin R.
Pt. Reyes
38°N
San Francisco


Legend
2007
2008
2009
2010
2011
43−year median
Releases
Flow at Bend Bridge Gauge (CMS)
200
400
600
800
1000
Dec−15
Jan−1
Jan−15
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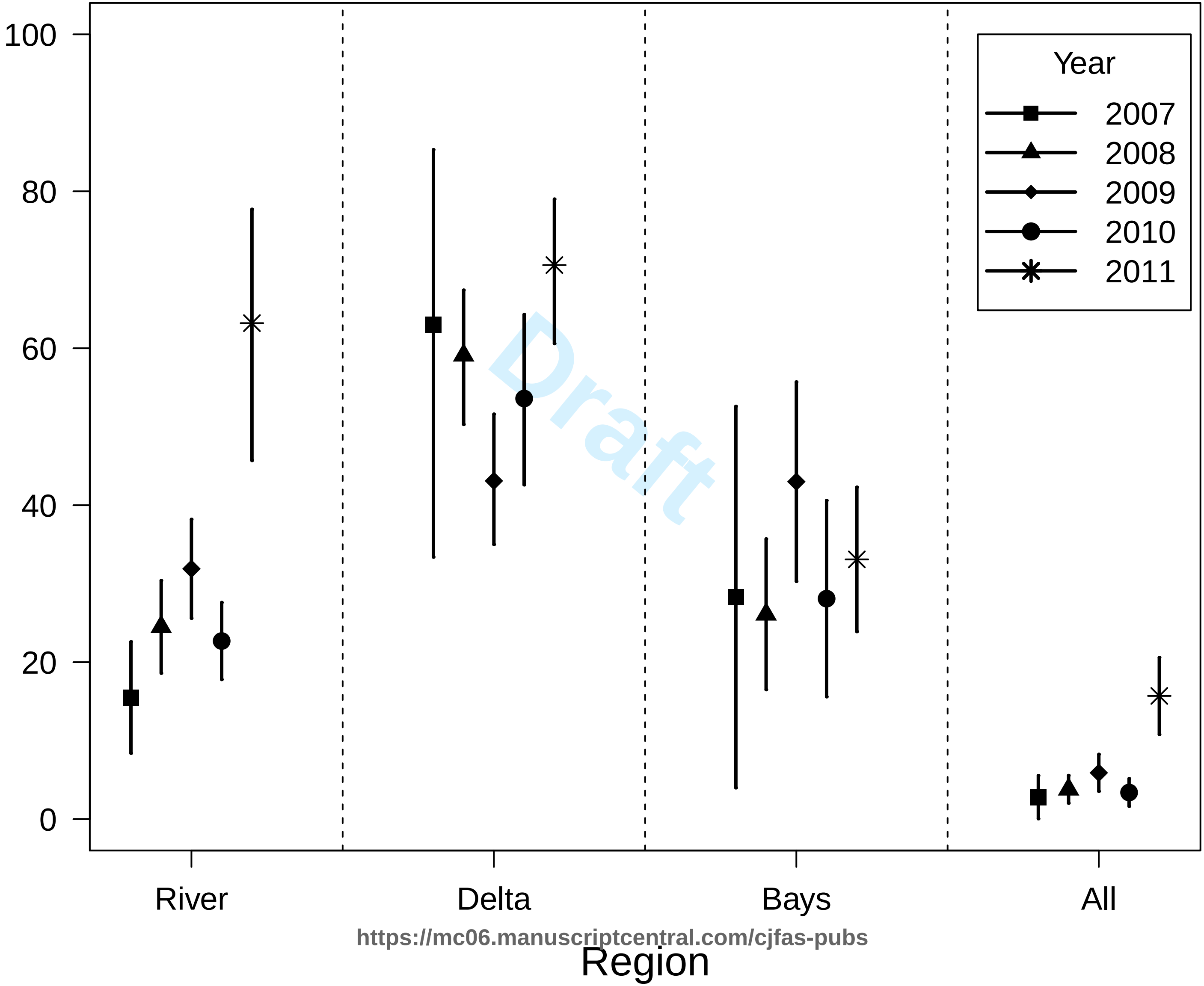
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Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: I. Model Description and Baseline Results

Kenneth A. Rose [a], Wim J. Kimmerer [b], Karen P. Edwards [c] & William A. Bennett [d]

[a] Department of Oceanography and Coastal Sciences, Louisiana State University, Energy, Coast, and Environment Building, Baton Rouge, Louisiana, 70803, USA

[b] Romberg Tiburon Center for Environmental Studies, San Francisco State University, 3152 Paradise Drive, Tiburon, California, 94920, USA

[c] Environment Agency, Manley House, Kestrel Way, Exeter, EX2 7LQ, UK

[d] Center for Watershed Sciences, John Muir Institute of the Environment, Bodega Marine Laboratory, University of California, Davis, Post Office Box 247, Bodega Bay, California, 94923, USA

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ARTICLE

Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: I. Model Description and Baseline Results

Kenneth A. Rose*
Department of Oceanography and Coastal Sciences, Louisiana State University,
Energy, Coast, and Environment Building, Baton Rouge, Louisiana 70803, USA

Wim J. Kimmerer
Romberg Tiburon Center for Environmental Studies, San Francisco State University,
3152 Paradise Drive, Tiburon, California 94920, USA

Karen P. Edwards
Environment Agency, Manley House, Kestrel Way, Exeter EX2 7LQ, UK

William A. Bennett
Center for Watershed Sciences, John Muir Institute of the Environment, Bodega Marine Laboratory,
University of California, Davis, Post Office Box 247, Bodega Bay, California 94923, USA

Abstract

Many factors have been implicated in the decline of Delta Smelt *Hypomesus transpacificus* in the upper San Francisco Estuary, and the importance of each factor is difficult to determine using field data alone. We describe a spatially explicit, individual-based population model of Delta Smelt configured for the upper estuary. The model followed the reproduction, growth, mortality, and movement of individuals over their entire life cycle on the same spatial grid of cells as the Delta Simulation Model (DSM2) hydrodynamics model. Daily values of water temperature, salinity, and densities of six zooplankton prey types were represented on the spatial grid. Reproduction was evaluated daily, and new individuals were introduced into the model as yolk sac larvae. Growth of feeding individuals was based on bioenergetics and zooplankton densities. Mortality sources included natural mortality, starvation, and entrainment in water diversion facilities. Movement of larvae was determined using a particle tracking model, while movement of juveniles and adults was based on salinity. Simulations were performed for 1995–2005. The baseline simulation was generally consistent with the available data. Predicted daily fractions of larvae entrained and annual fractions of adults entrained were similar in magnitude to data-based estimates but showed less interannual variation. Interannual differences in mean length at age 1 had large effects on maturity and subsequent egg production. Predicted and observed spatial distributions in the fall showed moderately good agreement for extremely low- and high-outflow years. As indicated by the population growth rate, 1998 was the best year and 2001 was the worst year. Water year 1998 (i.e., October 1997–September 1998) was characterized by fast growth in fall 1997, low entrainment, and high stage-specific survival rates, whereas water year 2001 had opposite conditions. Our analysis further shows how multiple factors can operate simultaneously to result in the decline in abundance of Delta Smelt.

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*Corresponding author: karose@lsu.edu
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Understanding the critical drivers and environmental changes that influence the population dynamics of fish is vital for effective resource management and restoration. Most fish species live multiple years and show ontogenetic shifts in the habitats they utilize, which exposes them to multiple environmental and biological factors spread over several points in their life cycle (Rose 2000). Identification of the relative importance of these factors and how they may interact with each other is an important step toward understanding and managing fish populations. A major debate is underway about the status of many harvested marine and coastal fish populations (Myers and Worm 2003; Hilborn 2007; Worm et al. 2009), as human development of coastal areas (McGranahan et al. 2007) and demand for high-quality freshwater (Vörösmarty et al. 2000) continue to accelerate. Identification of the major factors affecting population dynamics (especially declines in population) is critical because the high economic costs of protection and restoration demand efficient and effective responses.

The need to understand mechanisms of population decline for Delta Smelt *Hypomesus transpacificus* in the San Francisco Estuary is critical. This endemic species is listed as threatened under the U.S. Endangered Species Act and is listed as endangered under the California Endangered Species Act. Delta Smelt have generally been at low abundance since the 1980s and showed an even further sharp decrease starting in about 2002 (Bennett 2005; Sommer et al. 2007; Thomson et al. 2010). Delta Smelt have also become the focus of contentious debate because of perceived conflicts between the conservation of this species and the operation of facilities that divert water from the Delta Smelt's habitat for agricultural and urban uses (Brown et al. 2009; NRC 2010). These facilities alter seasonal patterns of flow, and they entrain and kill large numbers of Delta Smelt (Kimmerer 2008).

Many factors may be involved in the decline of Delta Smelt, and quantifying the importance of each factor has proven to be elusive despite the availability of extensive long-term field data (NRC 2012). Factors examined as possible contributors to the decline include entrainment of Delta Smelt by the two large water diversion facilities in the Sacramento–San Joaquin River Delta (hereafter, "the Delta"), shifts in the composition and densities of the zooplankton (prey) community, and changes in physical habitat related to salinity and turbidity (Baxter et al. 2010). A sharp decline in four fish species (juvenile Striped Bass *Morone saxatilis*; Longfin Smelt *Spirinchus thaleichthys*; Threadfin Shad *Dorosoma petenense*; and Delta Smelt) within the upper San Francisco Estuary beginning in approximately 2000 led to a substantial effort at synthesizing existing data to determine the cause (Sommer et al. 2007). The results to date have narrowed the possible factors to some extent (e.g., contaminant effects are likely small) and have facilitated the conclusion that the recent decline in Delta Smelt was due to multiple factors acting together (Baxter et al. 2010). Two statistical analyses (Mac Nally et al. 2010; Thomson et al. 2010) examined the dynamics of the four fish species by using monitoring data collected from the 1970s to 2007. Both analyses, which used similar data but different statistical methods, showed several covariates that were related to abundance of the fish, but they could not resolve the cause of the recent declines.

An alternative approach to the analysis of the effects of multiple factors on fish populations is simulation modeling of the growth, mortality, reproduction, and movement processes underlying the population dynamics. Population modeling allows the investigator to control everything and thus to perform simulation experiments for isolating the effects of individual factors and for exploring the effects of previously unobserved combinations of conditions (Rose et al. 2009). However, model results must be interpreted with caution because models are always simplifications of reality, and their predictions can be biased by decisions about which processes to include and at what temporal and spatial scales to represent those processes.

In this paper, we describe a spatially explicit, individual-based population model of Delta Smelt configured for the upper San Francisco Estuary. We chose this approach because many of the factors that are thought to contribute to the Delta Smelt's decline vary in space (Baxter et al. 2010), and simulating fish movement is more straightforward with an individual-based approach than with other modeling approaches (Tyler and Rose 1994). We first briefly describe the San Francisco Estuary and the life cycle of Delta Smelt. We then describe the spatial grid, environmental conditions, and reproduction, growth, mortality, and movement processes that are represented in the individual-based model. Hydrodynamic model output for the spatial grid and field data for temperature, salinity, and zooplankton densities were used as inputs to the population model for simulation of the period 1995–2005. The results of the baseline simulation are compared with the observed data, and we contrast the conditions between a "good year" and a "bad year" for Delta Smelt growth and survival within the baseline simulation. We conclude with a discussion of our results relative to other analyses and the strengths and weaknesses of our current model formulation. In our companion paper (Rose et al. 2013, this issue), we show that the results presented here are robust to alternative baseline assumptions, and we further explore the factors causing good and bad years by using a simulation experiment approach.

UPPER SAN FRANCISCO ESTUARY AND DELTA SMELT

The San Francisco Estuary is the largest estuary on the U.S. Pacific coast, with a watershed covering approximately 40% of California (Figure 1). The estuary connects the Sacramento and San Joaquin rivers through San Francisco Bay to the Pacific Ocean. Freshwater enters via the Sacramento River from the north and the San Joaquin River from the south; the confluence is roughly the landward limit of ocean salt penetration (Kimmerer 2004). We focus on the upper portion of the estuary (including the Delta and Suisun Bay), which encompasses the entire range of the Delta Smelt.

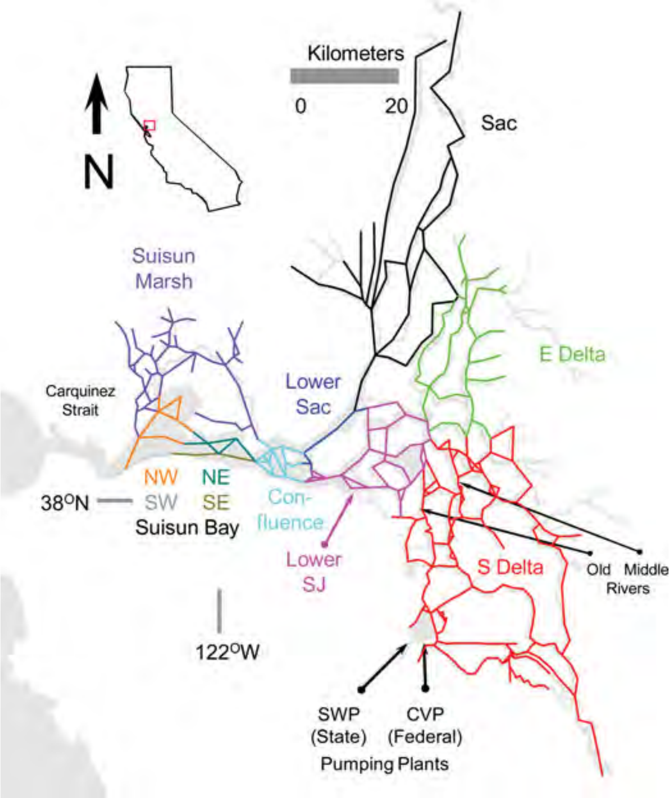

FIGURE 1. Location of the San Francisco Estuary, California, and the spatial grid and boxes used in the model. Gray represents the outline of the estuary. The 11 boxes are color coded and refer to (in numerical order): (1) Sacramento River region (Sac) of the Sacramento–San Joaquin Delta; (2) eastern Delta (E Delta); (3) southern Delta (S Delta); (4) lower Sacramento River region (Lower Sac); (5) lower San Joaquin River region (Lower SJ); (6) confluence (westernmost box in the Delta); (7) southeast Suisun Bay (SE); (8) northeast Suisun Bay (NE); (9) Suisun Marsh; (10) southwest Suisun Bay (SW); and (11) northwest Suisun Bay (NW). Additional labels show the Old River, Middle River, Carquinez Strait, and the State Water Project (SWP) and Central Valley Project (CVP) pumping plants.

The San Francisco Estuary has been described as one of the most highly altered estuarine ecosystems in the world (Nichols et al. 1986; Lund et al. 2010). Over the past 150 years, approximately 95% of the marshes surrounding the estuary have been isolated from tidal action, and numerous nonnative species have been introduced—some with substantial ecological effects (e.g., Nichols et al. 1990; Winder and Jassby 2011). The Delta, which formerly consisted of tidal marsh, is now a complex network of linked channels and sloughs surrounding islands that are protected by a constructed levee system. During the past 60 years, the upper estuary has increasingly been managed through large-scale manipulation of river flows in order to provide freshwater for agricultural, municipal, and industrial uses.

The two large water diversions in the south Delta have exported an average of 30% of the available flow into the Delta during 1960–2000, with the percentage generally increasing through time and exceeding 60% in some years and seasons (Kimmerer 2004). The State Water Project (SWP) facility provides drinking water for over 23 million Californians, and together the two diversion facilities (the SWP and the Central Valley Project [CVP]) fuel an estimated \$25 × 10^9 annual agricultural economy (Grimaldo et al. 2009). Elaborate fish recovery facilities attempt to screen fish from the diverted water but with mixed success (Kimmerer 2011). All of these changes have substantially altered both the physical and ecological aspects of the system (Nichols et al. 1986; Hollibaugh 1996; NRC 2012).

The life history of the Delta Smelt is summarized briefly here based on several sources (Moyle et al. 1992; Moyle 2002; Bennett 2005). The Delta Smelt has a relatively unusual life history strategy (Bennett 2005), as it exhibits the small size and short life span that are typical of an opportunistic life history strategy, but it has low reproductive rates that are more similar to those of an equilibrium strategist (Winemiller and Rose 1992). The Delta Smelt's life history also somewhat resembles those of salmonids (McCann and Shuter 1997) but without parental care. The geographic range of the Delta Smelt is confined to the upper San Francisco Estuary. It is primarily an annual species but with some small fraction of the population surviving a second year to spawn. Spawning takes place in freshwater during February–May at temperatures between 12°C and 20°C; spawning appears to be clustered in 2-week intervals, presumably related to the spring–neap tidal cycle. Eggs are demersal and attached; larval stages generally rear in freshwater before being transported to brackish waters, which are typically located between the confluence of the San Joaquin and Sacramento rivers and Carquinez Strait at the seaward margin of Suisun Bay (Figure 1). All life stages remain at a salinity of about 0.5–6.0 psu (the low-salinity zone) until the end of the year, when migration to freshwater begins. Delta Smelt eat primarily zooplankton throughout their lives, although adults also eat epibenthic crustaceans, such as amphipods. Delta Smelt are consumed by a variety of fish, principally visual predators.

MODEL DESCRIPTION

Overview

The model followed the reproduction, growth, mortality, and movement of individual Delta Smelt over their entire life cycle on a spatial grid of cells (Figure 1). The spatial grid was a one-dimensional network of 517 channels and 5 reservoirs used in the Delta Simulation Model (DSM2) hydrodynamic model (California Department of Water Resources [CDWR]). This one-dimensional model simulates non-steady-state hydrodynamics in a network of channels and has been widely used for analyses and water supply planning for the Delta (Kimmerer and Nobriga 2008). Simulations from DSM2 provided (1) hourly water velocities and water levels at the ends of channels and (2) hourly water flows into and out of the reservoirs. Daily water temperature, salinity, and densities of six zooplankton prey types as estimated from field data were also represented on the same spatial grid.

Each 365-d model year began on October 1, the start date for each water year. Individuals were aged on January 1 of each year. Whenever we refer to a year, it is the year that includes the summer period (e.g., model year 1996 extended from October 1, 1995, to September 30, 1996). Multiyear simulations were performed using reproduction to introduce the new individuals each year.

Reproduction was evaluated daily during the spring spawning season, and eggs developed as a daily cohort at a temperature-dependent rate. Upon hatching, new yolk sac larvae were pooled for each day and were introduced as model individuals. Individuals developed through life stages of yolk sac larva, larva, postlarva, juvenile, and adult. Growth was based on bioenergetics and zooplankton densities in the grid cells. Mortality included a stage-specific mortality rate, starvation, and mortality due to entrainment at the water diversion facilities. Movement of yolk sac larvae, larvae, and postlarvae was determined hourly by using a particle tracking model (PTM) that incorporates water velocities from the DSM2 hydrodynamic model. Movement of juveniles and adults was based entirely on a behavioral response to salinity, and the locations of individual fish on the grid were updated every 12 h.

All simulations used hydrodynamic conditions, temperature, salinity, and zooplankton densities for the period 1995–2005. This period was selected because (1) it encompasses the main period of Delta Smelt decline, (2) hydrodynamic simulations were available, and (3) field data on zooplankton and Delta Smelt were relatively complete.

Environment

A second grid of 11 coarser boxes was overlaid onto the channel grid (Figure 1) so that the more sparsely sampled field data could be used to specify daily water temperature, salinity, and zooplankton densities. The 11 boxes were determined based on previously identified regions of hydraulic similarity (e.g., Miller et al. 2012) and the availability of enough stations to ensure that at least several stations were present in each box.

Daily values of temperature, salinity, and zooplankton densities were estimated for each box and then were assigned to each channel within each box on each day (see details in Supplement A in the online version of this article). Final daily temperature and salinity values for each box are shown in Figure 2 for a year with high freshwater outflow (1998) and a year with low freshwater outflow (2001). All channels within a given box were assigned the box values. Temperature did not vary much among sampling stations within boxes, and the sampling density was too low to represent the within-box (channel-level) spatial gradients in salinity.

The food environment was represented by the biomasses of six zooplankton types: adults of *Limnoithona* spp. (calanoid copepods), calanoid copepodids, other calanoid adults, adult *Eurytemora* (calanoid copepods), adult *Acanthocyclops vernalis* (cyclopoid copepods), and adult *Pseudodiaptomus* (calanoid copepods). We included random variation when we used the boxwide mean to assign values to the channels within each box (see Supplement A). Daily zooplankton biomass densities in each box are presented for the same high-outflow (Figure 3) and low-outflow (Figure 4) years as were shown for temperature and salinity.

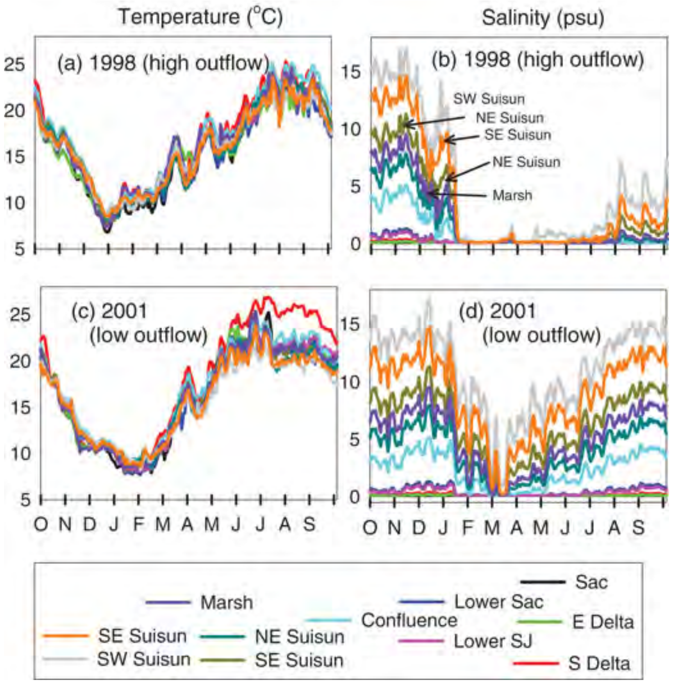

FIGURE 2. Daily temperature and salinity values in each box for **(a)**, **(b)** 1998 (a year of high outflow) and **(c)**, **(d)** 2001 (a year of low outflow). See Figure 1 for definition of box abbreviations. [Figure available online in color.]

Spawning

Each female individual that was longer than 60 mm TL at the start of the spawning season was allowed to spawn up to two times within the spawning season. We used a simple threshold of 60 mm because it was well supported by data (Bennett 2005) and because the manner in which maturity varies around the 60-mm length was uncertain. We explore a smoother maturity function in our companion paper (Rose et al. 2013).

The earliest day of spawning was first determined each year on October 1 by looking ahead at temperatures and finding the first day on which temperature exceeded 12°C in any box. On the earliest possible day of spawning in each year, a temperature of first actual spawning was assigned to each mature individual from a uniform distribution between 12°C and 20°C. To mimic the clustering of spawning on spring–neap tidal cycles, an individual spawned at the end of the 14-d tidal cycle that followed the day when water temperature in that individual's channel exceeded its assigned spawning temperature. By the time of spawning, the migratory movement algorithm based on salinity had put adults near or into freshwater boxes.

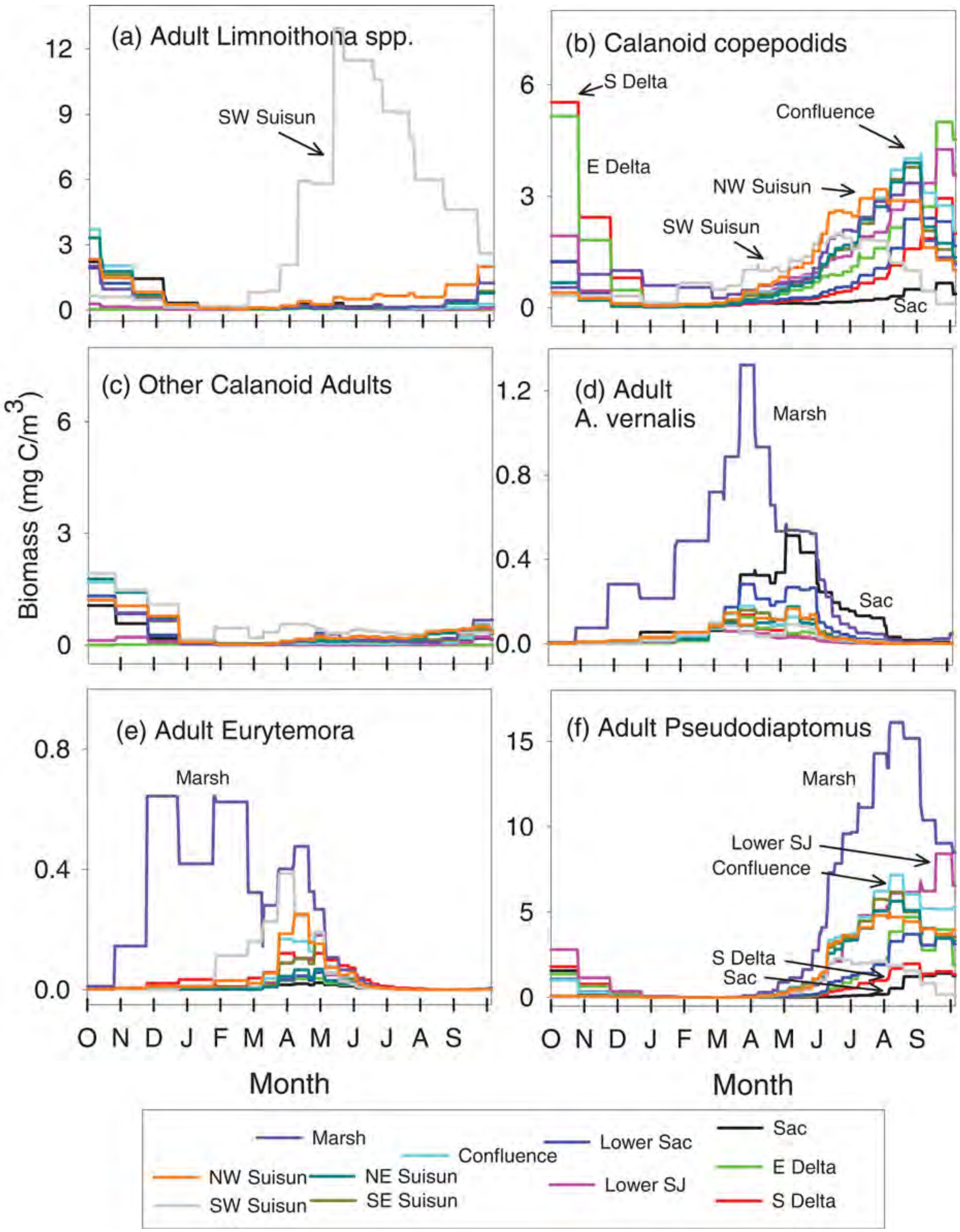

FIGURE 3. Daily biomass density values (mg C per m^3 of water) for each of the six zooplankton groups in each spatial box during a year of high outflow (1998): **(a)** adults of *Limnoithona* spp., **(b)** calanoid copepodids, **(c)** other calanoid adults, **(d)** adult *Acanthocyclops vernalis*, **(e)** adult *Eurytemora*, and **(f)** adult *Pseudodiaptomus*. See Figure 1 for definition of box abbreviations. [Figure available online in color.]

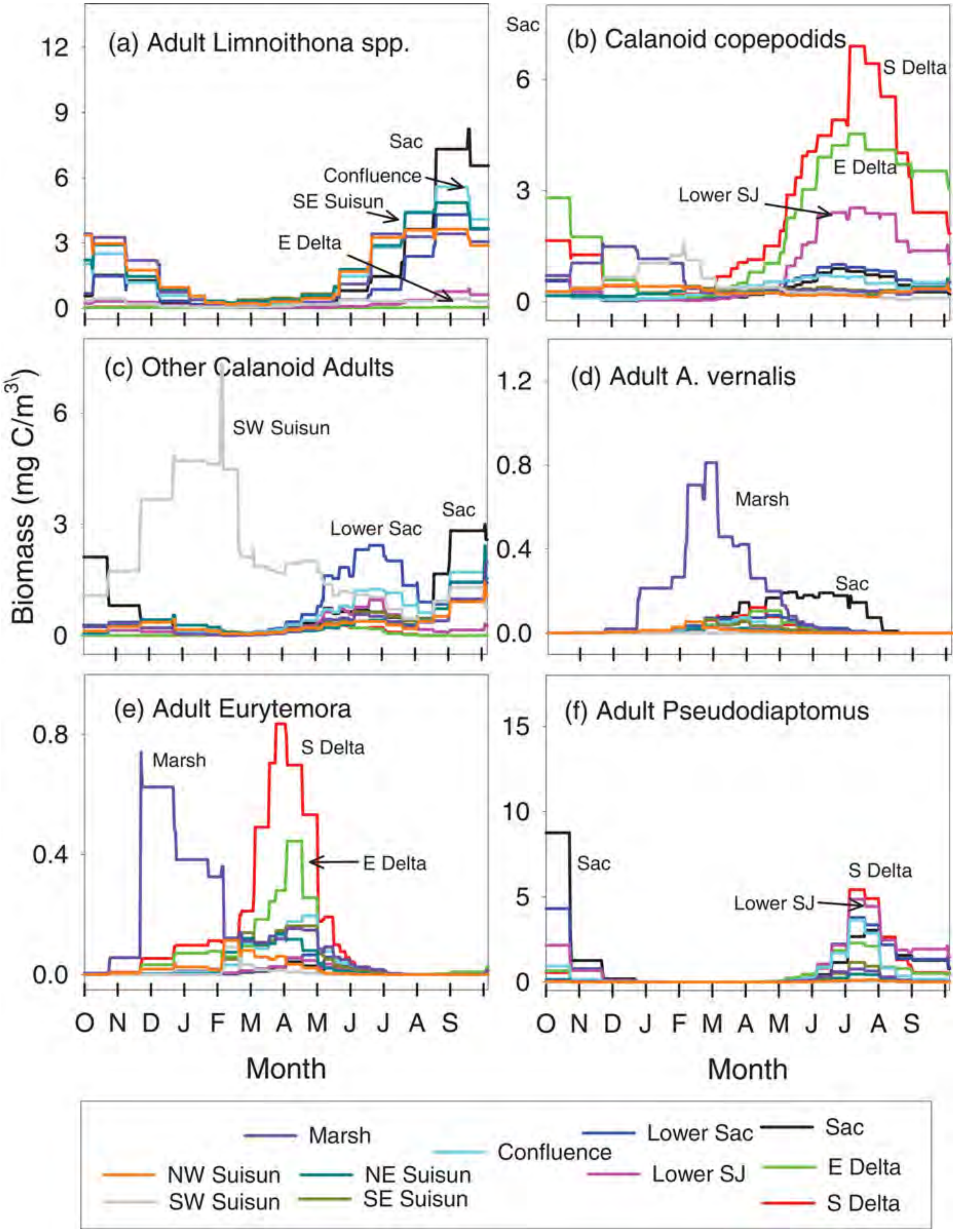

FIGURE 4. Daily biomass density values (mg C per m^3 of water) for each of the six zooplankton groups in each spatial box during a year of low outflow (2001): **(a)** adults of *Limnoithona* spp., **(b)** calanoid copepodids, **(c)** other calanoid adults, **(d)** adult *Acanthocyclops vernalis*, **(e)** adult *Eurytemora*, and **(f)** adult *Pseudodiaptomus*. See Figure 1 for definition of box abbreviations. [Figure available online in color.]

Fecundity (D; eggs/female) depended on the individual's weight on the day of spawning (Bennett 2005),

$$D = 175.4e^{\frac{L_{equiv}}{28.3}}, \tag{1}$$

where L_{equiv} (mm) is the length based on the actual weight of the fish. Upon spawning, the body weight of the individual Delta Smelt was reduced by 15%. We treated males the same as females (i.e., spawning temperatures and weight loss), but without any contribution of eggs, to produce similar weights at age.

After their first spawning event, females were evaluated daily to determine whether they would spawn a second time. Second spawning occurred if (1) the individual had regained enough weight (>95% of the weight expected from its length), (2) 14 or more days had passed since the first spawning, and (3) it was not too late (too warm) in the season for that individual to spawn in its box. The last possible day of spawning in each box was calculated as the first day after temperature exceeded 20°C plus 14 d to allow for the final tidal cycle to complete. The fecundity relationship used for the second spawning was the same as that for the first spawning, and weight was again reduced by 15%.

Eggs

Each female's first and second (if it occurred) spawns of eggs were followed separately as cohorts until hatching, when they became yolk sac larvae. Day of hatching was determined for each cohort by accumulating the daily fractional egg development (DV_e) until the degree of development exceeded 1.0. The daily fractional development towards hatching was based on temperature (Bennett 2005),

$$DV_e = \frac{1}{28.1 - 1.1 \cdot T}, \tag{2}$$

where T is the daily temperature (°C) in the box where spawning occurred. Spawning box temperature (which varied daily) was used because the eggs are attached. All eggs in each cohort that was spawned in a given box on a given day hatched on the same day. Daily egg mortality rates (M; d^{-1}) were calculated by converting hatch rates observed at constant temperature in the hatchery to daily mortality (Bennett 2005),

$$M = \frac{-\log(s)}{DV_e} \tag{3}$$

and

$$s = -2.35 + 0.45 \cdot T - 0.016 \cdot T^2, \tag{4}$$

where s is the survival fraction through the egg stage.

Yolk Sac Larvae

Beginning with yolk sac larvae, new model individuals were created and followed for the rest of their lives. New individuals were created from all those that hatched in each box on each day, and they were distinguished by whether they came from a first or second spawning event. Length (L; mm) at hatch depended on the temperature on the day of hatching (Bennett 2005),

$$L = 5.92 - 0.05 \cdot T. \tag{5}$$

Weight (g wet weight) at hatch was determined from a field-based length–weight relationship (Kimmerer et al. 2005):

$$W = 0.005 \cdot L^3. \tag{6}$$

Similar to the method used for eggs, the duration of the yolk sac larval stage was determined by accumulating the daily fractional development (DV_y) of each model individual based on the temperature in its box (Bennett 2005) until the cumulative development exceeded 1.0:

$$DV_y = \frac{1}{7.53 - 0.08 \cdot T}. \tag{7}$$

Daily mortality rate of yolk sac larvae was assumed constant (0.035 d^{-1}) and was a key parameter adjusted as part of model calibration.

Feeding Life Stages: Development and Bioenergetics

Larvae became postlarvae at 15 mm, and postlarvae became juveniles at 25 mm; juveniles then became age-1 adults and age-1 adults from the previous year advanced to age 2 on January 1 (Bennett 2005). Age-2 adults were removed from the model just before attaining age 3. Larval to postlarval development coincided with the development of a swim bladder, and the juvenile stage marked the appearance of fin folds and an association with the low-salinity zone.

The daily growth of each feeding individual was represented by a difference form of the Wisconsin bioenergetics model (Ney 1993; Hanson et al. 1997),

$$\begin{aligned} W_t = W_{t-1} + (C - R - F - U - SDA) \\ \cdot W_{t-1} \cdot \frac{e_p}{e_s} - Sp \cdot W_{t-1}, \end{aligned} \tag{8}$$

where W is the weight of each individual, C is the realized consumption rate, R is the total metabolic rate, F is egestion, U is excretion, SDA is specific dynamic action, and Sp is loss due to spawning. All rates except Sp were in units of grams of prey per gram of Delta Smelt per day (g prey·g smelt^{-1}·d^{-1} in wet weight); Sp was the fraction of weight lost (0.15) and occurred only on the day of spawning. The e_p and e_s terms (J/g) were used to convert grams of prey per gram of Delta Smelt to grams of smelt per gram of smelt, which was then multiplied by weight (W) to yield the weight change in grams of Delta Smelt per individual per day. The value of e_s was fixed at 4,814 J/g, while e_p was computed each day based on the fraction of *Limnoithona* in the diet. All zooplankton groups had an energy density of 2,590 J/g; the exception was *Limnoithona*, for which energy density was assumed to be 30% lower (1,823 J/g) because Delta Smelt grow more slowly when fed *Limnoithona* (Lindsay Sullivan, San Francisco State University, personal communication).

Total length (L; mm) was obtained from weight by using equation (6). Length was partially uncoupled from weight because length was allowed only to increase, whereas fish could lose weight. On days of weight gain, length was increased only after the individual's weight equaled that expected from its length. Thus, fish were allowed to become skinny but not fat.

Maximum consumption (C_{max}) depended on an individual's weight (W) and the water temperature (T):

$$C_{max} = a_c W^{b_c} f(T). \tag{9}$$

The temperature adjustment to maximum consumption ($f[T]$) increased from a value of CK_1 at temperature CQ to 0.98 at temperature T_O and then stayed at 0.98 until temperature reached T_M, after which the adjustment declined to CK_4 as temperature approached T_L (Table 1).

Realized consumption by the ith fish (C_i) was a functional response that depended on C_{max} and the densities of each zooplankton group j (prey density, PD_j) in the same channel as the fish:

$$C_{ij} = \frac{C_{max} W_i \left(\frac{PD_j \cdot V_{ij}}{K_{ij}}\right)}{1 + \sum_{k=1}^{6} \left(\frac{PD_k \cdot V_k}{K_{ik}}\right)} \tag{10}$$

and

$$C_i = \sum_{j=1}^{6} C_{ij}, \tag{11}$$

where C_{ij} is the daily rate of consumption of the jth prey type (six zooplankton groups) by individual fish i; V_{ij} is the vulnerability of prey type j to fish i; and K_{ik} is the half-saturation constant for fish i feeding on each prey type k. Equations (10) and (11) allowed an individual fish to consume multiple prey types without exceeding its maximum consumption. Vulnerabilities (V_{ij}) were set to 1.0 for all life stages eating all zooplankton types; the exception was Delta Smelt larvae, for which V_{ij} values of zero were used for all adult prey groups other than *Limnoithona* spp. The K-values were calibrated outside of the model to obtain diet and consumption rates that appeared realistic (Supplement B in the online version of this article).

The total metabolic rate (R) was an allometric function of weight and used an exponential relationship ($g[T]$) to adjust metabolism for temperature:

$$R = a_r W^{b_r} \cdot g(T), \tag{12}$$

where

$$g(T) = e^{(R_Q \cdot T)}. \tag{13}$$

Egestion (F) was a constant fraction of consumption, while *SDA* and excretion (U) were fractions of net assimilated energy

TABLE 1. Parameter values for each Delta Smelt life stage in the bioenergetics model.

Parameter	Description	Larvae	Postlarvae	Juveniles and adults
	Maximum consumption (C_{max})			
a_c	Weight multiplier	0.18	0.18	0.1
b_c	Weight exponent	−0.275	−0.275	−0.54
CQ (°C)	Temperature at CK_1 of maximum	7	10	10
T_O (°C)	Temperature at 0.98 of maximum	17	20	20
T_M (°C)	Temperature at 0.98 of maximum	20	23	23
T_L (°C)	Temperature at CK_4 of maximum	28	27	27
CK_1	Effect at temperature CQ	0.4	0.4	0.4
CK_4	Effect at temperature T_L	0.01	0.01	0.01
	Metabolism (R)			
a_r	Weight multiplier	0.0027	0.0027	0.0027
b_r	Weight exponent	−0.216	−0.216	−0.216
R_Q	Exponent for temperature effect	0.036	0.036	0.036
S_d	Fraction of assimilated food lost to *SDA*	0.175	0.175	0.175
	Egestion (F) and excretion (U)			
F_a	Fraction of consumed food lost to egestion	0.16	0.16	0.16
U_a	Fraction of assimilated food lost to excretion	0.1	0.1	0.1

($C - F$; Table 1):

$$F = F_a \cdot C, \tag{14}$$

$$SDA = S_d \cdot (C - F), \tag{15}$$

and

$$U = U_a \cdot (C - F). \tag{16}$$

During calibration, we adjusted the bioenergetics parameter values developed for Rainbow Smelt *Osmerus mordax* (Lantry and Stewart 1993) until we obtained growth that was realistic for Delta Smelt. We adjusted the allometric and temperature-related parameter values of maximum consumption (a_c, b_c, CQ, T_O, T_M, and T_L in Table 1) and the temperature parameter that affected respiration (R_Q in Table 1). We determined parameter values that satisfied two conditions: (1) realistic daily growth rates and optimal temperatures for growth for mid-stage-sized larvae, juveniles, and adults; and (2) realistic weights and lengths for an individual that had grown from first feeding through age 2 under daily average temperatures and a consumption rate (C) that was equal to 0.8 of the maximum (i.e., proportion of maximum consumption [p-value] = 0.8; $C = p\text{-value} \times C_{max}$). The final bioenergetics rates for the mid-stage-sized larvae, postlarvae, juveniles, and adults are shown in Supplement B.

Mortality

Mortality occurred from stage-specific mortality rates (M), starvation, entrainment losses at the two water export pumping facilities, and old age. Stage-specific mortality rates represented predation and other causes of mortality not explicitly calculated from starvation or entrainment. Daily instantaneous mortality was temperature dependent for eggs (equations 3 and 4); M was set at 0.035 for yolk sac larvae (calibrated), 0.05 for larvae, 0.03 for postlarvae, 0.015 for juveniles, and 0.006 for adults. Starvation occurred if the weight of an individual fell below 50% of the weight expected from its length. Upon reaching age 3 (i.e., the individual's third January 1), the individual died from old age and was removed from the population.

Entrainment mortality for all life stages except eggs occurred when an individual entered Clifton Court Forebay (reservoir number 4; SWP) or arrived at node 181 (CVP; Figure 1). Yolk sac larvae, larvae, and postlarvae were transported there by the PTM, whereas juveniles and adults were unaffected by hydrodynamic conditions except through salinity. Use of only those individual juveniles and adults that arrived at the SWP and CVP by behavioral movements based on salinity resulted in underestimation of the numbers entrained by the pumping facilities. Delta Smelt are recovered at the south Delta fish facilities at higher rates when daily net flow in the southern Delta (Middle and Old rivers) is southwards toward the SWP and CVP (Grimaldo et al. 2009; Kimmerer 2011). Therefore, juveniles and adults that were located in the south Delta box (box 3) of the model were exposed to additional entrainment mortality of 0.02 d^{-1} whenever the daily averaged flow in Middle River (downstream end of channel 90; Figure 1) was southward. The value of the added mortality (0.02 d^{-1}) was determined as part of model calibration.

Movement

Yolk sac larvae, larvae, and postlarvae were transported by water velocities on the spatial grid hourly by using a particle tracking approach, whereas juveniles and adults were moved every 12 h by using a kinesis approach to behavioral movement.

The PTM was a recoded version of the CDWR's PTM and used the same formulations (Wilbur 2000; Miller 2002). The CDWR's PTM has been used to examine entrainment impacts (e.g., Kimmerer and Nobriga 2008) and has been compared with other PTMs (Gross et al. 2010). Our recoded version used as input the hourly values of velocity at each end of each channel and the water level at each node that was generated by the DSM2 hydrodynamic model. The PTM kept track of the hourly positions of particles (the three larval stages) in three dimensions: along-channel (x = distance [m] from the upstream end of a channel), lateral (y = distance [m] from the center line of the channel), and vertical (z = distance [m] from the bottom of the channel). The y and z positions within a channel were altered by random perturbations and were used to adjust the x-direction velocity (Supplement C in the online version of this article).

Day-to-day movements and seasonal migrations of juveniles and adults were based on a kinesis approach (Humston et al. 2000, 2004), with salinity used as the cue. Salinity was used to simulate reasonable distributions of individuals within the system, but salinity did not directly affect growth or mortality. Rather, salinity was used to distribute individuals realistically, and individuals then experienced the local conditions (temperature and prey densities) in the channels.

Only the along-channel (x) position was tracked for juveniles and adults. At each 12-h time step, each individual's x position was updated, and its channel or reservoir location was determined. Kinesis represents the distance moved by each individual as the sum of an inertial component (IC) and a random component (RC), with the inertial component dominating when conditions (salinity) are good and the random component dominating when conditions are poor. The position in the x dimension (m from the upstream end of the channel) was updated every 12 h as

$$x_{t+1} = x_t + \Delta x_t \tag{17}$$

and

$$\Delta x_t = IC + RC, \tag{18}$$

where IC is the inertial component that depends on the movement velocity at the last time step (Δx_{t-1}), and RC is the random component based on fish swimming speed.

To compute *IC* and *RC*, we first computed the functions (f and g) that defined the degree to which salinity (S) in the box deviated from optimal salinity,

$$f(S) = H_1 \cdot e^{-0.5 \cdot \left(\frac{S - S_O}{\sigma_S}\right)^2} \tag{19}$$

and

$$g(S) = 1 - H_2 \cdot e^{-0.5 \cdot \left(\frac{S - S_O}{\sigma_S}\right)^2}, \tag{20}$$

where S_O is the optimal value of salinity (2.0 psu); σ_S $(= 3.0)$ determines how quickly the function decreases as salinity deviates from its optimal value; and the H-values are constants (0.75 and 0.90) that define the maximum values of the functions. Inertial velocity (*IC*) was then computed using the distance moved in the last time step (Δx_{t-1}) and $f(S)$:

$$IC = \Delta x_{t-1} \cdot f(S), \tag{21}$$

Equation (21) results in the individual moving at the same total velocity (inertial and random combined) as in the last time step to the degree that conditions (salinity) are favorable; $f(S)$ is larger when salinity is near the optimal value (equation 19).

The random component of distance moved (*RC*) was computed based on $g(S)$ and a random component (r):

$$RC = r \cdot g(S). \tag{22}$$

The random component r was calculated as

$$r = N(0, 1) \cdot \frac{d}{2} + d \tag{23}$$

with

$$d = \sqrt{\frac{(0.001 \cdot L \cdot \Delta t \cdot 60 \cdot 60)^2}{2}}, \tag{24}$$

where r is a normal deviate with a mean of d and an SD of $d/2$. The numerator in equation (24) represents the distance (m) moved during one 12-h time step, assuming a swimming speed of 1.0 body length/s. The parameter d computed by equation (24) is typically about 70% of the distance to account for fish not swimming in a straight line. The probability of up-estuary movement (P_{up}) was specified as 0.50; for each individual and each time step, a random uniform number was compared with P_{up} to determine the x direction of movement (seaward or up-estuary) in a channel. The distance moved in that direction was determined by the computed velocity of the individual (Δx_t; equation 18).

If individuals moved past the end of a channel, they then entered a node where they either continued into a new channel or entered a reservoir. The new channel or reservoir was randomly selected from all those connected to the node, regardless of flow (Supplement C). Individuals were simply started at the beginning of a new channel. Supplement D (in the online version of this article) shows the results of testing the behavioral movement with simplified salinity patterns on the model grid.

Up-estuary migrations of adults and seaward migrations of juveniles were simulated using the above kinesis approach by changing S_O (equations 19 and 20) and P_{up}. On December 15 of each year, the spawning migration to freshwater began by changing S_O from 2 to 0 psu and by setting P_{up} to 0.85 (rather than 0.50) so that more moves were in the up-estuary direction. On May 1, the migration of adults and juveniles back to low-salinity water was simulated by setting S_O back to 2 psu and setting P_{up} to 0.15. Once individuals reached their new optimal salinity, P_{up} was switched back to 0.50.

Numerics

We used a super-individual approach (Scheffer et al. 1995) in order to accurately simulate the addition of new yolk sac larvae each year while ensuring that we did not exceed computer limitations (Supplement E in the online version of this article). Each super-individual represented some number of identical individuals in the population, which we term its "worth." Each year during spawning, the same number of super-individuals was added, but with their initial worth adjusted to reflect the yolk sac larvae produced. Mortality acted to decrement the worth of an individual, with the worth then being used to determine population-level numbers of eggs spawned and Delta Smelt densities and abundances. We used a complicated algorithm for determining how to allocate the fixed number of super-individuals each year among hatch dates and boxes (Supplement E). In all simulations, we used 150,000 super-individuals per age-class (450,000 super-individuals total) because this was sufficient for convergence (i.e., almost identical results were obtained when we followed more super-individuals). The model was coded in FORTRAN90.

Computation of Population Growth Rate

We used the individual-based model output to estimate a simple Leslie age-based matrix model for each year, which allowed us to summarize the multidimensional individual-based model results with a single variable of annual finite population growth rate (λ). The value of λ was based on the detailed dynamics of the individual-based model but allowed for easier comparison among years. A 2×2 matrix model was estimated for each year by computing the average maturity, fecundity, and age-specific survival rates (Supplement F in the online version of this article); eigenvalue analysis was then used to determine λ. The value of λ for a specific year is a measure of the conditions for Delta Smelt during that year. The λ value is also a reflection of conditions from the previous year by indicating how growth in the fall prior to spawning affected the elements related to maturity and fecundity in the matrix.

TABLE 2. Calculation of the major model output variables examined in Delta Smelt model simulations and the calculations for the data when model–data comparisons were performed. The corresponding figures for the results are noted; "text" means the results are described in the text.

Variable	Model calculations	Data calculations
(a) January adult abundance (Figure 5)	Summed worth of all individuals on January 1; includes young of the year that just became age 1 and age-1 fish that just became age 2 but does not include age-2 fish that were just removed as they became age 3.	Catch per trawl from the spring Kodiak trawl survey for 2002–2006 was averaged for January and February (first two trawls) and expanded to population size using volume sampled, 100% efficiency, and volume of Sacramento–San Joaquin Delta and Suisun Bay less than 4 m deep. November and December midwater trawl (MWT) abundance was computed the same way but by using volume of Delta and Suisun Bay less than 4 m deep. Log(Kodiak trawl abundance) was then regressed against log(MWT abundance), and the MWT values were used to estimate Kodiak trawl values for 1995–2001.
(b) Mean length of young-of-the-year, age-1, and age-2 fish (Figure 6)	Computed the weighted mean lengths on January 1 (just before their birthdays) using worth as the weighting factor in the averaging.	Mean length of fish in the December MWT samples, excluding fish greater than 100 mm, which were assumed to be age 1 or older.
(c) Annual number of adults entrained in diversion facilities (Figure 7)	Summed worth of individuals that were killed by arrival at reservoir 4 (State Water Project) or node 181 (Central Valley Project), plus the worth associated with the added mortality of all individuals in box 3 (South Delta) when Middle River flow is negative. The amount of worth (w) attributable to Middle River-related mortality (R) versus natural mortality (M) is $w(\frac{R}{M+R})(1-e^{-M+R})$.	Methods are described by Kimmerer (2008), and results used here are shown in Figure 12a of that paper.
(d) Fraction of adults on January 1 subsequently entrained during that year	Ratio of numbers entrained (see variable c) divided by the January adult abundance (see variable a)	Methods are described by Kimmerer (2008), and results used here are shown in Figure 12c of that paper.
(e) Fraction of age-1 individuals that were mature and the number of eggs per entering age-1 individual (Figure 8)	Fraction mature was computed as the summed worth of age-1 individuals greater than 60 mm at the time of projected spawning divided by the summed worth of all age-1 individuals on the same day. The ratio of eggs to entering age-1 fish was computed as the cumulative number of eggs produced by age-1 individuals divided by the summed worth of age-1 fish on January 1 prior to spawning.	No data.
(f) Salinity weighted by densities of larvae, juveniles, and adults (Figure 9)	First, the worth of larvae (including postlarvae) was summed for each box on each day and then divided by the volume of the box to obtain number per m^3 by box on each day. Salinity in each box on each day was used to compute average salinity across boxes, weighted by the larval densities in each box. This process was repeated for juveniles and for adults. This was done for calendar years to better match following a year-class from the early spring spawning.	Number per trawl in each sample of the 20-mm, summer townet, fall MWT, and spring Kodiak trawl surveys was used to weight the salinity value measured with the trawls. Data values include a mix of larvae, juveniles, and adults that varied throughout the year depending on the survey.
(g) Proportion of individuals in and seaward of the confluence box for adults on December 14 and April 30, for postlarvae on June 24, and for juveniles and adults on September 1 (Figure 10)	For each stage and day, we summed the worth of individuals in each box and then divided the sum of worth in the confluence box and seaward boxes by the total summed worth over all boxes.	All of the fall MWT data from all stations during September–December were aggregated for each year, assigned to up-estuary of the confluence box (47 stations) or in or seaward of the confluence box (39 stations). The proportion in Figure 10f was computed from these two totals.

TABLE 2. Continued.

Variable	Model calculations	Data calculations
(h) Daily fraction of larvae plus postlarvae entrained in diversion facilities (Figure 11)	Summed worth of larval and postlarval individuals reaching reservoir 4 and node 181 divided by the summed worth of larvae and postlarvae at the end of the day plus the numbers lost to pumping plant entrainment during that day.	Methods are described by Kimmerer (2008), who used the 20-mm survey data, and the results are shown in Figure 14 of that paper. Note: Kimmerer's (2008) estimates included some juveniles as well as larvae and postlarvae. Also see recent papers about the estimation by Kimmerer (2011) and Miller (2011).
(i) Diets (text)	Computed averaged diets for each life stage using the biomass of zooplankton types eaten by every 500th individual on every 30th day. We first computed the proportions for each individual and then averaged the proportions over individuals. This resulted in individuals covering all life stages for the time periods during which the stages were present.	Diets reported by Lott (1998), Nobriga (2002), and Baxter et al. (2010), who summarized unpublished data from Steven Slater (California Department of Fish and Game); data were only sufficient for qualitative and general comparison.
(j) Annual finite population growth rate (λ; Figure 12)	The λ value was computed from a 2×2 Leslie matrix model with parameter values determined from the individual-based model output each year (see Supplement F).	No data.
(k) Stage-specific survival rates (Figure 13)	Summed worth of individuals entering each life stage during the year divided by the summed worth of individuals entering the next life stage.	No data.
(l) Averaged temperature and proportion of maximum consumption (*p*-values; text)	Computed average temperature and average *p*-value for all individuals (weighted by their worth) each day and then computed seasonal averages weighting the daily values for total daily worth of age-1 individuals during February 27–June 7 (spawning) and total daily worth of juveniles during April 18–October 1 (growing season) and October 1–December 30 (fall).	

MODEL SIMULATIONS

Calibration

The model was calibrated in three steps. We first tested the movement of juveniles and adults on test grids with fixed salinity patterns to understand movement in contrived situations where we knew the correct movement patterns (Supplement D). Once the entire model had been calibrated, we again evaluated the movement patterns among years to confirm that simulated movement was realistic under dynamic salinity conditions. The results using the full model are presented below as part of the 1995–2005 historical simulation.

The second step was to determine the *K*-values (equation 10) for each Delta Smelt life stage and each zooplankton prey group (Supplement B). We averaged daily temperature and the biomass of each zooplankton group in each box over the periods when each life stage would be in the system. We assumed that larvae, juveniles, and adults remained in each of the 11 boxes, and we then iteratively adjusted the *K*-values so that the average consumption rate (i.e., with *p*-value = 0.8) and diets were reasonably close to the available observations.

The third and final step was to put the above two calibrated components (movement and growth) into the full model and then to simulate the period 1995–2005 by adjusting only the yolk sac larval mortality rate and the entrainment mortality multiplier based on Middle River flow. The mortality rate of yolk sac larvae was adjusted because this mortality was relatively simple (i.e., only temperature dependent and of short duration). The entrainment mortality multiplier was adjusted because the role of Middle River flow in affecting entrainment is well documented (Grimaldo et al. 2009), although the magnitude is uncertain, and we had data on adult entrainment mortality (Kimmerer 2011). We adjusted the yolk sac larval mortality rate until the predicted average January abundance for 1995–2005 was close to the data average of 2.7×10^6; we then adjusted the entrainment mortality multiplier until the average annual fraction of adults removed by diversions was close to the data average of 10%. We did not try to fit to individual years or to the pattern in the time series of annual abundances. Thus, any interannual differences in model output were generated by differences in temperature, salinity, entrainment, and zooplankton densities.

Historical Simulation

We report the results from the last step of the calibration: the 1995–2005 historical simulation. The calculations that were performed to obtain all reported model outputs and to summarize the field data used for model–data comparisons are shown in Table 2. The field data for Delta Smelt originate mostly from four surveys that are conducted annually by the California Department of Fish and Game (www.dfg.ca.gov/delta/): (1) the fall midwater trawl (MWT) survey began in 1967 and samples juveniles and adults monthly during September–December at 116 stations; (2) the spring Kodiak trawl survey began in 2002 and samples adults every 2–4 weeks during winter and spring at 39 stations; (3) the 20-mm survey (larval net) began in 1995 and samples larvae at 48 stations between March and July; and (4) the summer townet survey began in 1959 and samples mostly juveniles at up to 32 stations during June–August. These field data have been described and used extensively in previous analyses (e.g., Bennett 2005; Kimmerer et al. 2009; Sommer et al. 2011; Miller et al. 2012).

The model outputs and the model–data comparisons in Table 2 confirmed various aspects of the calibration or served to assess the realism of model behavior. None of the model–data comparisons can be considered as true model validation because no data were kept aside for independent comparison. Comparisons a–d in Table 2 were related to the three steps in model calibration as described above. Maturity of age-1 individuals and the number of eggs per entering age-1 individual (Table 2, comparison e) integrated the effects of growth differences (due to temperature and prey biomass) from the previous year on reproduction. Movement patterns were confirmed by using averaged salinities weighted by Delta Smelt density (comparison f) and the proportions of individuals in and seaward of the Sacramento River–San Joaquin River confluence box (comparison g). We used monthly Delta outflows (m^3/s) from DAYFLOW (www.water.ca.gov/dayflow/) to help interpret the spatial distributions in comparison g. Comparison h, the daily fraction of larvae lost to entrainment, confirmed the realism of the pumping-related mortality determined by the PTM. Overall average diets (comparison i) were examined to confirm reasonable shifts in diet from larvae to juveniles to adults. The λ values (comparison j) and stage survival rates (comparison k) provided condensed summaries of the differences among years. Finally, comparison l identified the between-year differences in temperature and food as actually experienced by the simulated fish.

MODEL RESULTS

Dynamics within the Historical Simulation

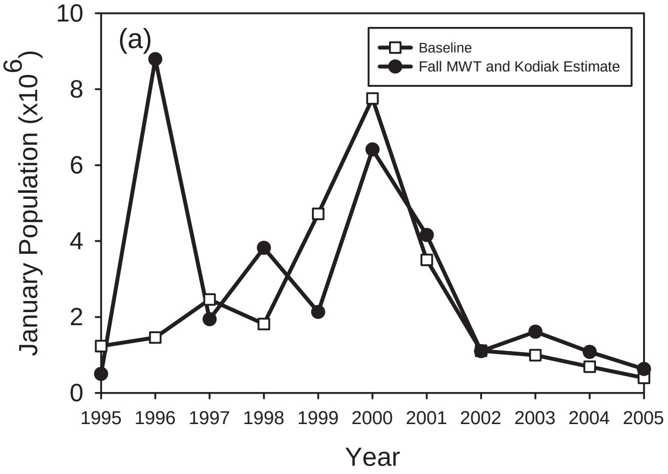

FIGURE 5. Annual abundance of adult Delta Smelt in January for 1995–2005 from the baseline simulation and as estimated from the fall midwater trawl (MWT) and spring Kodiak trawl sampling.

For the simulated period 1995–2005, calibration resulted in an average January adult abundance of 2.7×10^6 (compared to the data target of 2.3×10^6) and an average fraction of adults lost to the pumps of 11% (the target was 10%). The final calibrated mortality rates were 0.035 d^{-1} for yolk sac larvae and 0.02 d^{-1} for Middle River-related pumping mortality. Annual January abundances varied from year to year in a pattern similar to that of data-based estimates, with a peak in 2000, a decline in 2001, and then low abundances in 2002–2005 (Figure 5). One exception was that the January adult abundance in 1996 had the highest data-based estimate but a relatively low simulated value.

Simulated lengths at age on January 1 were similar to data values for young of the year about to become age 1, with both model and data values varying between 55 and 65 mm (Figure 6). Faster growth was predicted for the summer and fall of 1995 (shown as the January 1996 value), 1997 (the January 1998 value), and 2001–2004. Simulated growth was slow in 1996, 1999, and 2000, resulting in shorter fish recorded during the

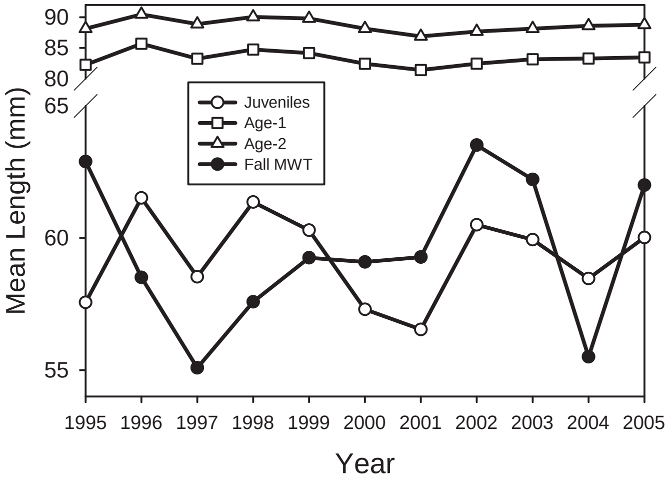

FIGURE 6. Mean total length of juvenile, age-1, and age-2 Delta Smelt on January 1 in each year (just prior to birthdays) of the 1995–2005 baseline simulation. Also included are the mean lengths of young-of-the-year fish from fall midwater trawl (MWT) sampling.

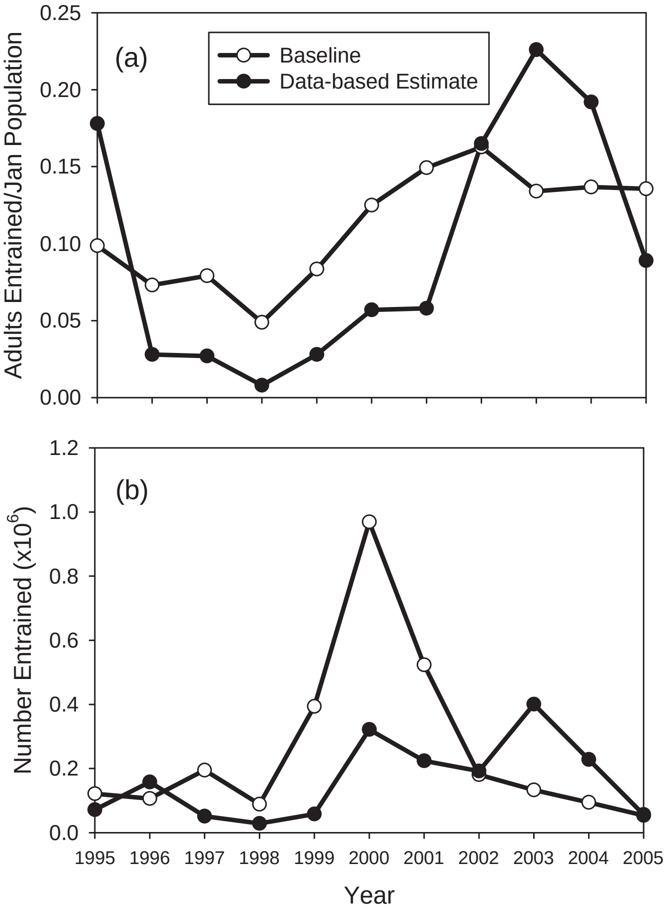

FIGURE 7. Predicted and observed annual values in 1995–2005 for **(a)** the fraction of adult Delta Smelt present in January that were entrained in pumping plants during the next few months (i.e., winter) and **(b)** the number of adults that were entrained during the same time period.

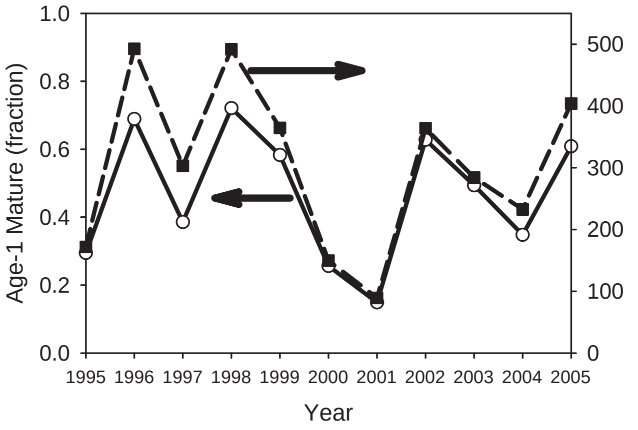

FIGURE 8. Annual fraction of age-1 individual Delta Smelt that were mature (solid line, open circles) and the number of eggs produced per entering age-1 individual (dashed line, black shaded squares) for the 1995–2005 baseline simulation.

next January. Mean lengths of about 82 mm for age-1 fish (about to become age 2) and 90 mm for age-2 fish (about to become age 3) were consistent with the results of Bennett (2005).

The predicted annual fraction of adults entrained showed less interannual variation than the data-based values (Figure 7a), and the predicted numbers entrained were as much as two times the data values for 1999–2001 (Figure 7b). Predicted and estimated annual fractions entrained were low (<10%) for 1996–1999 and then increased to 15–20% for 2002–2004. Predicted fractions showed less variation and were higher than estimated values during the earlier, low-entrainment-loss years and were lower than estimated values during the latter, high-entrainment-loss years (i.e., in Figure 7a, the line connected by open circles is flatter than the line connected by black shaded circles). Substantially more model adults were entrained during 1999–2001 than were shown by the data (Figure 7b) because the fraction entrained was higher, and in two of those years the population estimate (Figure 5a) was higher than that in the data. Overestimation of the fraction entrained in early years and underestimation of the fraction entrained in later years suggested inaccuracies in the simulated adult spatial distributions or in the use of a single value for the pumping mortality at any southward Middle River flow.

Even though the variation in mean length of age-1 adults was small (± 5 mm; Figure 6), interannual differences had large effects on maturity (Figure 8, solid line) and subsequent egg production (Figure 8, dashed line) by age-1 individuals. Age-1 individuals at the beginning of the spawning season (about 3 months into age 1) varied above and below 60 mm from year to year. This hovering around 60 mm caused the fraction of age-1 fish that were mature to range from 0.15 (in 2001) to 0.60–0.70 (in 1996, 1998, and 2002; Figure 8), tracking the slow and fast age-0 growth from the previous year (Figure 6). A greater fraction of individuals becoming mature and a higher weight of these individuals (equation 1) resulted in a fivefold difference among years in the number of eggs produced per entering age-1 individual (Figure 8). Egg production per entering age-1 fish was highest in 1998 (491.8) due to the fast growth of juveniles in 1997 and the high proportion (72%) of age-1 fish being mature at spawning; egg production per entering age-1 individual was lowest in 2001 (89.3; 15% maturity) due to slow juvenile growth in 2000. Such large variation in the fraction mature and eggs produced per entering age-1 fish seems extreme and may partially reflect the all-or-none maturity rule (100% mature if longer than 60 mm) we used. We further investigate the maturity rule in our companion paper (Rose et al. 2013).

Simulated Delta Smelt density-weighted salinities showed the up-estuary spawning migration of adults and the subsequent larval and juvenile movement seaward (Figure 9). Note that the years in Figure 9 are calendar years (i.e., they start on January 1) in order to follow a year-class. Salinity slowly rose for larvae and postlarvae during June–September as they were transported seaward (Figure 9a). Salinity also rose for juveniles during June–October (Figure 9b) after the S_O for juveniles was changed from 0 to 2 psu on May 1. Salinity for adults went from near zero in January–May to approaching 2–6 psu beginning in June

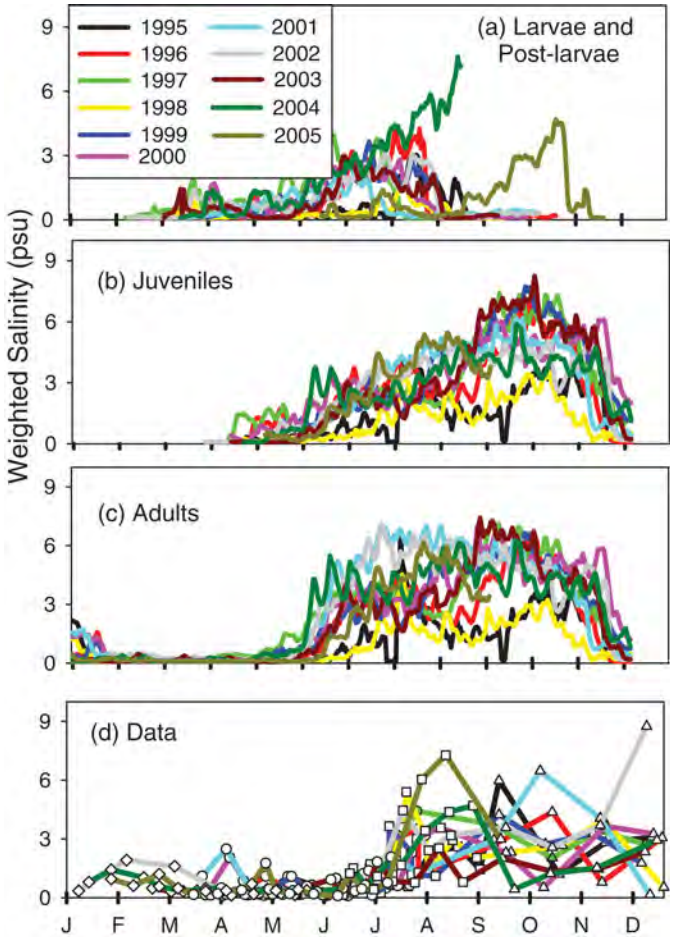

FIGURE 9. Average salinity (psu) weighted by Delta Smelt density computed daily during calendar years 1995–2005 for **(a)** larvae and postlarvae combined, **(b)** juveniles, and **(c)** adults in the baseline simulation. Panel **(d)** shows the weighted salinity values obtained by merging catch per unit effort data from the 20-mm, summer townet, fall midwater trawl (MWT), and spring Kodiak trawl surveys for 1995–2005. Years are calendar years rather than water years (e.g., 1997 refers to January–December). [Figure available online in color.]

(Figure 9c), triggered by a change in the adults' S_O back to 2 psu on May 1. During most years, the density-weighted salinity values for juveniles and adults caused their seaward migration to occur earlier than was shown in the data (June in Figure 9c versus 9d), and they occupied water during the late summer and fall with salinities of 2–6 psu, whereas the data suggested somewhat lower-salinity waters of 1–4 psu during the late summer and fall (August–October in Figure 9c versus 9d).

The interannual influence of Delta outflow on the proportion of individuals in each spatial box is shown in Supplement G (in the online version of this article) and is summarized here by using a single metric: the proportion of fish that were within or seaward of the confluence box (Figure 10). In December, prior to their up-estuary spawning migration, adults were distributed based on salinity, which was roughly correlated with average October outflow (Figure 10a). During the high-outflow years of 1996 and 1999, more than 80% of adults were in or seaward of the confluence box, whereas during the remaining years fewer than 60% were in or seaward of the confluence box.

Spawning migration (including young-of-the-year fish that became age 1 on January 1) began in January and ended by April 30, with almost all individuals located up-estuary of the confluence box (Figure 10b). Once hatched, larvae were transported by the PTM; by June 24, when postlarvae were about to become juveniles, proportions again roughly reflected outflow conditions (Figure 10c). During 1995 and 1998, which were years of high May outflow, over 80% of postlarvae were in or seaward of the confluence box, whereas during relatively low-outflow years (2001, 2002, and 2004) only 20–30% of postlarvae were located in or seaward of the confluence box. Data for 1997 appear anomalous relative to May outflow because that year had a low May outflow but the highest June outflow over the simulation time period (2,033 m^3/s versus less than 1,327 m^3/s). Juvenile and adult distributions on September 1 (Figure 10d, e) resembled each other because both reflected behavioral movement towards 2-psu water. Juveniles and adults were farthest seaward during the high outflow of August 1998 and were situated up-estuary during the low-outflow years of 2001, 2002, and 2004.

Finally, the predicted and observed proportions of adults that were in or seaward of the confluence during the fall showed moderately good agreement for extremely low- and high-outflow years but not for years of intermediate flow (Figure 10f). Predicted and observed proportions showed relatively more fish in and seaward of the confluence during 1996 and 1999 and more fish being relatively up-estuary during 1995, 2004, and 2005. October outflow was highest in 1996 and 1999 and was low in 1995 and 2004 (Figure 10a); October outflow for 2005 was not low, but the summed October–December outflow in 2005 was relatively low. However, predicted proportions were flatter than observed proportions (proportions under low outflow were above the 1-to-1 line, and proportions under high outflow were below the 1-to-1 line in Figure 10f), indicating that simulated adults were generally too far seaward under low outflow and too far up-estuary under high outflow.

The simulated daily proportion of larvae and postlarvae entrained, which results from transport by the PTM, generally agreed with the data-based estimates (Figure 11). Model predictions showed less interannual variation than the data-based values. A few extreme model values of 0.2–0.3 were predicted, whereas data values never exceeded 0.1. In both the simulation and in the data, entrainment was relatively low during 1995, 1996, and 1998 and was high during 2002 and 2003. Model-predicted entrainment was also high during 2000, 2001, and 2005, which were intermediate entrainment years in the data.

Simulated diets were reasonable and consistent among years, even between the most extreme years (not shown). Larvae consumed *Limnoithona* spp. (20% of consumed biomass) and calanoid copepodids (80%) because other prey had vulnerabilities of zero. As Delta Smelt increased in size, they consumed

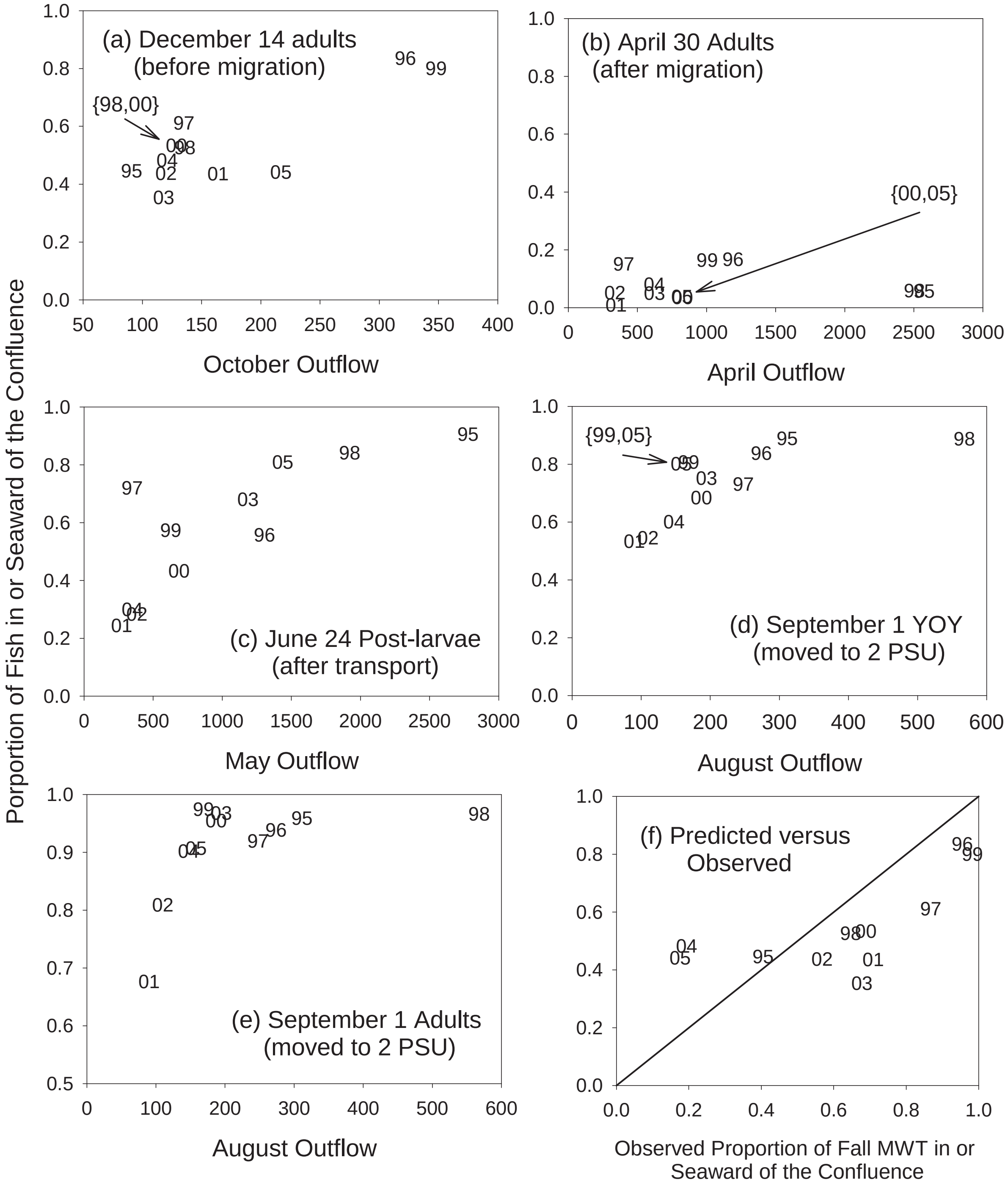

FIGURE 10. Predicted proportion of Delta Smelt individuals in the confluence and seaward boxes (see Figure 1) versus monthly Sacramento–San Joaquin Delta outflow (m^3/s) in the immediately preceding months for 1995–2005 of the baseline simulation: **(a)** adults on December 14 (before the spawning migration), **(b)** adults on April 30 (after the spawning migration), **(c)** postlarvae on June 24 (after particle tracking model transport), **(d)** juveniles (young of the year) on September 1, and **(e)** adults on September 1. Two-digit numbers indicate water years (e.g., 96 = 1996; 02 = 2002). Panel **(f)** is a comparison of the predicted proportion of Delta Smelt in and seaward of the confluence box from December 14 versus the proportion estimated from the fall midwater trawl (MWT) survey. Panel (a) uses outflow from October of the previous year (e.g., October 2001 outflow for the year 2002).

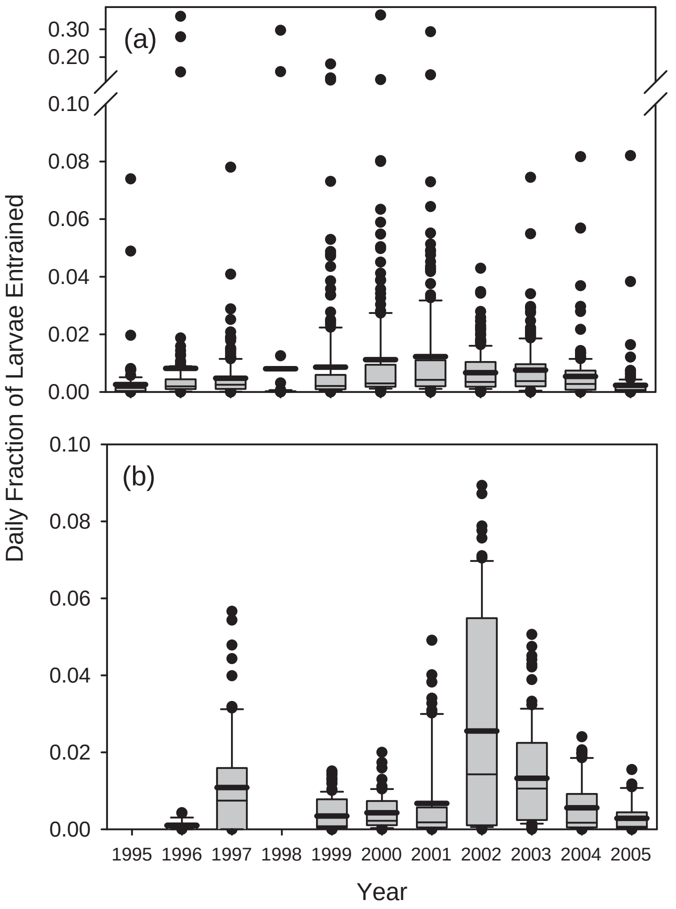

FIGURE 11. Daily entrained fraction of **(a)** Delta Smelt larvae and postlarvae combined as determined by the particle tracking model for 1995–2005 of the baseline simulation and **(b)** larvae (and some juveniles) as estimated by Kimmerer (2008). The thin line within each box is the median, the thick line is the mean, the ends of the box represent the 25th and 75th percentiles, the ends of the whiskers represent the 10th and 90th percentiles, and the black circles are points outside of the 10th and 90th percentiles.

less *Limnoithona* spp. and calanoid copepodids and more of the other four adult zooplankton types (50% [*Limnoithona* spp. and calanoid copepodids] and 50% [other types] for postlarvae; 79% and 21% for juveniles; 92% and 8% for adults). *Pseudodiaptomus* increased in the diet as fish transitioned from postlarvae to juveniles, but the *Pseudodiaptomus* contribution then decreased slightly between juvenile diets and adult diets as the biomass of this zooplankton type decreased in the fall. These results qualitatively agreed with several diet studies of Delta Smelt (Table 2), but more rigorous comparison was not attempted because of the difficulties in interpreting field diets involving rapidly digested zooplankton and without simultaneous measurement of zooplankton densities.

Best versus Worst Years in the Historical Simulation

Population growth rate (λ) from the Leslie matrix model showed that water year 1998 was the best year and water year 2001 was the worst year for the simulated Delta Smelt population (Figure 12). The λ in each year resulted from a combination of (1) growth in the prior year affecting subsequent reproduction and (2) higher stage-specific survival rates in the current year for most of the life stages. Thus, water year 1998 extended from October 1997 to September 1998 and included the fall of 1997, which led up to spawning in spring 1998. Fast growth in fall 1997 resulted in large new adults at the beginning of 1998 (Figure 6) and therefore a high fraction of mature age-1 fish and a high number of eggs per entering age-1 individual (Figure 8). The year 1998 also had moderately high growth during summer (Figure 6), the lowest entrainment losses (Figure 7a, 11), and the highest stage-specific survival rates for all life stages (Figure 13). The bad year, 2001, had the second slowest growth in the prior year (2000; Figure 6) and consequently had the lowest number of eggs per entering age-1 fish (Figure 8). In addition, 2001 had moderately high entrainment losses (Figure 7) and low survival of eggs (Figure 13a), juveniles (Figure 13e), and adults (Figure 13g, h).

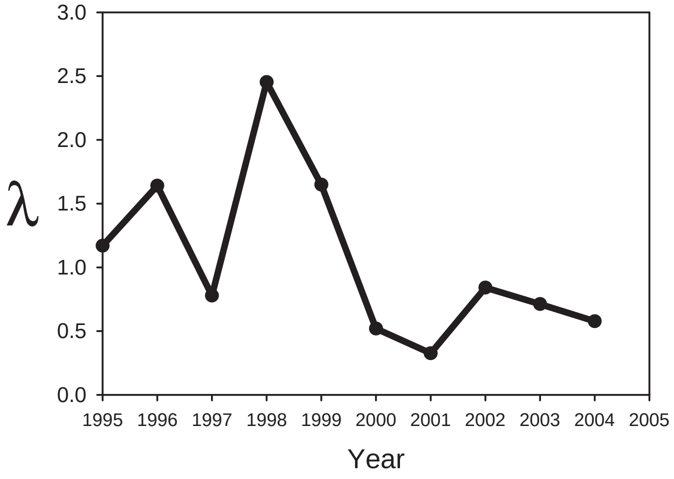

FIGURE 12. Population growth rate (λ; fraction per year) of Delta Smelt as determined by the age-based Leslie matrix model applied to individual-based model output for each year of the 1995–2005 baseline simulation. No value for 2005 was possible because the simulations ended on September 30, 2005; information through December 31, 2005, would be needed to estimate the matrix model for 2005.

Compared with 2001, water year 1998 had a relatively cool and delayed warming in spring that benefited Delta Smelt larvae, but both years had similar growth conditions for juveniles during summer. Mean temperature experienced by age-1 individuals during February 27–June 7 (spawning) was 14.8°C in 1998 versus 16.4°C in 2001. Average day of spawning was April 28 in 1998 versus April 6 in 2001, and average duration of the larval stage (inversely related to growth rate) was 25.2 d (1998) versus 28.6 d (2001). Although juveniles also experienced cooler temperatures during the early summer (16.7°C versus 22.2°C for April 18–June 7), differences became smaller when viewed over the entire growing season. Average temperature experienced by juveniles during April 18–October 1 was slightly cooler during 1998 than during 2001 (20.9°C versus

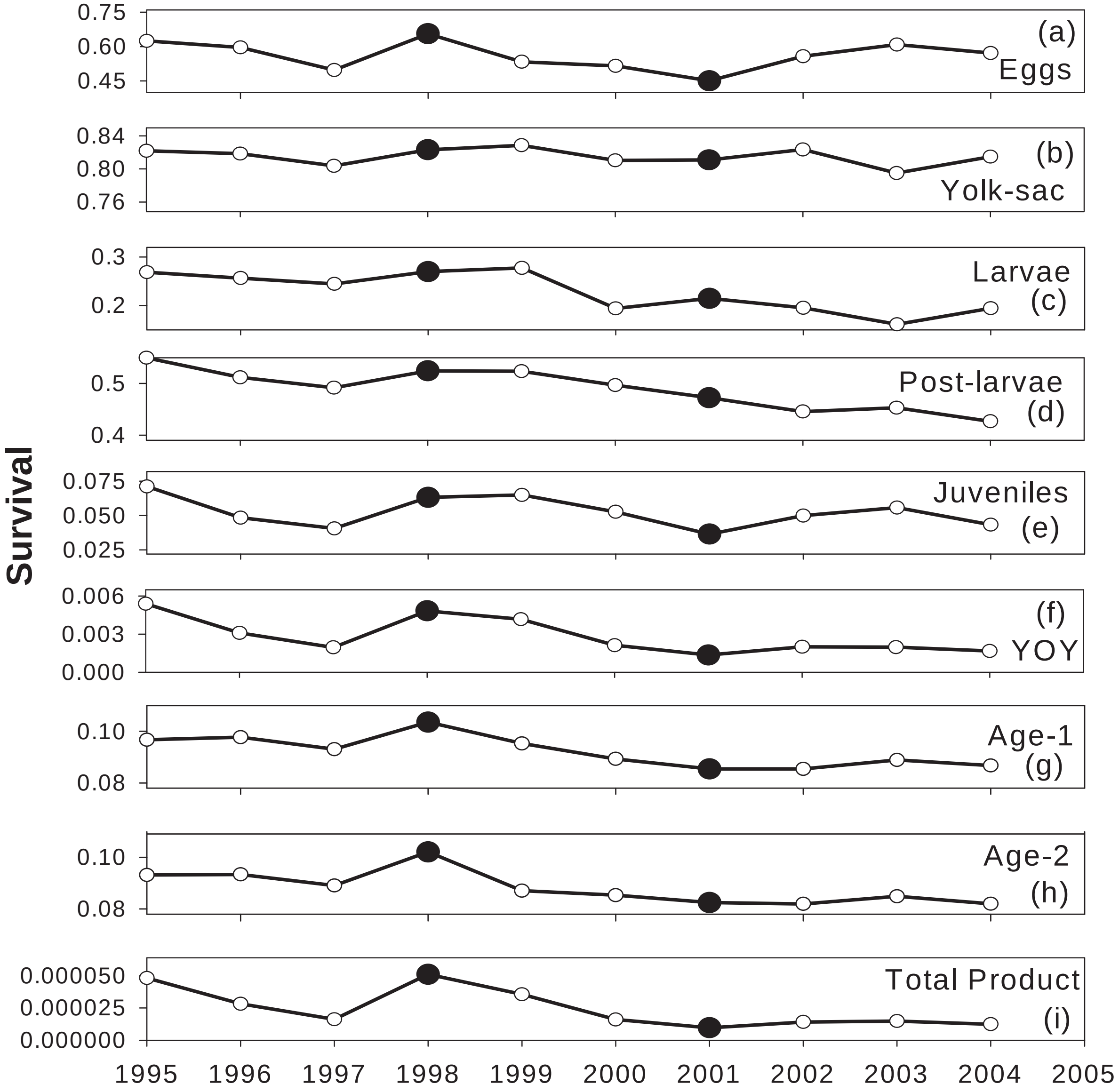

FIGURE 13. Delta Smelt stage-specific survival (fraction) from the 1995–2005 baseline simulation for **(a)** eggs, **(b)** yolk sac larvae, **(c)** larvae, **(d)** postlarvae, **(e)** juveniles, **(f)** total young of the year (product of a–e), **(g)** age 1, **(h)** age 2, and **(i)** total (product of f–h).

22.1°C), and the average *p*-value was higher in 1998 (0.89 versus 0.84). However, mean lengths of juveniles were similar between 1998 and 2001 (60.3 mm in 1999 versus 60.5 mm in 2002; Figure 6), so the difference in summer growth of juveniles between 1998 and 2001 was not a major factor.

The higher number of eggs per age-1 individual in 1998 compared with 2001 was due to faster growth during fall 1997 compared to fall 2000. Mean length of juveniles on January 1 (just before their birthday to age 1) was 61.4 mm for 1998 versus 56.5 mm for 2001. The mean *p*-value for October 1–December 30 was 0.76 in 1997 versus 0.68 in 2000; 1997 was also warmer than 2000 (15.9°C versus 15.0°C).

Delta outflow was generally higher in 1998 than in 2001 (Figure 10), so individuals were farther seaward, resulting in lower entrainment mortality during 1998. The PTM put 84% of postlarvae in or seaward of the confluence box on June 24 in 1998 compared with 24% on June 24 in 2001 (Figure 10c). Similarly, behavioral movement of juveniles resulted in about 88% of them occurring in or seaward of the confluence box on September 1, 1998, versus 53% on September 1, 2001 (Figure 10d). Almost no larvae were predicted to be entrained during 1998, whereas a daily average loss of 1.2% was predicted for 2001 (Figure 11a); the fraction of January adults entrained was 0.05 in 1998 versus 0.14 in 2001 (Figure 7a).

DISCUSSION

We used a detailed, individual-based approach to model the population dynamics of Delta Smelt during a time period that included a major population decline. The model was completely density independent; a density-dependent version is analyzed by Rose et al. (2013). The Delta Smelt has been declining since the 1980s and was one of four species to show a step decline around 2002 (Sommer et al. 2007). The choice of a detailed individual-based model may seem odd because of the extensive data demands of this general approach. Survey data-based modeling approaches are easier to justify in terms of calibration and in testing the degree of fit (e.g., Thomson et al. 2010; Miller et al. 2012); however, unlike our process-based approach, survey data-based approaches do not provide a means of assessing cause-and-effect relationships and so far have not helped to settle the controversy over the causes of the decline.

We opted for a spatially explicit, individual-based approach to explore the potential causes for the Delta Smelt's decline and the conditions that result in good versus bad years for Delta Smelt. The term "spatially explicit" refers to multiple, linked spatial boxes with different conditions among them. The individual-based approach allows for relatively easy simulation of movement and for local experiences to accumulate as each individual moves among the spatial boxes. A spatially explicit approach was required to enable a model that could (1) represent feeding, growth, reproduction, and movement in some detail; and (2) simulate how interannual variation in spatial distributions by life stage interacted with dynamic habitat. The chief disadvantage of such a complicated mechanistic model is that describing how it works can be difficult (Grimm et al. 2006), and many of the assumptions and parameter values must be based on judgment; thus, replication of the modeling by others is a challenge (Wilensky and Rand 2007). Indeed, the output of our model was sufficiently complicated that we chose to fit an age-structured matrix model to its output to provide a more straightforward summary of each year's condition. Our model is designed for exploring hypotheses about some of the factors affecting Delta Smelt population dynamics but is not designed for forecasting future Delta Smelt population abundances. Hypotheses about future conditions can be explored with our model but in a relative way, whereby simulated values are compared with some simulated baseline condition.

Maunder and Deriso (2011) also fitted a stage-based model of Delta Smelt by using the same extensive long-term monitoring data used here. By including covariates such as annual entrainment rate in their model, Maunder and Deriso (2011) were able to evaluate the relative importance of different factors. Their data-based modeling approach is relatively easy to describe (mathematically compact) and can be easily judged for its performance and skill (fit to data), but the approach also inherits problems with the monitoring data in terms of bias and process versus observation errors and is heavily correlation based. Clearly, the data-based approach of Maunder and Deriso (2011) and the detailed, process-based approach used here can complement each other, and detailed comparison between the two approaches would likely allow for more insights than either approach alone can provide.

Calibration of complicated individual-based models is always a challenge. Our approach was first to adjust the movement and feeding algorithms externally under simplified conditions and then calibrate by adjusting two mortality-related parameters for the 1995–2005 historical simulation to get the averaged population abundance and averaged fraction entrained to match the data. None of the calibration steps involved adjustments to fit the model to specific years.

Model results were generally consistent with the available data and information (Table 2) about Delta Smelt. The model reasonably matched a variety of measures related to growth, mortality, and movement. Predicted growth resulted in realistic lengths at age (Figure 6). The PTM produced reasonable larval entrainment rates (Figure 11), and a simple function of Middle River flow yielded annual adult entrainment fractions that mimicked the observed values (Figure 7). Movement was confirmed both based on salinity experienced by individuals (Figure 9) and geographically (Figure 10). The fraction of individuals in the confluence box and seaward boxes during the fall agreed with estimates from fall MWT sampling. Thus, the calibrated model is a good descriptor of the 1995–2005 conditions and is useful for comparing Delta Smelt dynamics among those years. We caution that our bioenergetics model was sufficient for relating prey and temperature to growth, but it must be re-evaluated for other purposes.

There were several major discrepancies between model results and observed values. First, the model underestimated the January abundance in 1996 (Figure 5), and the reason for this is unclear. Second, the model overestimated the degree of adult entrainment in early years and underestimated the degree of adult entrainment in later years (Figure 7). This lack of sufficient interannual variation in simulated adult entrainment may be attributable to the simulated movement of adults being too similar among years (Figure 10f); the center of distribution for simulated adults was less variable across years than the center of distribution for fish caught by the fall MWT. Another possible explanation is that adult entrainment mortality was switched on or off depending on the sign of Middle River flow, whereas analyses showed that the actual entrainment rate probably increases with the magnitude of southward flow toward the diversion facilities (Kimmerer 2011).

A third discrepancy between the model and the data was that movement in the model tended to put juveniles and adults in water that was too saline during late summer to winter (Figure 9). This could reflect a conceptual difference between the data-based and modeled density-weighted salinities. Because the model tracks each individual, an individual-weighted salinity is unbiased by any sampling error. In contrast, the sampling programs catch relatively few fish and do not sample all salinities equally. However, even with the sampling issues, the results suggest that the model is contributing to this discrepancy. Two possibilities are that (1) behavioral movement of juveniles in the model may be too slow to react to local salinity changes (Supplement D) and (2) the starting locations from the PTM were too far seaward. Some of the movement of late larval Delta Smelt in nature likely is a result of both transport (which we assumed) and behavior as the fish gain competence to direct their movements.

Finally, the model showed wide fluctuations in the fraction of age-1 individuals that were mature and the number of eggs per entering age-1 individual (Figure 8) from small changes in mean length (Figure 6). Although we lack data with which to compare these results, these differences among years seemed larger than what we would expect to see in the real population. We partially address this in Rose et al. (2013) by including length-dependent maturation as one of the alternative baselines.

We performed many comparisons of model results with the available data (Table 2), but we did not perform the classical model calibration and validation comparisons and we did not compare model predictions with commonly used abundance indices from the monitoring programs. We focused on using most of the data for calibration and often in a pattern-matching mode (Grimm et al. 2005) rather than a more traditional comparison of predicted values versus observed data (Stow et al. 2009); thus, some of the consistency between the model and the data was a result of calibration. While Delta Smelt abundance indices from the various monitoring programs have been used extensively as indicators of population abundance and survival (Bennett 2005; Maunder and Deriso 2011; Miller et al. 2012), we found the model–data comparisons using the indices to be uninformative due to the sensitivity of the indices to calculation details, such as the months included and the gear selectivity (e.g., Newman 2008).

Our analysis of model results and data for 1995–2005 clearly illustrated why it has been difficult to ascribe the Delta Smelt's decline to a single causative factor, either over the long term or as part of the recent 2002 decline. Interannual variation in λ (Figure 12) was due to a combination of the effects of temperature, salinity, larval growth, hydrodynamics, and growth of juveniles in the prior year affecting the movement, growth, mortality, and reproduction in various combinations of life stages. Small changes in mean length of young-of-the-year fish from the previous year (Figure 6) were amplified into large effects on egg production (Figure 8), and temperature affected the timing of spawning and the subsequent growth of larvae.

We did not include an explicit representation of turbidity in the final version of our model. Turbidity affects spatial distributions (Feyrer et al. 2007; Nobriga et al. 2008) and larval growth (Baskerville-Bridges et al. 2004) of Delta Smelt. We initially included turbidity (estimated from extensive Secchi depth measurements) in the same way that we included salinity and temperature (Supplement A). Turbidity showed the expected decrease during the modeled time period, which is part of a longer-term downward trend (Kimmerer 2004; Wright and Schoellhamer 2004; Nobriga et al. 2008). However, we had no basis upon which to determine relationships between turbidity and growth rate or mortality rate, and thus we could have simulated a decline in the Delta Smelt population based solely on the lower turbidity in the later years. Because we predicted the decrease in Delta Smelt without turbidity (i.e., based on hydrodynamics, temperature, salinity, and zooplankton), a turbidity effect was not included.

In the companion paper (Rose et al. 2013), we further explore Delta Smelt dynamics using the individual-based model. We configure alternative baseline simulations and perform a simulation experiment to further refine our understanding of bad versus good years for Delta Smelt. We vary salinity, temperature, zooplankton, hydrodynamics, and eggs per entering age-1 individual between the best year (1998) and the worst year (2001) to systematically quantify the effects of each factor and their combined effects on λ. We then show that these results are robust to alternative baseline configurations.

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Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: II. Alternative Baselines and Good versus Bad Years

Kenneth A. Rose [a] , Wim J. Kimmerer [b] , Karen P. Edwards [c] & William A. Bennett [d]

[a] Department of Oceanography and Coastal Sciences , Louisiana State University , Energy, Coast, and Environment Building, Baton Rouge , Louisiana , 70803 , USA

[b] Romberg Tiburon Center for Environmental Studies , San Francisco State University , 3152 Paradise Drive, Tiburon , California , 94920 , USA

[c] Environment Agency, Manley House , Kestrel Way , Exeter , EX2 7LQ , UK

[d] Center for Watershed Sciences, John Muir Institute of the Environment, Bodega Marine Laboratory , University of California , Davis, Post Office Box 247, Bodega Bay , California , 94923 , USA

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ARTICLE

Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: II. Alternative Baselines and Good versus Bad Years

Kenneth A. Rose*
Department of Oceanography and Coastal Sciences, Louisiana State University,
Energy, Coast, and Environment Building, Baton Rouge, Louisiana 70803, USA

Wim J. Kimmerer
Romberg Tiburon Center for Environmental Studies, San Francisco State University,
3152 Paradise Drive, Tiburon, California 94920, USA

Karen P. Edwards
Environment Agency, Manley House, Kestrel Way, Exeter EX2 7LQ, UK

William A. Bennett
Center for Watershed Sciences, John Muir Institute of the Environment, Bodega Marine Laboratory,
University of California, Davis, Post Office Box 247, Bodega Bay, California 94923, USA

Abstract

We used a previously described individual-based population model to further explore the population dynamics of Delta Smelt *Hypomesus transpacificus* in the upper San Francisco Estuary. We formulated four alternative baseline configurations of the model and used a factorial design to systematically isolate the effects of factors that determined a good versus bad year. The alternative baseline conditions were obtained by substituting different assumptions about growth, maturity, and mortality into the original baseline configuration. In the simulation experiment, we varied five factors by setting each value to its 1998 (best year) or 2001 (worst year) value: salinity, temperature, zooplankton densities, hydrodynamics, and eggs per age-1 individual at spawning. Although some of the alternative baselines resulted in lower January abundances, estimated finite population growth rates were very similar for all versions. The simulation experiment showed that juvenile growth in the winter prior to spawning (i.e., eggs per age-1 individual) was the most important single factor in making 2001 a bad year, although no single factor alone was sufficient to fully account for the poor conditions in 2001 relative to 1998. Temperature played an important secondary role, and hydrodynamics played a more minor role. The results of the simulation experiment were robust, as similar results were obtained under the four alternative baselines. We compare our results with previous modeling and statistical analyses of the long-term monitoring data; we also discuss some implications of our results for Delta Smelt management and suggest future directions for analyses.

The Delta Smelt *Hypomesus transpacificus* resides only in the San Francisco Estuary and is listed as threatened under the U.S. Endangered Species Act and as endangered under the California Endangered Species Act. Abundance of Delta Smelt started to decline in the 1980s, and a sharp decrease starting in 2001 led to a series of management actions that were intended to benefit the species but that also involved reducing the water available to be diverted for irrigation and water supply (NRC

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*Corresponding author: karose@lsu.edu
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2012). The State Water Project and the Central Valley Project have exported an average of 30% of the freshwater flowing into the estuary during 1960–2000, with the percentage generally increasing through time and exceeding 60% in some years and seasons (Kimmerer 2004). The State Water Project facility provides drinking water for over 23 million Californians; combined, the two diversion facilities fuel an estimated $\$25 \times 10^9$ annual agricultural economy (Grimaldo et al. 2009).

A suite of factors has been identified as important in contributing to the decline of Delta Smelt. These factors include entrainment by water diversion facilities (Kimmerer 2008, 2011; Miller 2011), contaminant effects (Kuivila and Moon 2004; Connon et al. 2009; Brooks et al. 2012), shifts in the zooplankton (prey) community (Nobriga 2002; Feyrer et al. 2003; Winder and Jassby 2011), and changes in physical habitat (Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009). The role of these factors in contributing to the Delta Smelt's decline has been examined by using statistical analysis of long-term field data (Mac Nally et al. 2010; Thomson et al. 2010; Miller et al. 2012) and population dynamics modeling (Maunder and Deriso 2011). These analyses have led to what many consider to be contradictory conclusions about the relative importance of various factors in affecting Delta Smelt population dynamics (NRC 2010; Kimmerer 2011; Miller 2011).

Determining the factors that affect Delta Smelt population dynamics is critical for formulating effective remediation actions. Remediation actions under the federal Endangered Species Act are termed "reasonable and prudent alternatives" (RPAs), and specific actions were proposed as part of the recent biological opinion for Delta Smelt (USFWS 2008) and were subsequently argued in court (NRC 2010). One RPA restricts water diversions during the winter to limit losses of Delta Smelt at the diversion facilities (Grimaldo et al. 2009; Kimmerer 2011). Another controversial RPA was designed to protect fall habitat by using reservoir releases to maintain the estuarine salinity field in certain spatial regions (NRC 2010). The high economic costs of these various management actions, coupled with uncertainty about how they may affect Delta Smelt population dynamics, have led to controversy (NRC 2012).

In a companion paper (Rose et al. 2013, this issue), we described an individual-based population model of Delta Smelt and used a historical baseline simulation for 1995–2005 to identify the factors leading to good and bad years for Delta Smelt. In the present paper, we extend the analysis of Rose et al. (2013) by formulating alternative baseline configurations of the model and by using a factorial design to systematically isolate the effects of factors that determined a good year versus a bad year. We formulated four alternative baseline conditions by substituting different assumptions about growth, maturity, and mortality into the baseline configuration. The four alternative baselines were (1) fixed larval growth instead of food-dependent larval growth, (2) size-dependent mortality instead of stage-dependent mortality, (3) density-dependent mortality instead of density-independent mortality, and (4) length-dependent maturity rather than a length threshold for maturity. Each of these assumptions was important to baseline dynamics, and each was uncertain. Our earlier identification of good and bad years was from the historical simulation, and the effects of some factors can be confounded by the autocorrelation that is inherent in a historical simulation. Here, we follow up with a designed simulation experiment in which we systematically varied the factors that are potentially important in determining good and bad years, and we further show the robustness of the simulation experiment results by repeating the experiment for each of the four alternative baseline conditions. We demonstrate that the results obtained under the original baseline conditions were similar under the four alternative baseline conditions (i.e., robust), and we further refine the role of various factors in determining good and bad years.

MODEL DESCRIPTION

Overview

The individual-based model followed the reproduction, growth, mortality, and movement of super-individuals over their entire life cycle (from eggs to age 3) on the same spatial grid as the Delta Simulation Model (DSM2) hydrodynamics model that was developed by and is widely used by the California Department of Water Resources (baydeltaoffice.water.ca.gov/modeling/deltamodeling/models/dsm2/dsm2.cfm). A model year was defined as a water year: October 1 of the previous year to September 30 (e.g., model year 2001 extends from October 1, 2000, to September 30, 2001). The model is described in detail by Rose et al. (2013) and is briefly summarized here.

The spatial grid was one-dimensional, with 517 channels and 5 reservoirs (Figure 1 in Rose et al. 2013). The DSM2 hydrodynamics model provided hourly values of water velocities and flows into and out of channels and reservoirs, which were used as inputs to a particle tracking model (PTM) that was embedded in the Delta Smelt individual-based model. A second grid of 11 coarser boxes was overlaid onto the channel grid, and values of daily temperature, salinity, and biomass densities of six zooplankton groups in each box were used to assign values to each channel.

For each super-individual, we tracked a suite of traits, including life stage, growth rate, weight, length, age, diet, location on the grid, maturity status, fecundity, and worth. Worth was the number of identical population individuals represented by the super-individual. Rather than following every individual and removing them upon death, we followed a fixed number of super-individuals and decreased their worth in each time step to account for mortality (Scheffer et al. 1995). All computations were scaled from the super-individuals to the population by multiplying by the worth of the super-individuals. Individuals were assigned to five life stages: egg, yolk sac larva, postlarva, juvenile, and adult. Advancement to the next life stage (development) was based on (1) temperature for egg to yolk sac larva

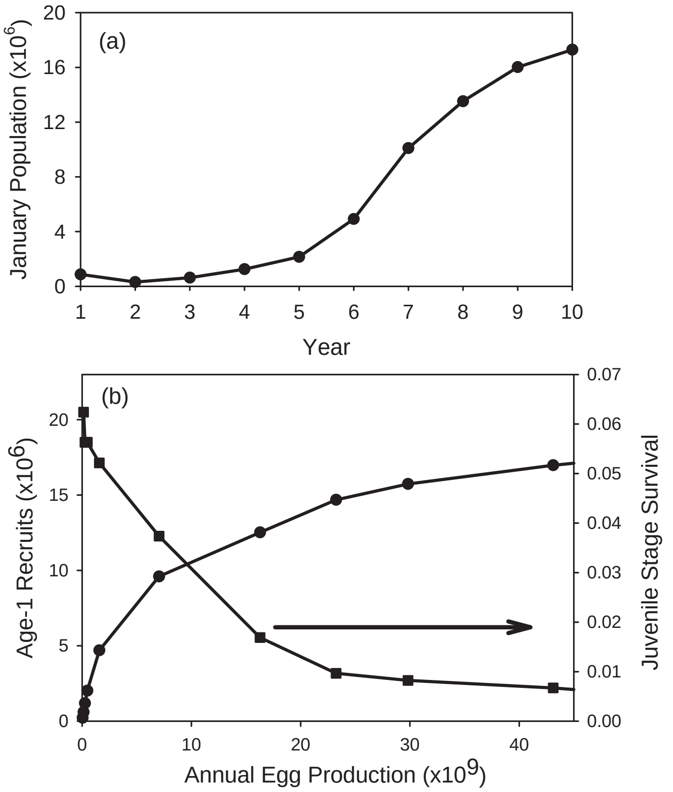

FIGURE 1. Simulated adult Delta Smelt abundance over time and juvenile survival from each year in a 15-year model run with artificially increasing egg production every year and density-dependent juvenile mortality: **(a)** adult abundance in January of each year and **(b)** age-1 recruits (circles, primary *y*-axis) and juvenile-stage survival (squares, secondary *y*-axis) versus annual egg production for each year.

to larva; (2) length for larva to postlarva to juvenile; and (3) date (January 1) for juvenile to age 1 and for age 1 to age 2.

Growth increments at each time step were determined from body weight, temperature, and the biomass densities of the six zooplankton groups (adult *Limnoithona* spp.; calanoid copepodids; other calanoid adults; adult *Eurytemora*; adult *Acanthocyclops vernalis*; and adult *Pseudodiaptomus*). Length was then increased if fish weight had increased sufficiently. Mortality was a stage-specific, fixed rate plus starvation (if the weight of an individual fell below 50% of the weight expected for its length) and entrainment by the two water diversion facilities. Movement on the spatial grid was by physical transport using a PTM for yolk sac larvae, larvae, and postlarvae; movement was behavioral (in response to salinity) for juveniles and adults. Development, reproduction, growth, and mortality were updated daily, whereas movement of eggs and all larval stages was updated hourly and movement of juveniles and adults was updated every 12 h.

Model Outputs

In our companion paper (Rose et al. 2013), we presented a detailed comparison between individual-based model outputs and data. We focus here on model predictions involving a small subset of those output variables. The major outputs presented for all simulations in this paper are the annual adult abundance in January and the annual finite population growth rate (λ). Annual adult abundance in January was computed as the summed worth of all individuals on January 1, including the young of the year that just became age 1 and the age-1 fish that just became age 2; it did not include age-2 fish that were just removed as they became age 3. We used the individual-based model output to estimate a Leslie age-based matrix model for each year to summarize the complicated individual-based model results with a single variable, λ. The value of λ was based on the detailed dynamics of the individual-based model but allowed for easier comparison among years. A 2×2 matrix model was estimated each year by computing the average maturity, fecundity, and age-specific survival rates and by using eigenvalue analysis to determine λ (see Supplement F in the online version of Rose et al. 2013).

Additional model outputs were used selectively to configure or confirm the alternative baselines and to provide some explanation for how the factors in the simulation experiment (described below) affected Delta Smelt. These outputs were defined and their calculations were described by Rose et al. (2013): stage-specific survival rates, recruitment (number of entering age-1 individuals on January 1), fraction of entering age-1 fish that were mature at the time of spawning, number of eggs per entering age-1 individual, percentage of individuals in and seaward of the Sacramento River–San Joaquin River confluence box at various times during the year (together with monthly average Sacramento–San Joaquin River Delta [hereafter, "Delta"] outflows), average daily fraction of larvae that were entrained in water diversions during a year, and annual fraction of adults that were entrained. Finally, we used a Lagrangian approach and reported the averaged values of p (proportion of maximum consumption) and temperature experienced by individuals for selected time periods in the simulations.

MODEL SIMULATIONS

Alternative Baselines

We configured four additional versions of the baseline model: fixed larval growth, size-dependent mortality, density-dependent mortality, and length-dependent maturity. We used the historical baseline simulation of 1995–2005 to help configure and calibrate the alternative baselines.

Fixed larval growth.—Model predictions of Delta Smelt abundance in the historical simulation were sensitive to larval growth rates, and we were uncertain about our formulation of larval feeding and bioenergetics. Use of a fixed duration for the larval stage eliminated variation in larval growth as a factor in year-to-year differences. Larval growth was fixed by specifying the larval duration in days rather than letting the transition from larva to juvenile be determined by length. We used the average larval duration over years from the baseline simulation (26 d) for all simulations with the fixed larval growth rate.

Size-dependent mortality.—Mortality in the original baseline version was constant within each stage but decreased with successive stages, so penalties in survival for slow growth occurred only through the delay in transition from larvae to postlarvae and from postlarvae to juveniles. Making mortality length dependent reflected the idea that vulnerability to predation mortality decreases with increasing size (Sogard 1997; Bailey and Duffy-Anderson 2010; Gislason et al. 2010), so that faster growth would increase cumulative survival regardless of how stage transitions were triggered. We assumed that mortality rate was a function of length (M_L; d^{-1}) for larvae through adults; we then fit the function to the constant stage-specific mortality rates from the baseline simulation, associating the rate with the midpoint length of each stage:

$$M_L = -0.034 + 0.165 \cdot L^{-0.322}. \tag{1}$$

We re-ran the 1995–2005 simulation and compared averaged annual stage-specific fractional survival rates between the baseline and the alternative with size-dependent mortality (Table 1) to confirm that this alternative produced mortality rates that were generally similar to those from the original baseline. Survival from yolk sac larva through age 2 was similar (4.4×10^{-5} in the baseline versus 3.5×10^{-5} under size-dependent mortality); juvenile survival increased (0.054 in the baseline; 0.073 under size-dependent mortality), and age-1 survival was approximately halved (0.092 in the baseline; 0.044 under size-dependent mortality).

Density-dependent mortality.—The original baseline version was set up as density independent because the recent Delta Smelt population is at such a low level that density-dependent effects seem unlikely. To allow for subsequent simulations at higher Delta Smelt densities, we included an alternative baseline with density-dependent mortality. The juvenile stage is the likely stage for density dependence based on general theory (Rothschild 1986; Cowan et al. 2000). Bennett (2005) and Maunder and Deriso (2011) found evidence for a density-dependent relationship between summer and fall Delta Smelt indices, and this relationship occurs in our simulation for the juvenile life stage. We assumed a multiplier of the juvenile daily mortality rate based on the normalized density of juveniles in each box on each day,

$$M' = M \cdot e^{3.0\left(\frac{D_t}{0.005}\right)}, \tag{2}$$

where D_t is the density of juveniles (number/m^3) and 0.005 is an average juvenile density (number/m^3).

We calibrated the value of 3.0 in equation (2) to obtain realistic maximum January adult abundances of about 20–25 million; the highest abundance estimate from the spring Kodiak trawl and fall midwater trawl (MWT) data during 1968–2006 was 24.3 million in 1981. We ran the model by repeating 1995 conditions from the historical simulation (high Delta Smelt survival) but with artificially increased egg production each year to generate a spawner–recruit curve under ever-increasing January adult abundances. We adjusted the multiplier in the exponent within equation (2) (final value = 3.0) until it generated a leveling off at high egg production that occurred roughly with about 20–25 million adults in January (Figure 1a). Juvenile-stage survival decreased with increasing population abundance from 0.06 to less than 0.01, resulting in a leveling off of age-1 recruits at about 20 million (Figure 1b). Abundance of age-1 recruits was similar to January adult abundance because most of the adults were age-1 individuals.

TABLE 1. Stage-specific durations (d) and survival (fraction) of Delta Smelt averaged over the 1995–2005 simulations for the original baseline and the alternative baseline that used size-dependent mortality.

	Duration (d)		Survival (fraction)	
Stage	Baseline	Size dependent	Baseline	Size dependent
Eggs	10.5	10.4	0.56	0.57
Yolk sac larvae	4.88	4.87	0.82	0.71
Larvae	26.3	26.0	0.23	0.25
Postlarvae	21.7	22.2	0.49	0.50
Juveniles	186	187	0.054	0.073
Age 1	365	365	0.092	0.044
Age 2	365	365	0.088	0.11

Length-dependent maturity.—The simple maturity rule (fish > 60 mm TL are mature) in the original baseline was substituted with a smoother, length-dependent maturity relationship (Figure 2). Model results were potentially sensitive to small

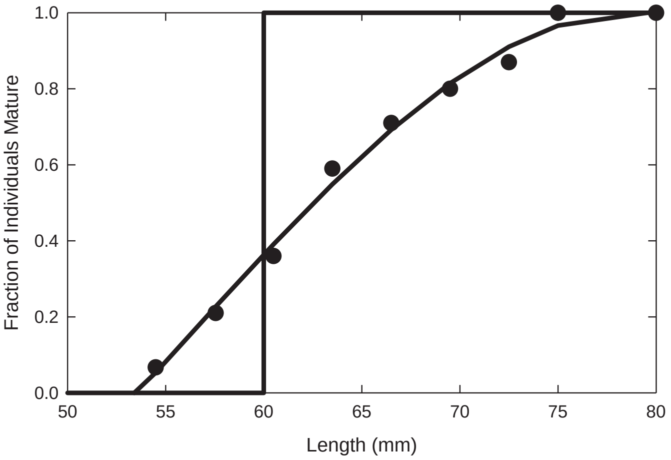

FIGURE 2. Fraction of Delta Smelt individuals that were mature as function of length for the baseline (60-mm cutoff) and the length-dependent maturity alternative. The points (circles) represent the fractions mature by length, estimated by assigning females (from the spring Kodiak trawl survey for 2002–2010) to 3-mm length bins and using ripe or spent individuals (condition codes 4–6) as mature.

changes in length of young of the year causing large changes in the mature fraction of individuals because typical lengths varied around 60 mm when maturity was determined. The relationship between fraction mature and fish length was fitted by allocating females that were sampled in the spring Kodiak trawl survey during 2002–2010 into 3-mm length bins and using ripe or spent individuals (codes 4–6) as mature. This resulted in an asymmetric relationship of fraction mature at around 60 mm (Figure 2). Use of other definitions for maturity resulted in relationships that were more symmetric at around 55–65 mm. We used the asymmetric relationship because it was justifiable based on the data and it provided a better test of model robustness.

Simulations under alternative baselines.—The 1995–2005 historical simulation with the original baseline (analyzed by Rose et al. 2013) was repeated with each of the four alternative baselines. We compared simulated January adult abundances and λ values among the original baseline and the four alternative versions. Results from a single simulation are presented. The individual-based model has stochastic aspects in assigning zooplankton biomass densities to channels and spawning temperatures to females, the y and z movements of the PTM, and the random component of behavioral movement. Because of the summing and averaging over many individuals and over time, population-level outputs (e.g., mean length at age, spatial distributions, and λ) varied by less than 5%—and often by less than 2%—among replicate simulations.

Good versus Bad Years

In this paper, we further explore the factors affecting the good year (1998) and bad year (2001) for Delta Smelt recruitment as identified in the analysis of the historical simulation (Rose et al. 2013). We performed a factorial simulation experiment to identify the conditions that caused the differences between water year 1998, which had the largest λ (2.45) within the baseline historical simulation, and water year 2001, which had the smallest λ (0.33) in the simulation. We varied five factors: salinity (S), temperature (T), zooplankton densities (Z), hydrodynamics (H), and eggs per entering age-1 individual (i.e., recruit) on January 1 (E). Each of these five factors was set to either its 1998 value or its 2001 value, resulting in a total of 32 (2^5) combinations.

Salinity.—Salinity affected the movement patterns of juveniles and adults and thus affected their spatial distribution and vulnerability to entrainment. The year 1998 was a high-outflow year, and salinities were very low for the modeled area from roughly March to August, after which salinity increased but remained below 5 psu (Figure 2b in Rose et al. 2013). Salinity in boxes down-estuary from the confluence was higher during the low-outflow year, 2001, than during 1998; this higher salinity occurred throughout 2001 except for a short period in March (Figure 2d in Rose et al. 2013). In the original baseline historical simulation, adults were located farther seaward with the salinity distribution in 1998. Average August outflow was 568 m^3/s in 1998 versus 90 m^3/s in 2001, and the percentage of adults that were in or seaward of the confluence box on September 1 was 97% during 1998 versus 67% during 2001 of the original baseline simulation (Figure 10e in Rose et al. 2013). The fraction of January adults that were entrained was 0.05 in 1998 versus 0.14 in 2001.

Temperature.—Temperature affected the initial date and duration of the spawning period; the egg and yolk sac development and mortality rates; and the bioenergetics (growth) of larvae, postlarvae, juveniles, and adults. When viewed systemwide, differences in temperature between 1998 and 2001 were not obvious (Figure 2a, c in Rose et al. 2013). More detailed analysis of the historical simulation using the average temperature experienced by model individuals showed two major differences between 1998 and 2001: (1) warmer fall and winter at the beginning of the water year and (2) cooler and delayed warming in the spring. Fall 1997 and winter 1998 were warmer than fall 2000 and winter 2001. During October 1–December 30, juveniles experienced an average temperature of 15.9°C in 1997 versus 15.0°C in 2000. Mean temperature experienced by these individuals (which became adults after January 1) during February 27–June 7 (the spawning period) was 14.8°C in 1998 versus 16.4°C in 2001. The warming in the spring also occurred later in 1998, and the average day of spawning was April 28 in 1998 versus April 6 in 2001.

Zooplankton.—The effect of switching 1998 and 2001 zooplankton densities would seem to be the simplest to interpret because this factor only affected feeding rate and therefore growth rate; however, the use of multiple prey groups made interpretation difficult. Dominant prey groups in the annual diets of postlarval, juvenile, and adult Delta Smelt in the baseline simulation were other calanoid adults and adult *Pseudodiaptomus*. The differences between 1998 and 2001 in the biomass densities of these two key prey groups were complicated (see Figure 3c versus 4c and Figure 3f versus 4f in Rose et al. 2013). Although adult *Pseudodiaptomus* biomasses were generally higher during summer and fall in 1998 than in 2001, biomasses of other calanoid adults during summer and fall were higher in 2001 and biomass in the southwest Suisun Bay box during winter and spring was much higher in 2001. Biomass densities of the other zooplankton groups also showed complicated differences. For example, the biomass density of adult *A. vernalis* was higher (and occurred at high levels for a longer period) in the Suisun Marsh box during 1998, but adult *Eurytemora* biomass density was higher in the southern Delta and eastern Delta boxes during 2001 (see Figure 3d versus 4d and Figure 3e versus 4e in Rose et al. 2013).

We relied on the p-value from the bioenergetics model to infer prey availability. The p-value reflects prey availability scaled for maximum consumption rate, which also depends on temperature. The historical simulation using the original baseline version showed that average p-values experienced by juveniles during the faster fall–winter growth (October 1–December 30) was 0.76 in 1997–1998 versus 0.68 in 2000–2001. This difference, in combination with warmer temperatures, led to longer recruits

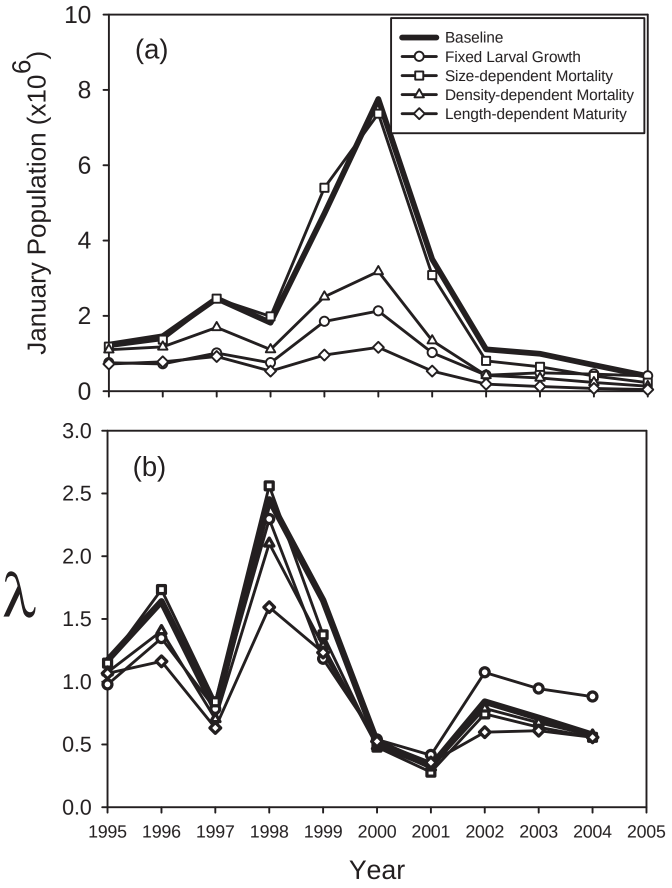

FIGURE 3. Simulated **(a)** annual adult Delta Smelt abundance in January and **(b)** finite population growth rate (λ; fraction per year), 1995–2005, for the original baseline simulation and the four alternative baseline simulations. The values of λ were determined by using an age-based Leslie matrix model applied to individual-based model output for each year. No value for 2005 is possible because the simulations ended on September 30, 2005; information through December 31, 2005, would be needed to estimate the matrix model for 2005.

on January 1 in 1998 than in 2001 (mean TL = 61.4 mm versus 56.5 mm). Averaged *p*-values in 1998 were also somewhat higher during the summer growth period (April 18–October 1) for young of the year (0.89 in 1998 versus 0.84 in 2001), although by October the mean lengths of young of the year were only slightly greater in 1998 than in 2001 (54 mm versus 52 mm).

Hydrodynamics.—Hydrodynamics affected the entrainment of yolk sac larvae, larvae, and postlarvae via the PTM; the entrainment of juveniles and adults; and the starting locations of new juveniles by determining the transport of larval life stages. Average May outflow was 1,922 m^3/s in 1998 versus 273 m^3/s in 2001, and the percentage of postlarvae that were in or seaward of the confluence box after transport (June 24) was 84% in 1998 versus 24% in 2001. Almost no larvae were predicted to be entrained during 1998, whereas the daily average entrainment loss was 1.2% in 2001.

Eggs per age-1 individual.—Unlike the other factors, which had readily available values for 1998 and 2001, the number of eggs per age-1 individual required additional calculations in the model to achieve 1998 or 2001 values in the factorial simulation experiment. The number of eggs per age-1 fish reflected growth that occurred in the fall and winter leading up to spawning. In the original historical simulation, the mean length of young of the year on October 1 was somewhat greater in 1997 (starting value for 1998) than in 2000 (54.0 mm versus 52.0 mm) due to the more favorable summer conditions in 1997 than in 2000. This small difference was amplified by warmer temperature and higher prey densities in the fall and winter of 1997, resulting in a mean length of 61.4 mm on January 1, 1998, versus 56.5 mm on January 1, 2001. These lengths straddled the 60-mm maturity cutoff, and whereas 72% of entering age-1 individuals were mature in 1998, only 15% of entering age-1 fish were mature in 2001 of the historical baseline simulation. Thus, although there were fewer recruits on January 1, 1998, than on January 1, 2001 (0.159×10^7 versus 0.258×10^7), the number of mature age-1 female spawners was greater in 1998 (0.287×10^6 versus 0.1105×10^6) and egg production was about 1.5 times higher in 1998 (0.942×10^9 versus 0.641×10^9).

In the historical baseline simulation, the average number of eggs per age-1 individual was 491.8 for 1998 versus 89.3 for 2001. We did not explicitly simulate the previous year's conditions for the simulation experiment, in which either 1998 or 2001 conditions were repeated year after year. Rather, we adjusted the fecundity of entering age-1 individuals each year when we projected spawning so that the total projected number of eggs divided by the number of simulated entering age-1 individuals would be either 491.8 or 89.3.

Simulations in the good year versus bad year experiment.—Simulations were for 15 years, with 4 years of spin-up using 1999 conditions as in the baseline simulations, followed by 11 years of 1 of the 32 combinations of 1998 or 2001 conditions repeated every year. We used the two extreme years because they provided the best contrast for separating out the effects of multiple factors and thus for identifying which factors were most important in determining year-class strength. Eleven years of repeated conditions were simulated in order to ensure that we had the long-term (equilibrium) population responses to the specified conditions; shorter simulations could be affected by initial conditions and still reflect aspects of the transient solutions. We refer to the 32 combinations by using the letters of the factors that were set to 2001 values (i.e., *S* for salinity, *T* for temperature, *Z* for zooplankton, *H* for hydrodynamics, and *E* for eggs per entering age-1 individual). For example, in the simulation labeled "*EH*," eggs per age-1 fish and hydrodynamics were set at 2001 values, while salinity, temperature, and zooplankton were set at 1998 values. We report λ averaged over years 10–14 of each 15-year simulation. As with the baseline simulations, results from a single simulation are presented because replicate simulations differed by less than 5% in their population-level outputs. Values of λ that were 25% and 50% higher than the

2001 value are shown for reference to aid in judging how close the other λ values were to the 2001 value.

Robustness

To confirm the robustness of results based on the original baseline, we also repeated all of the 32 simulation combinations under each of the four alternative baseline conditions. We only report the averaged λ for years 10–14 for four combinations (*ET*, *EH*, *ETH*, and *ETHS*) that resulted in low λ values to illustrate that the full set of combinations was robust to the alternative baselines. We focused on these four combinations because they resulted in low λ values near the 2001 value and because their robustness is particularly important, as they form the basis for identifying which factors determine how a good year differs from a bad year.

RESULTS

Alternative Baselines

The use of size-dependent mortality resulted in January adult abundances similar to those in the original baseline, while the alternative baselines with fixed larval growth, density-dependent mortality, and length-dependent maturity resulted in January abundances that were lower than those in the original baseline (Figure 3a). Lower peak abundances were expected for the density-dependent mortality version because juvenile survival was specified to decrease under high abundances. Larval growth (and therefore larval-stage survival) had an important influence on both good and bad years. Lower abundances under length-dependent maturity occurred because the maturity relationship was not symmetric around 60 mm (Figure 2) and thus would, on average, result in a lower fraction of young of the year becoming mature than was observed with the simple 60-mm rule in the original baseline.

Despite these differences in January abundances, λ values were very similar for all versions of the baseline, with the length-dependent maturity alternative differing the most from the original baseline (Figure 3b). Relatively high January adult abundance occurred in 2001 (Figure 3a), despite the lowest λ being observed in that year, because January abundance was related to conditions in the previous summer and fall and was not reflective of the spring and summer conditions in 2001. The high λ values during years prior to 2001 led to high January adult abundance in 2001. The temporal pattern in λ values for length-dependent maturity was the same as that for the original baseline, but values in all years were lower than baseline values, with the largest difference occurring in 1998 ($\lambda = 1.59$ for length-dependent maturity versus 2.45 for the original baseline). The original baseline and the four alternatives all identified 1998 as the best model year and 2001 as the worst model year for Delta Smelt.

Systematic Comparison of Best versus Worst Years

The intersimulation variability in λ values decreased and more combinations approached the 2001 value as the number of factors set to 2001 values increased (Figure 4). The percentage of combinations that resulted in λ values within 50% of the 2001 λ value increased from 0% when one factor was set to the 2001 value to 10% for two factors at 2001 values, 50% for three factors at 2001 values, and 60% for four factors at 2001 values. All but one of the combinations that generated a λ value within 50% of the 2001 value involved either eggs per age-1 individual or temperature being set at the 2001 value.

Juvenile growth in the fall prior to spawning (i.e., as reflected by the number of eggs per age-1 fish) was the most important single factor in making 2001 a bad year, although no single factor alone was sufficient to fully account for the poor conditions in 2001 relative to 1998 (Figure 4). Temperature (*T*) played an important secondary role (Figure 4, shaded circles), and hydrodynamics (*H*) played a more minor role; salinity (*S*) and zooplankton (*Z*) as single factors were unimportant. When one factor at a time was switched from 1998 to 2001 values (Figure 4, leftmost section), only eggs per age-1 fish (*E*) resulted in a λ value less than 1.0. The single factors *T* and *H* (each at the 2001 value) generated the second- and third-lowest λ values (1.1 and 1.5). As a single factor, *Z* (which determined

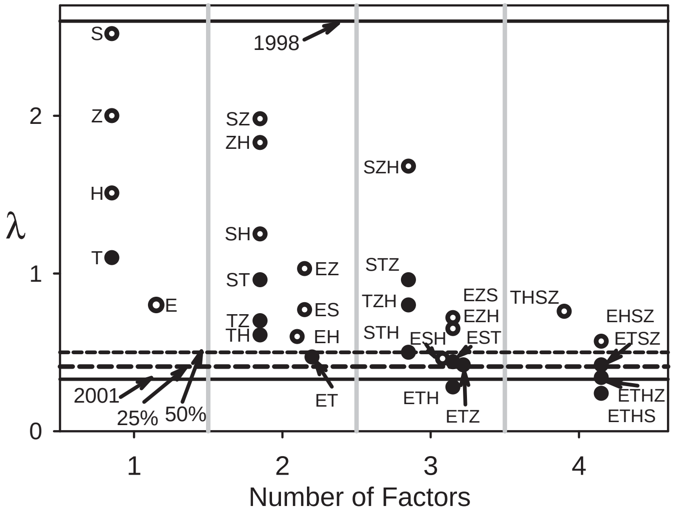

FIGURE 4. Contributions of five factors to differences between the best year (1998) and worst year (2001) for Delta Smelt. Each circle represents the mean finite population growth rate (λ) for years 10–14 of a 15-year simulation of repeated conditions for each factor (salinity [*S*], temperature [*T*], zooplankton [*Z*], hydrodynamics [*H*], and number of eggs per age-1 individual [*E*]) at either 1998 or 2001 values. Results are organized by the number of factors that were set to 2001 values (i.e., 1–4 factors; each combination code [e.g., “*STZ*”] lists the factors set at 2001 values); within each section, results with the number of eggs per age-1 individual at its 1998 value are shown on the left and results with that factor at its 2001 value are shown on the right. Shaded circles denote all combinations that included the 2001 temperature. The 1998 and 2001 values of λ are indicated by solid horizontal lines; the dotted horizontal lines represent λ values that are 25% and 50% higher than the 2001 value.

growth) generated a λ of 2.0, which was lower than the value for 1998 (λ = 2.6) but still much higher than the value for 2001 (λ = 0.33). When only *S* was set to the 2001 value, there was almost no effect on λ (2.52 versus 2.60).

All combinations of two factors set at 2001 values with eggs per age-1 individual at its higher 1998 value (left-side points in Figure 4, second section) generated λ values above 0.6; among these two-factor combinations, temperature and hydrodynamics at 2001 values together (*TH*) resulted in the lowest λ (0.61). The three lowest λ values all included 2001 temperature (Figure 4, shaded circles). The two-factor combinations that included the 2001 value for eggs per age-1 fish (right-side points in Figure 4, second section) resulted in λ values less than 1.0, and the *ET* and *EH* combinations produced λ values less than 0.6. Again, the lowest of these λ values was from the combination *ET* (Figure 4, shaded circle) and approached the λ value predicted for 2001 (0.47 versus 0.33).

Among the three-factor combinations set at 2001 values with eggs per age-1 individual set at the 1998 value (left-side points in Figure 4, third section), temperature and hydrodynamics were important. The highest λ (1.68) was predicted for the one combination that did not include 2001 temperature (*SZH*). The combinations with the three lowest λ values included the 2001 value for temperature (*STZ*, *TZH*, and *STH*; Figure 4, shaded circles); the two lowest of these λ values were from combinations that also included 2001 hydrodynamics (λ = 0.8 for *TZH* and 0.5 for *STH*).

When the number of eggs per age-1 fish was included as one of the three factors set at 2001 values (right-side points in Figure 4, third section), all λ values were less than 1.0. The combinations also including 2001 temperature (*ETH*, *ETZ*, and *EST*) generated the lowest λ values (0.28, 0.42, and 0.44, respectively), which were close to the λ value for 2001. The combinations that did not include 2001 temperature (Figure 4, open circles) generally had higher λ values (0.72 for *EZS* and 0.65 for *EZH*); the exception was *ESH*, which yielded a λ value (0.46) similar to those from the three combinations that included the 2001 temperature.

The number of eggs per age-1 individual and temperature continued to be very important in four-factor combinations. All four-factor combinations that included the 2001 value for eggs per age-1 fish (right-side points in Figure 4, fourth section) resulted in λ values less than 0.5, and those combinations that also included 2001 temperature (Figure 4, shaded circles) generated λ values that were close to the 2001 value. Of the four combinations that included the 2001 value for eggs per age-1 fish, the three combinations that also included 2001 temperature (*ETSZ*, *ETHZ*, and *ETHS*) all generated λ values less than 0.45, whereas the combination without temperature (*EHSZ*) generated the highest λ value (0.60). The remaining four-factor combination (*THSZ*; left-side point in Figure 4, fourth section), in which the number of eggs per age-1 individual was set at the 1998 value, generated the highest λ (0.85) observed for any four-factor combination.

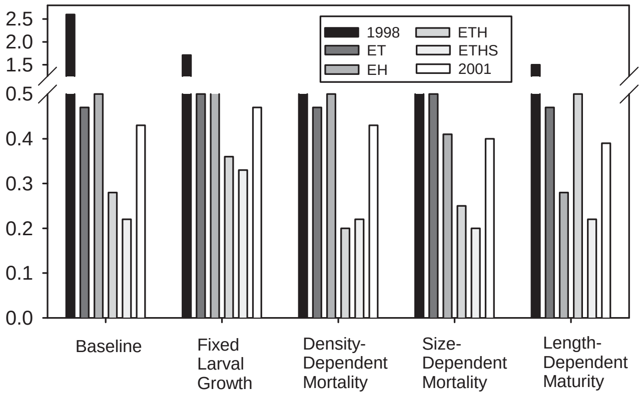

FIGURE 5. Averaged finite population growth rate (λ; years 10–14) of Delta Smelt under the four alternative baselines and the four factor combinations that resulted in low λ values near the value for 2001. Factors are salinity (*S*), temperature (*T*), zooplankton (*Z*), hydrodynamics (*H*), and number of eggs per age-1 individual (*E*); each combination code (e.g., "*ETH*") lists the factors that were set at 2001 values, and the remaining factors (i.e., with letters not shown) were set at 1998 values.

Robustness

The conditions leading to the good year (1998) were more sensitive to alternative baselines than the poor conditions leading to the bad year (2001; Figure 5). The four combinations (i.e., selected from Figure 4) that produced low λ values when set to their 2001 values under the original baseline generated similarly low λ values under the four alternative baselines. In contrast, the λ values varied more among the 1998 simulations. The alternative of density-dependent mortality produced the greatest reduction in λ for 1998 (λ decreased from 2.45 to 1.00). Larval growth and length-dependent maturity were also important in attaining the high λ predicted for 1998 in the original baseline. When larval growth was fixed at the overall average value (fixed duration), λ was reduced from 2.45 in the original baseline to 1.7; under length-based maturity, λ was reduced to 1.5. Size-dependent mortality was associated with the smallest reduction in the λ value for 1998 (λ decreased from 2.45 to 2.13).

DISCUSSION

Our analysis using a simulation experiment approach further clarified the relative influence of factors affecting Delta Smelt recruitment and population dynamics. In our companion paper (Rose et al. 2013), we compared conditions in 1998 with those in 2001 by using the 1995–2005 historical simulation. The five factors analyzed were inferred to be important in the historical simulation because their values differed, at least in some ways, between the best year and the worst year. In this paper, we systematically varied the five factors in a factorial simulation experiment to look for main and interaction effects. We moved away from the historical sequence of years and performed 15-year simulations with either 1998 or 2001 values repeated every year to allow the simulated population to reach a quasi-steady-state response. We also showed that our results, when viewed in a comparative mode, were generally robust to alternative versions of the baseline model.

Our results demonstrated that among the factors we examined, no single factor completely accounted for the difference between the high λ in the best year (1998) and the low λ in the worst year (2001). Growth of juveniles in the fall–winter, temperature, and hydrodynamics clearly had the strongest effects, but λ could not be brought down from its 1998 value to near its 2001 value without some combination of factors. Thus, our results support the growing consensus that no single factor explains the Delta Smelt decline that occurred during 1995–2005 (Bennett and Moyle 1996; Bennett 2005; Baxter et al. 2010; Thomson et al. 2010).

Although we have shown that growth conditions in fall–winter were an important factor, there are many ways to achieve the faster growth that was predicted for 1998 relative to 2001. The growth conditions in winter affected the lengths of entering age-1 fish on January 1, with a 1998 value of 60.2 mm versus a 2001 value of 58.8 mm, and consequently affected the fraction mature (0.55 versus 0.41) and the egg production per entering age-1 fish (502.6 versus 107.6). These values for 1998 and 2001 differ from those reported in Rose et al. (2013) because the present values are averaged from the repeated years in the simulation experiment, whereas in our other paper (Rose et al. 2013) we reported values for 1998 and 2001 within the historical simulation. The difference in predicted mean lengths between 1998 and 2001 was well within the range of observed interannual values (see Figure 6 in Rose et al. 2013). Our analysis did not, however, distinguish how juveniles attained greater lengths prior to becoming age 1 and spawning. We used 1998 and 2001 conditions, but other years can also generate similar differences in growth based on combinations of zooplankton conditions and temperature; essentially, any mechanism that allows new age-1 recruits to have a greater length prior to spawning would result in a high number of eggs per age-1 fish and would set the stage for a good year. This can be achieved via warmer winter temperature (as in 1998) or by higher zooplankton densities causing faster growth at any time from the previous summer through early spring. If zooplankton conditions are better at higher salinity (seaward), then hydrodynamics (via its effect on transport) or salinity could also produce faster growth by putting individuals in boxes with higher prey biomass densities. We did not systematically examine how temperature, zooplankton, hydrodynamics, and salinity during the growing season of the year before or during the winter–spring period could potentially combine to promote faster growth and larger spawners in the spring. Rather, we used the suite of conditions for 1998 and 2001 to contrast a good year with a bad year.

A second way to increase egg production without faster growth of spawners would be to increase young-of-the-year survival prior to spawning. Total egg production was calculated as the number of eggs per entering age-1 fish times the number of age-1 fish. Our results were robust to the size-dependent mortality and length-based maturity versions of the baseline, so the growth of adults affected the number of eggs per age-1 individual but not the abundance of age-1 fish. Higher Delta outflow at key times resulted in reduced entrainment, and hydrodynamics were consistently an important factor. Further analysis should explore spatial (box-scale) differences in mortality, which, if sufficient, could benefit the Delta Smelt via management manipulation of hydrodynamics and salinity, generating differences in starting age-1 abundances for spawning. We assumed that except for entrainment losses, mortality was stage dependent but not spatially variable.

Our results for the importance of food (zooplankton) are similar to those of Maunder and Deriso (2011), but we disagree about the roles of entrainment and density dependence. Maunder and Deriso (2011) used a stage-based life cycle model, and by introducing covariates into life stage survival (spawner–recruit) relationships, they determined that food abundance, temperature, predator abundance, and density dependence were the most important factors controlling the population dynamics of Delta Smelt. They further stated that there was some support for negative effects of water clarity and adult entrainment.

Our simulation experiment contrasting the best year versus the worst year agrees with the important role of temperature and zooplankton, but we did not examine the effects of predator abundance or water clarity. Maunder and Deriso (2011) used spring and summer zooplankton conditions: minimum *Eurytemora* and *Pseudodiaptomus* densities for April–June; average *Eurytemora* density for July; and average *Pseudodiaptomus* density for July–August. We found that fall, winter, and early spring growth was potentially important, at least for the comparison between 1998 and 2001. Maunder and Deriso (2011) examined a longer time period (1970–2006) that covered larger changes in the zooplankton community, and this could emphasize the importance of spring and summertime zooplankton relative to other factors, such as winter growth and its consequences for spring reproduction. We recommend that conditions in the winter and early spring and conditions from the year before be further evaluated for their potential to benefit Delta Smelt.

We disagree to some extent with Maunder and Deriso (2011) about the role of entrainment and density dependence. Examination of Figure 8 of Maunder and Deriso (2011) to assess the role of entrainment showed more agreement with our analysis than did their general statement of "some support for a negative relationship with . . . adult entrainment." They showed an approximately twofold increase in adults during 2002–2006 by eliminating entrainment. This agrees with our analysis, showing higher entrainment mortality during the same years as in our simulation; however, we would term their Figure 8 results as providing more than "some" support for a negative effect of adult entrainment. The Maunder and Deriso (2011) analysis covered a longer time period (1970–2006) than our analysis (1995–2005); thus, the role of covariates can differ and density dependence likely played a larger role at the earlier, higher abundance levels (see Bennett 2005). In addition, direct comparisons between the models are somewhat confounded because our analysis and the

Maunder and Deriso (2011) analysis shared some information, such as the entrainment estimates from Kimmerer (2008) and the spawner–recruit information from long-term monitoring.

Several statistical analyses of similar monitoring and covariate data as used by Maunder and Deriso (2011) also implicated various indicators of spring and summer zooplankton food availability as being important. Thomson et al. (2010) used Bayesian change point analysis to examine variation in the fall MWT index; Mac Nally et al. (2010) used multivariate autoregressive modeling to analyze the fall MWT index in a multispecies approach; and Miller et al. (2012) used Ricker spawner–recruit relationships to analyze the ratio of indices as survival indicators. These analyses all inferred that various combinations of water temperature, water clarity, zooplankton indicators, and entrainment were correlated to various degrees with the historical pattern in the Delta Smelt abundance indices.

Other assumptions that are inherent in our modeling merit further analyses as possible alternative versions of baseline conditions. The representation of predation on Delta Smelt was partially explored by using size-dependent mortality, but there are also temporal trends and spatial patterns to the key predators of Delta Smelt that could be important. Striped Bass *Morone saxatilis* and Largemouth Bass *Micropterus salmoides* show distinct spatial distributions within the San Francisco Estuary and have also exhibited recent temporal trends, with young Striped Bass declining and Largemouth Bass increasing (Nobriga and Feyrer 2007). Furthermore, exotic Mississippi Silversides *Menidia audens* are known to readily consume larval Delta Smelt and have increased substantially in recent years (Baerwald et al. 2012).

Another assumption worthy of investigation is that the Delta Smelt population in the individual-based model consisted of individuals that all exhibit the same migratory behavior. Limited field data indicate that there is partial or divergent migration (Secor 1999; Chapman et al. 2012) within the Delta Smelt population, with some individuals possibly remaining year-round in the Cache Slough region, which is located in the southwestern portion of our Sacramento River model box (Merz et al. 2011; Sommer et al. 2011). An alternative version of the baseline individual-based model could include some proportion of individuals that remain resident in some areas. Resident individuals, or individuals with reduced or altered migrations, could exhibit different growth because of spatial variation in temperature, zooplankton, and susceptibility to entrainment.

Our detailed individual-based approach is not commonly used to simulate the population dynamics of endangered fish species, although it can be adapted for use in the more traditional population viability analysis (PVA) and risk framework. The individual-based approach is increasingly being used to simulate fish population and community dynamics for purposes of answering ecological and fisheries management questions (DeAngelis and Mooij 2005). However, although the individual-based approach is usually mentioned in reviews of PVA approaches (e.g., Akçakaya and Sjögren-Gulve 2000; Morris et al. 2002; Petersen et al. 2008), the number of examples of its use specifically for PVA remains quite limited. Some commonly used general models apply an individual-based approach, but they employ a very simple representation of processes (e.g., Jarić et al. 2010). Examples in which a more mechanistic individual-based model approach was used include models of endangered birds (Letcher et al. 1998), turtles (Mazaris et al. 2005), and recruitment of Colorado Pikeminnow *Ptychocheilus lucius*. Using an individual-based approach very similar to our Delta Smelt modeling, Jager et al. (2001) analyzed the effects of habitat fragmentation by dams on the White Sturgeon *Acipenser transmontanus*, which is a species of concern and has been listed as endangered elsewhere. Population viability analysis usually involves many realizations of a modeled population trajectory to generate risk values. Our individual-based model cannot easily be used to perform thousands of simulations. A possible link to a PVA-type analysis of Delta Smelt would be to (1) use the individual-based model in a systematic way to create crude probability distributions for the elements of the Leslie matrix model (which can generate λ values with Monte Carlo simulation) or (2) use the coupled individual-based model and Leslie model to directly generate distributions of λ values. Once sets of λ values are obtained for a variety of environmental and biological conditions, they can be used in more traditional PVA projections of long-term persistence (see Morris et al. 2002).

Our analysis addresses several ongoing methodological issues in fish population dynamics: spatial dynamics in complex habitats, coupled biological–physical modeling, and recruitment and population dynamics at low abundances. The need for studies of long-term population dynamics to deal with spatial dynamics has recently been discussed (Giske et al. 1998; Struve et al. 2010), and approaches that deal with spatial variation explicitly are receiving greater attention (e.g., Kerr et al. 2010). Increasingly, fish-related management issues require an integrated approach that combines the physics of water with the biology of the fish and other biota (Shenton et al. 2012), and one method is the direct coupling of fine-scale hydrodynamics with long-term fish population dynamics (Buckley and Buckley 2010; Rose et al. 2010; Hinrichsen et al. 2011; Stock et al. 2011).

Our model expands on the classical particle tracking approach by simulating detailed biological processes, relatively complicated behavioral movement, and multiple generations. Our Delta Smelt model simulated growth, survival, reproduction, and movement of individual fish on the same spatial grid as the hydrodynamics, and the super-individual method allowed for 15-year simulations. Although PTMs are commonly embedded within hydrodynamics models (North et al. 2009; Hinrichsen et al. 2011), the PTMs typically do not include detailed descriptions of growth and reproduction. Rather, these studies usually invoke, at most, simple movement behavior as an addition to passive transport and are mostly used for short-term (<1 year) simulations (Miller 2007; Lett et al. 2009; Gallego 2011). However, a consequence of full life cycle modeling that includes juveniles and adults within a detailed spatial grid is that now we must simulate behavioral movement on relatively fine scales. Modeling behavioral movement is critical to ensure that individuals experience the appropriate conditions over time, but this remains a challenge (Watkins and Rose 2013). Delta Smelt movement patterns in our simulations were generally realistic but require further refinement.

Finally, much fish population modeling has focused on the effects of harvesting from high-number populations, whereas there is an increasing need to examine dynamics of fish populations at low abundances due to overharvest and in support of recovery plans for listed species (Keith and Hutchings 2012). The focus on harvesting leads to an emphasis on density-dependent mortality, often via the spawner–recruit relationship (Rose et al. 2001). Our approach differs from this by focusing on Delta Smelt population dynamics under density-independent conditions. We emphasized how individuals were transported through or navigated through their spatially complex and temporally varying habitat. Our analysis can be viewed as part of the broader idea of multiple factors within the match–mismatch theory of controls on young-of-the-year survival and therefore recruitment (Peck et al. 2012), coupled with the idea that adult bioenergetics are important for determining maturity and annual egg production (Neil et al. 1994; Rose et al. 2001). Because our model was density independent, all of the predicted variation in stage-specific survival rates was due to variation in how spatial distributions interacted with dynamic environmental conditions. Our results showed how the spatial and temporal positioning of all life stages each year (based on physical transport and salinity), combined with the pattern in daily water temperature and the amount of Delta outflow, affected the magnitude and location of egg production and the subsequent dynamic matching of larval and juveniles with their prey types, thus affecting recruitment success. However, even our modeling results were not simple to interpret, and therefore they also illustrate how spatially and temporally dynamic habitat can create complicated match–mismatch situations.

Delta Smelt have been at the center of escalating controversy in the San Francisco Estuary region for several decades (NRC 2010; Kimmerer 2011; Miller 2011). What initially arose as a conflict between water demands for export versus for the environment (including Delta Smelt) has metastasized as the number of ostensible factors behind the decline of Delta Smelt has grown (e.g., Mac Nally et al. 2010; Maunder and Deriso 2011; Miller et al. 2012). The conflict has now evolved into a complicated situation in which multiple factors operate in interactive ways and are continually being argued over in court (Delta Smelt Consolidated Cases 2010). Our results contribute to the growing number of examples showing that multiple factors affect aquatic ecosystems (Breitburg and Riedel 2005; Ormerod et al. 2010; Cloern and Jassby 2012) and that the search for a single factor controlling fish population dynamics is unlikely to be successful (e.g., Rose 2000; Krebs 2002; Hecky et al. 2010; Lindegren et al. 2011).

Our results to date suggest that management actions to benefit Delta Smelt must deal with multiple stressors that occur at different points in the life cycle. An increase in prey would induce relatively large responses in reproduction but may not be feasible. We showed that growth leading up to spawning was important for subsequent population growth; it remains to be seen whether it is possible to promote growth of Delta Smelt or higher young-of-the-year survival prior to spawning (fall–spring) via management actions. We also showed that no single factor can alone account for the differences between good and bad years and that promoting growth should be done in combination with other actions (if feasible) to (1) ensure good temperatures for summer growth and delayed spawning and (2) ensure sufficient outflow and avoidance of high entrainment (see results in Rose et al. 2013). Our results also demonstrate that expectations should be clearly stated, as most management actions are unlikely to generate large, immediate responses because the influence of stressors varies from year to year and because the reduction in a single stressor during any one year may be moderated by the conditions in other, non-manipulated stressors occurring in that year.

We envision two other areas for future analyses using the individual-based model. First, extending the model simulations for the periods before 1995 and after 2005 would allow for more comparisons and contrasts of good versus bad years to determine other combinations of factors that may be important; climate change scenarios should be included in these simulations to allow for future-looking comparisons. This would require use of the DSM2 hydrodynamic model or another hydrodynamic model and the development of synthetic temperature, salinity, and zooplankton data. Second, a more rigorous side-by-side comparison of the Maunder and Deriso (2011) model and our individual-based model would facilitate an understanding of the relative effects of key stressors on Delta Smelt population dynamics. The population dynamics and reasons for the decline of Delta Smelt are complex. However, complexity is not a reason to avoid rigorous quantitative analyses—indeed, it is perhaps the best reason to develop and compare alternative modeling approaches.

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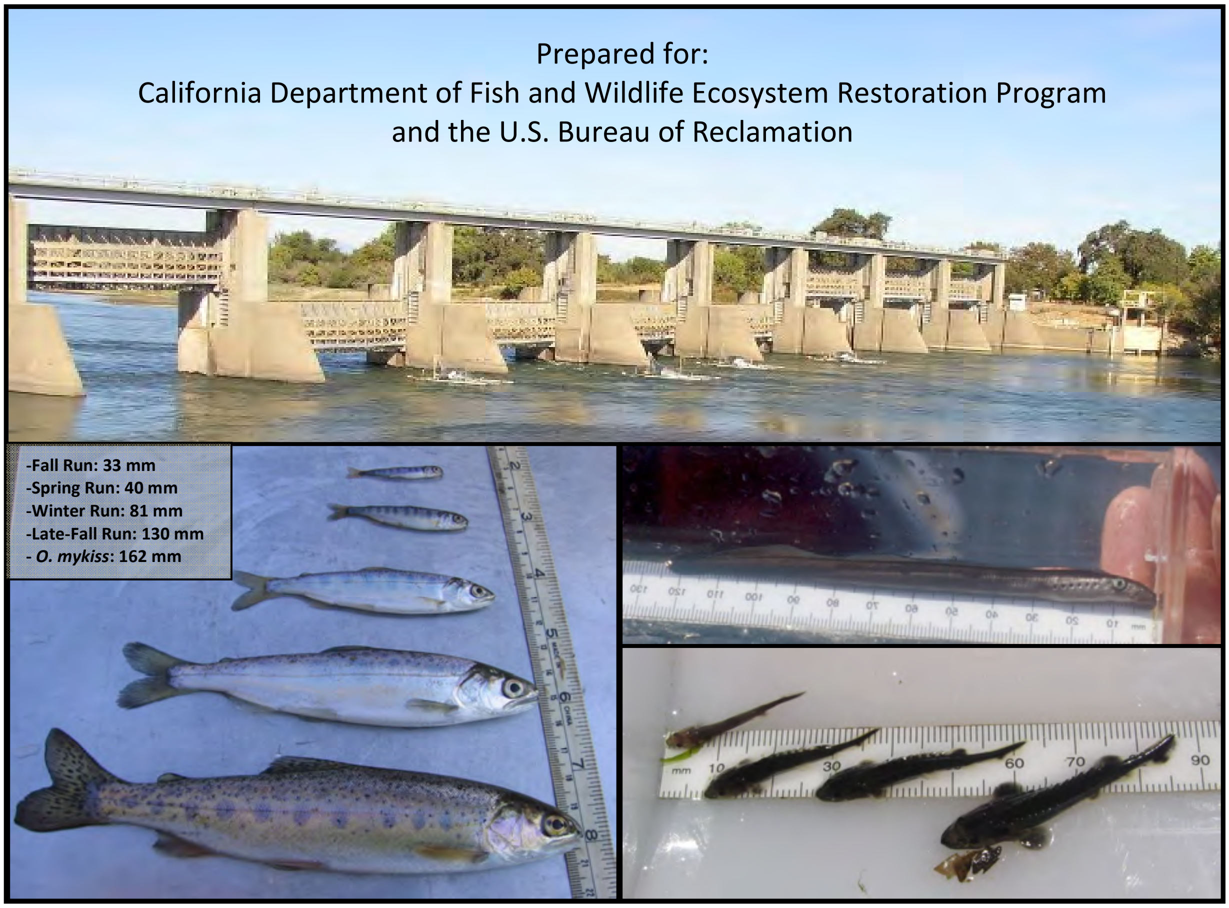
COMPENDIUM REPORT OF RED BLUFF DIVERSION DAM ROTARY TRAP JUVENILE ANADROMOUS FISH PRODUCTION INDICES FOR YEARS 2002-2012



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Prepared by:
William R. Poytress
Joshua J. Gruber
Felipe D. Carrillo
And
Scott D. Voss

U.S. Fish and Wildlife Service
Red Bluff Fish and Wildlife Office
10950 Tyler Road
Red Bluff, CA 96080

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Compendium Report of Red Bluff Diversion Dam Rotary Trap Juvenile Anadromous Fish Production Indices for Years 2002-2012

William R. Poytress, Joshua J. Gruber, Felipe D. Carrillo and Scott D. Voss

U.S. Fish and Wildlife Service
Red Bluff Fish and Wildlife Office

Abstract.— Fall, late-fall, spring, and winter-run Chinook salmon (*Oncorhynchus tshawytscha*) and Steelhead/Rainbow trout (*Oncorhynchus mykiss*) spawn in the Sacramento River and tributaries in California's Central Valley upstream of Red Bluff Diversion Dam (RBDD) throughout the year. Sampling of juvenile anadromous fish at RBDD allows for year-round quantitative production and passage estimates of all runs of Chinook and *O. mykiss*. Incidental capture of Green Sturgeon (*Acipenser medirostris*) and various Lamprey species (*Lampetra spp. and Entosphenus tridentatus)* has occurred throughout juvenile Chinook monitoring activities since 1995. This compendium report addresses, in detail, juvenile anadromous fish monitoring activities at RBDD for the period April 4, 2002 through September 30, 2013.

Sampling was conducted along a transect using four 8-foot diameter rotary-screw traps attached via aircraft cables directly to RBDD. Trap efficiency (i.e., the proportion of the juvenile salmonid population passing RBDD captured by traps) was modeled with percent of river discharge sampled (%*Q*) to develop a simple least-squares regression equation. Chinook and *O. mykiss* passage were estimated by employing the trap efficiency model. The ratio of fry to pre-smolt/smolts passing RBDD was variable among years. Therefore, juvenile passage was standardized to determine juvenile production by estimating a fry-equivalent Juvenile Production Index (JPI) for among-year comparisons. Catch per unit volume (CPUV) was used as an index of relative abundance for Green Sturgeon and Lamprey species. Abiotic data collected or calculated throughout sample efforts included: water temperature, flow, turbidity, and moon illuminosity (fraction of moon illuminated). The abiotic variables were analyzed to determine if relationships existed throughout the migration periods of the anadromous species.

A trap efficiency model developed in 2000 to estimate fish passage demonstrated improved correlation between 2002 and 2013 with the addition of 85 mark-recapture trials. The model's *r*-squared value improved greatly with the addition of numerous mark-recapture trials that used wild fry size-class salmon over a variety of river discharge levels. Total passage estimates including annual effort values with 90% confidence intervals (CI) are presented, by brood year, for each run of Chinook. Fry and pre-smolt/smolt Chinook passage estimates with 90% CI's are summarized annually by run in Appendix 1. Comparisons of relative variation within and between runs of Chinook were performed by calculating Coefficients of Variation (CV). Fall Chinook annual total passage estimates ranged between 6,627,261 and 27,736,868 juveniles for brood years 2002-2012 ($\bar{y}$ = 14,774,923, CV = 46.2%). On average, fall Chinook passage was composed of 74% fry and 26% pre-smolt/smolt size-class fish (SD = 10.3). Late-fall

Chinook annual total passage estimates ranged between 91,995 and 2,559,519 juveniles for brood years 2002-2012 (ȳ = 447,711, CV = 159.9%). On average, late-fall Chinook passage was composed of 38% fry and 62% pre-smolt/smolt size-class fish (SD = 22.5). Winter Chinook annual total passage estimates ranged between 848,976 and 8,363,106 juveniles for brood years 2002-2012 (ȳ = 3,763,362, CV = 73.2%). On average, winter Chinook passage was composed of 80% fry and 20% pre-smolt/smolt size-class fish (SD = 11.2). Spring Chinook annual total passage estimates for spring Chinook ranged between 158,966 and 626,925 juveniles for brood years 2002-2012 (ȳ = 364,508, CV = 45.0%). On average, spring Chinook passage was composed of 54% fry and 46% pre-smolt/smolt size-class fish (SD = 20.0). Annual total passage estimates for *O. mykiss* ranged between 56,798 and 151,694 juveniles for calendar years 2002-2012 (ȳ = 116,272, CV = 25.7).

A significant relationship between the estimated number of adult females and fry-equivalent fall Chinook production estimates was detected (r^2 = 0.53, df = 10, *P* = 0.01). Recruits per female were calculated and ranged from 89 to 1,515 (ȳ = 749). Egg-to-fry survival estimates averaged 13.9% for fall Chinook. A significant relationship between estimated number of females and fry-equivalent late-fall Chinook production estimates was detected (r^2 = 0.67, df = 10, *P* = 0.002). Recruits per female were calculated and ranged from 47 to 243 (ȳ = 131). Egg-to-fry survival estimates averaged 2.8% for late-fall Chinook. A significant relationship between estimated number of females and fry-equivalent winter Chinook production estimates was detected (r^2 = 0.90, df = 10, $P < 0.001$). Recruits per female were calculated and ranged from 846 to 2,351 (ȳ = 1,349). Egg-to-fry survival estimates averaged 26.4% for winter Chinook. No significant relationship between estimated number of females and fry-equivalent spring Chinook production estimates was detected (r^2 = 0.00, df = 10, *P* = 0.971). Recruits per female were calculated and ranged from 1,112 to 8,592 (ȳ = 3,122). Egg-to-fry survival estimates averaged 61.5% for spring Chinook. Spring Chinook juvenile to adult correlation values appear unreasonable and well outside those found for other runs and from other studies.

Catch of Green Sturgeon was highly variable, not normally distributed and ranged between 0 and 3,701 per year (median = 193). Catch was primarily composed of recently emerged, post-exogenous feeding larvae. The 10-year median capture total length averaged 27.3 mm (SD = 0.8). Green Sturgeon annual CPUV was typically very low and ranged from 0.0 to 20.1 fish/ac-ft (ȳ = 2.5 fish/ac-ft, SD = 5.9). Data were positively skewed and median annual CPUV was 0.8 fish/ac-ft.

Lamprey species sampled included adult and juvenile Pacific Lamprey (*Entosphenus tridentatus*) and to a much lesser extent River Lamprey (*Lampetra ayresi*) and Pacific Brook Lamprey (*Lampetra pacifica*). Unidentified lamprey ammocoetes and Pacific Lamprey composed 99.8% of all captures, 24% and 75%, respectively. River Lamprey and Pacific Brook Lamprey composed the remaining 0.2%, combined. Lamprey captures occurred throughout the year between October and September. Lamprey ammocoete annual relative abundance ranged from 3.6 to 11.7 fish/ac-ft (ȳ = 6.8 fish/ac-ft, SD = 2.6). Overall, these data were normally distributed as median annual CPUV was 6.5 fish/ac-ft, similar to the mean value. Pacific Lamprey macropthalmia annual relative abundance was generally higher than ammocoete relative abundance and ranged from 2.1 to 112.8 fish/ac-ft ($\bar{y}$ = 41.0 fish/ac-ft, SD = 34.7). Overall, Pacific Lamprey data was slightly positively skewed and median CPUV was 34.1 fish/ac-ft.

Tabular summaries of the abiotic conditions encountered during each annual capture period were summarized for each run of salmon, *O. mykiss*, Green Sturgeon and Lamprey species. The range of temperatures experienced by Chinook fry and pre-smolt/smolts in the last 11 years of passage at RBDD have been within the optimal range of temperature tolerances for juvenile Chinook survival. Green Sturgeon have likely benefitted from temperature management efforts aimed at winter Chinook spawning and production, albeit less comprehensively. Lamprey species have also likely benefitted from temperature management as temperatures for early life stages of Lamprey in the mainstem Sacramento River appear to have been, on average, optimal in the last 11 years.

The relationship between river discharge, turbidity, and fish passage are complex in the Upper Sacramento River where ocean and stream-type Chinook of various size-classes (i.e., runs, life stages and ages) migrate daily throughout the year. Fish passage increases often coincided with an increase in turbidity which were sampled more effectively than increases in river discharge. A positive bias of fish passage estimates may result if the peak turbidity event was sampled following an un-sampled peak flow event. The importance of the first storm event of the fall or winter period cannot be overstated. Smolt passage and juvenile Lamprey passage increase exponentially and fry passage can be significant during fall storm events.

Rotary trap passage data indicated fry size-class winter Chinook exhibit decreased nocturnal passage levels during and around the full moon phase in the fall. Pre-smolt/smolt winter Chinook appeared less influenced by nighttime light levels and much more influenced by changes in discharge levels. Spring, fall and late-fall Chinook fry exhibited varying degrees of decreased passage during full moon periods, albeit storms and related hydrologic influx dominated peak migration periods.

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Introduction

The United States Fish and Wildlife Service (USFWS) has conducted direct monitoring of juvenile Chinook salmon (*Oncorhynchus tshawytscha)* passage at Red Bluff Diversion Dam (RBDD; RM 243) on the Sacramento River, CA since 1994 (Johnson and Martin 1997). Martin et al. (2001) developed quantitative methodologies for indexing juvenile Chinook passage using rotary-screw traps to assess the impacts of the RBDD Research Pumping Plant. Absolute abundance (production and passage) estimates were needed to determine the level of impact from the entrainment of salmonids and other fish community populations through experimental 'fish friendly' Archimedes and internal helical pumps (Borthwick and Corwin 2001). The original project objectives were met by 2000 and funding of the project was discontinued.

In 2001, funding was secured through a CALFED Bay-Delta Program grant for three years of annual monitoring operations to determine the effects of restoration activities in the Upper Sacramento River aimed primarily at winter Chinook[1] salmon. Through various amendments, extensions, and grant approvals by the CALFED Ecosystem Restoration Program, the State of California based funding source lasted until 2008. At this point, the State of California defaulted on their funding agreement and internal USFWS funding sources through the Central Valley Project Improvement Act (CVPIA) bridged the gap for a period of time until State funding was restored. The US Bureau of Reclamation, the primary proponent of the Central Valley Project (CVP) of which this project provides monitoring and abundance trend information, has funded this project since 2010 due to regulatory requirements contained within the Biological Opinion for the Operations and Criteria Plan for the CVP (NMFS 2009).

Protection, restoration, and enhancement of anadromous fish populations in the Sacramento River and its tributaries is an important element of the CVPIA Section 3402. The CVPIA has a specific goal to double populations of anadromous fishes in the Central Valley of California. Juvenile salmonid production monitoring is an important component authorized under Section 3406 (b)(16) of CVPIA and has funded many anadromous fish restoration actions which were outlined in the CVPIA Anadromous Fisheries Restoration Program (AFRP) Working Paper (USFWS 1995), and Draft Restoration Plan (USFWS 1997; finalized in 2001).

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[1] The National Marine Fisheries Service first listed Winter-run Chinook salmon as threatened under the emergency listing procedures for the ESA (16 U.S.C.R. 1531-1543) on August 4, 1989 (54 FR 32085). A proposed rule to add winter Chinook salmon to the list of threatened species beyond expiration of the emergency rule was published by the NMFS on March 20, 1990 (55 FR 10260). Winter Chinook salmon were formally added to the list of federally threatened species by final rule on November 5, 1990 (55 FR 46515), and they were listed as a federally endangered species on January 4, 1994 (59 FR 440). Critical habitat for winter Chinook salmon has been designated from Keswick Dam (RM 302) to the Golden Gate Bridge (58 FR 33212; June 16, 1993). Winter Chinook salmon have been listed as endangered under the CESA since September 22, 1989 (California Code of Regulations, Title XIV, Section 670.5). Their federal endangered status was reaffirmed in June 2005 (70 FR 37160).

Since 2002, the USFWS rotary trap winter Chinook juvenile production indices (JPI's) have primarily been used in support of production estimates generated from carcass survey derived adult escapement data using the National Oceanic and Atmospheric Administration's (NOAA) Juvenile Production Estimate Model. Martin et al. (2001) stated that RBDD was an ideal location to monitor juvenile winter Chinook production because (1) the spawning grounds occur almost exclusively above RBDD (Vogel and Marine 1991; Snider et al. 1997, USFWS 2011), (2) multiple traps could be attached to the dam and sample simultaneously across a transect, and (3) operation of the dam could control channel morphology and hydrological characteristics of the sampling area providing for consistent sampling conditions for purposes of measuring juvenile fish passage.

Fall, late-fall, spring, and winter-run Chinook salmon and Steelhead/Rainbow Trout (*Oncorhynchus mykiss*) spawn in the Sacramento River and tributaries upstream of RBDD throughout the year resulting in year-round juvenile salmonid passage (Moyle 2002). Sampling of juvenile anadromous fish at RBDD allows for year-round quantitative production and passage estimates of all runs of Chinook and Steelhead/Rainbow trout. Timing and abundance data have been provided in real-time for fishery and water operations management purposes of the CVP since 2004[2]. Since 2009, confidence intervals, indicating uncertainty in weekly passage estimates, have been included in real-time bi-weekly reports to allow better management of available water resources and to reduce impact of CVP operations on both federal Endangered Species Act (ESA) listed and non-listed salmonid stocks. Currently, Sacramento River winter Chinook are ESA listed as endangered. Central Valley spring Chinook and Central Valley Steelhead (hereafter *O. mykiss)* are listed as threatened within the Central Valley Endangered Species Unit.

Incidental capture of Green Sturgeon (*Acipenser medirostris*) and various Lamprey species (*Lampetra spp. and Entosphenus sp.)* has occurred throughout juvenile Chinook monitoring activities at RBDD since 1995 (Gaines and Martin 2002). Although rotary traps were designed to capture outmigrating salmonid smolts, data from the incidental capture of sturgeon and lamprey species has become increasingly relied upon for basic life-history information and as a measure of relative abundance and species trend data. The Southern distinct population segment of the North American Green Sturgeon was proposed for listing as threatened under the Federal ESA on April 7, 2006 (FR 17757) which then took effect June 6, 2006. Pacific Lamprey (*Entosphenus tridentatus*) are thought to be extirpated from at least 55% of their historical habitat and have been recognized by the USFWS as a species needing a comprehensive plan to conserve and restore these fish (Goodman and Reid 2012).

The objectives of this compendium report are to: (1) summarize the estimated abundance of all four runs of Chinook salmon and *O. mykiss* passing RBDD for brood

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[2] Real-time biweekly reports located for download at: http://www.fws.gov/redbluff/rbdd_biweekly_final.html

years (BY) 2002 through 2012, (2) estimate annual relative abundance of Green Sturgeon and Lamprey species production for eleven consecutive years, (3) define temporal patterns of abundance for all anadromous species passing RBDD, (4) correlate juvenile salmon production with adult salmon escapement estimates, (5) perform exploratory data analyses of potential environmental covariates driving juvenile fish migration trends, and (6) describe various life-history attributes of anadromous juvenile fish produced in the Upper Sacramento River as determined through long-term monitoring efforts at RBDD.

This compendium report addresses, in detail, our juvenile anadromous fish monitoring activities at RBDD for the period April 4, 2002 through September 30, 2013. This report includes JPI's and relative abundance estimates for the 2002-2012 brood year emigration periods and will be submitted to the California Department of Fish and Wildlife to comply with contractual reporting requirements for Ecosystem Restoration Program Grant Agreement Number P0685507 and to the US Bureau of Reclamation who funded in part or in full the surveys from years 2008 through 2013 (Interagency Agreement No. R10PG20172).

Study Area

The Sacramento River originates in Northern California near Mt. Shasta from the springs of Mt. Eddy (Hallock et al. 1961). It flows south through 370 miles of the state draining numerous slopes of the coast, Klamath, Cascade, and Sierra Nevada ranges and eventually reaches the Pacific Ocean via San Francisco Bay (Figure 1). Shasta Dam and its associated downstream flow regulating structure, Keswick Dam, have formed a complete barrier to upstream anadromous fish passage since 1943 (Moffett 1949). The 59-river mile (RM) reach between Keswick Dam (RM 302) and RBDD (RM 243) supports areas of intact riparian vegetation and largely remains unobstructed. Within this reach, several major tributaries to the Sacramento upstream of RBDD support various Chinook salmon spawning populations. These include Clear Creek and Cottonwood Creek (including Beegum Creek) on the west side of the Sacramento River and Cow, Bear, Battle and Payne's Creek on the east side (Figure 1). Below RBDD, the river encounters greater anthropogenic impacts as it flows south to the Sacramento-San Joaquin Delta. Impacts include, but are not limited to, channelization, water diversion, agricultural and municipal run-off, and loss of associated riparian vegetation.

RBDD is located approximately 1.8 miles southeast of the city of Red Bluff, California (Figure 1). The dam is 740-feet (ft) wide and composed of eleven, 60-ft wide fixed-wheel gates. Between gates are concrete piers 8-ft in width. The USBR's dam operators were able to raise the RBDD gates allowing for run-of-the-river conditions or lower them to impound and divert river flows into the Tehama-Colusa and Corning canals. USBR operators generally raised the RBDD gates from September 16 through May 14 and lowered them May 15 through September 15 during the years 2002-2008. As of the spring of 2009, the RBDD gates were no longer lowered prior to June 15 and were raised by the end of August or earlier (NMFS 2009) in an effort to reduce the impact to spring Chinook salmon and Green Sturgeon. Since the fall of 2011, the RBDD gates have been left in the raised position allowing unobstructed upstream and downstream passage of adult and juvenile anadromous fish. The RBDD has been replaced by a permanent pumping plant upstream of the RBDD and the facilities have been relinquished to the Tehama Colusa Canal Authority as of spring 2012. Mothballing of the RBDD infrastructure was scheduled to occur in 2014.

Methods

Sampling Gear.—Sampling was conducted along a transect using four 8-ft diameter rotary-screw traps (E.G. Solutions® Corvallis, Oregon) attached via aircraft cables directly to RBDD. The horizontal placement of rotary traps across the transect varied throughout the study but generally sampled in the river-margin (east and west river-margins) and mid-channel habitats simultaneously (Figure 2). Rotary traps were positioned within these *spatial zones* unless sampling equipment failed, river depths were insufficient (< 4-ft), or river hydrology restricted our ability to sample with all traps (water velocity < 2.0 ft/s).

Sampling Regimes.—In general, rotary traps sampled continuously throughout 24-hour periods and samples were processed once daily. During periods of high fish abundance, elevated river flows, or heavy debris loads, traps were sampled multiple times per day, continuously, or at randomly pre-selected periods to reduce incidental mortality. When abundance of Chinook was very high, sub-sampling protocols were implemented to reduce listed species take and incidental mortality in accordance with National Marine Fisheries Service (NMFS) Section 10(a)(1)(A) research permit terms and conditions. The specific sub-sampling protocol implemented was contingent upon the number of Chinook captured or the probability of successfully sampling various river conditions. Initially, rotary trap cones were structurally modified to only sample one-half of the normal volume of water entering the cones (Gaines and Poytress 2004). If further reductions in capture were needed, the number of traps sampled was reduced from four to three. During storm events and associated elevated river discharge levels, each 24-hour sampling period was divided into four or six non-overlapping strata and one or two strata was randomly selected for sampling (Martin et al 2001). Estimates were extrapolated to un-sampled strata by dividing catch by the strata-selection probability (i.e., $P = 0.25$ or 0.17). If further reductions in effort were needed or river conditions were intolerable, sampling was discontinued or not conducted. When days or weeks were unable to be sampled, mean daily passage estimates were imputed for missed days based on weekly or monthly mean daily estimates (i.e., interpolated).

Data Collection.—All fish captured were anesthetized, identified to species, and enumerated with fork lengths (FL) measured to the nearest millimeter (mm). When capture of Chinook juveniles exceeded approximately 200 fish/trap, a random sub-sample of the catch to include approximately 100 individuals was measured, with all additional fish being enumerated and recorded. Chinook salmon race was assigned using length-at-date criteria developed by Greene[3] (1992). Juvenile salmon were assigned to a fry or pre-smolt/smolt life stage based on their fork length. Individuals ≤ 45 mm were classified as fry, and individuals ≥ 46 mm were classified as pre-smolt/smolts.

O. mykiss between 80 and 200-mm fork length were weighed to the nearest gram using a digital scale with a stated accuracy of +/- 0.5 grams. This size range was selected to reduce the influence of measurement error for fish lengths <80 mm (Pope and Kruse 2007). Additionally, state and federal permit regulations restricted the use of anesthetizing agents for fish that may be consumed by the public (i.e., fish >200mm). *O. mykiss* were visually assessed and assigned a life-stage rating based on morphological features following protocols developed by the Comprehensive Assessment and Monitoring Program (CAMP; USFWS 1997). Furthermore, *O. mykiss* annual weight-length regression coefficients were generated by transforming (Log_{10}) the weight and fork length data to create a linear regression equation:

$$\mathrm{Log}_{10}(\text{Total Weight}) = b(\mathrm{Log}_{10}\text{Fork Length}) + a$$

Confidence interval overlap between the annual slope coefficients was used to test if the annual *O. mykiss* growth rates between years were significantly different (Pope and Kruse 2007). If the 95% confidence intervals around any two slope coefficients did not overlap they were considered significantly different.

Green Sturgeon and Lamprey species were measured for total length (TL) to the nearest mm. Identification of Green Sturgeon larvae was possible based on meristics for individuals > 46 mm TL and assumed for all individuals <46 mm[4]. Lamprey species were identified to the genus level during the ammocoete stage and described as ammocoetes. Adult and macropthalmia (eyed juveniles) were identified to the genus and species level using dentition patterns, specifically by the number of inner lateral horny plates on the sucking disk (Moyle 2002).

Trap Effort. Data quantifying effort by each rotary trap were collected at each trap sampling and included the length of time each trap sampled (expressed as sample weight with 1440 minutes equal to 1.0 for 24-hour samples), water velocity immediately in front of the cone at a depth of 2-ft, and depth of cone “opening” submerged. Water velocity was measured using a General Oceanic® Model 2030 flowmeter. These data collectively were used to calculate the estimated volume of water sampled by traps (X_i)

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[3] Generated by Sheila Greene, California Department of Water Resources, Environmental Services Office, Sacramento (May 8, 1992) from a table developed by Frank Fisher, California Department of Fish and Game, Inland Fisheries Branch, Red Bluff (revised February 2, 1992). Fork lengths with overlapping run assignments were placed with the latter spawning run.

[4] To confirm the identification of larval sturgeon, samples were transferred to UC Davis to be grown-out between 1996 and 1997 (Gaines and Martin 2002) and annual subsamples of larvae were sent to UC Davis for genetic analyses between 2003 and 2012 (Israel et al 2004, Israel and May 2010). To date, all samples have been confirmed to be Green Sturgeon.

in acre-feet (ac-ft). Trap effort data were then standardized to a sample weight of 1.0 for within- and between-day comparisons. Individual (X_i) data were summed for the number of traps operating within a 24-hour sample period to estimate daily water volume sampled (X_d). The percent river volume sampled by traps ($\%Q_d$) was estimated as the ratio of river volume sampled (X_d) to total river volume passing RBDD in acre-feet. River volume (Q_d) was obtained from the United States Geological Survey gauging station at Bend Bridge at RM 258 (USGS site no. 11377100, http://waterdata.usgs.gov/usa/nwis/uv?site_no=11377100). Daily river volume at RBDD was adjusted from Bend Bridge river flows by subtracting daily RBDD diversions, when applicable.

Sampling Effort.— Annual rotary trap sampling effort was quantified by assigning a value of 1.00 to a sample consisting of four, 8-ft diameter rotary-screw traps sampling 24 hours daily, three hundred and sixty-five days a year. Annual values <1.00 represent occasions where less than four traps were sampling, traps were structurally modified to sample only one-half the normal volume of water, or when less than the entire year were sampled. Annual passage estimate effort was calculated by summing the total number of days passage was estimated, based on 3 or 4 traps sampling (minimum required to generate passage estimate; Martin et al. 2001), and divided by the sum of the annual total number of days sampled plus the number of days unsampled.

Mark-Recapture Trials.— Chinook collected as part of daily samples were marked with bismark brown staining solution (Mundie and Traber 1983) prepared at a concentration of 21.0 mg/L of water. Fish were stained for a period of 45-50 minutes, removed, and allowed to recover in fresh water. Marked fish were held for 6-24 hours before being released 2.5-miles upstream from RBDD after official sunset. Recapture of marked fish was recorded for up to five days after release. Trap efficiency was calculated based on the proportion of recaptures to total fish released (i.e., mark-recapture trials). Trials were conducted as fish numbers and staffing levels allowed under a variety of river discharge levels and trap effort combinations.

Trap Efficiency Modeling.— To develop a trap efficiency model, mark-recapture trials were conducted as noted above. Estimated trap efficiency (i.e., the proportion of the juvenile population passing RBDD captured by traps; $\hat{T}_d$) was modeled with $\%Q$ to develop a simple least-squares regression equation (eq. 5). The equation (slope and intercept) was then used to calculate daily trap efficiencies based on daily estimated river volume sampled. Each successive year of mark-recapture trials were added annually to the original trap efficiency model developed by Martin et al. (2001) on July 1 of each year.

Daily Passage Estimates ($\hat{P}_d$).—The following procedures and formulae were used to derive daily and weekly estimates of total numbers of unmarked Chinook and *O. mykiss* passing RBDD. We defined C_{di} as catch at trap i (i = 1,…,t) on day d (d = 1,…,n), and X_{di} as volume sampled at trap i ($i = 1,\ldots t$) on day d ($d = 1,\ldots n$). Daily salmonid catch and water volume sampled were expressed as:

1. $$C_d = \sum_{i=1}^{t} C_{di}$$

and,

2. $$X_d = \sum_{i=1}^{t} X_{di}$$

The $\%Q$ was estimated from the ratio of water volume sampled (X_d) to river discharge (Q_d) on day d.

3. $$\%\hat{Q}_d = \frac{X_d}{Q_d}$$

Total salmonid passage was estimated on day d ($d = 1,\ldots,n$) by

4. $$\hat{P}_d = \frac{C_d}{\hat{T}_d}$$

where,

5. $$\hat{T}_d = (a)(\%\hat{Q}_d) + b$$

and, $\hat{T}_d =$ estimated trap efficiency on day d.

Weekly Passage ($\hat{P}$).—Population totals for numbers of Chinook and *O. mykiss* passing RBDD each week were derived from $\hat{P}_d$ where there are N days within the week:

6. $$\hat{P} = \frac{N}{n} \sum_{d=1}^{n} \hat{P}_d$$

Estimated Variance.—

7. $$Var(\hat{P}) = (1 - \frac{n}{N}) \frac{N^2}{n} s_{\hat{p}_d}^2 + \frac{N}{n} \left[\sum_{d=1}^{n} Var(\hat{P}_d) + 2 \sum_{i \neq j}^{n} Cov(\hat{P}_i, \hat{P}_j) \right]$$

The first term in eq. 7 is associated with sampling of days within the week.

8. $$s^2_{\hat{P}_d} = \frac{\sum_{d=1}^{n}(\hat{P}_d - \hat{\bar{P}})^2}{n-1}$$

The second term in eq. 7 is associated with estimating $\hat{P}_d$ within the day.

9. $$Var(\hat{P}_d) = \frac{\hat{P}_d(1-\hat{T}_d)}{\hat{T}_d} + Var(\hat{T}_d)\frac{\hat{P}_d(1-\hat{T}_d) + \hat{P}_d{}^2\hat{T}_d}{\hat{T}_d^3}$$

where,

10. $Var(\hat{T}_d) =$ error variance of the trap efficiency model

The third term in eq. 7 is associated with estimating both $\hat{P}_i$ and $\hat{P}_j$ with the same trap efficiency model.

11. $$Cov(\hat{P}_i, \hat{P}_j) = \frac{Cov(\hat{T}_i, \hat{T}_j)\hat{P}_i\hat{P}_j}{\hat{T}_i\hat{T}_j}$$

where,

12. $$Cov(\hat{T}_i, \hat{T}_j) = Var(\hat{\alpha}) + x_i Cov(\hat{\alpha}, \hat{\beta}) + x_j Cov(\hat{\alpha}, \hat{\beta}) + x_i x_j Var(\hat{\beta})$$

for some $\hat{T}_i = \hat{\alpha} + \hat{\beta}x_i$

Confidence intervals (CI) were constructed around $\hat{P}$ using eq. 13.

13. $$P \pm t_{\alpha/2,n-1}\sqrt{Var(\hat{P})}$$

Annual JPI's were estimated by summing $\hat{P}$ across weeks.

14. $$JPI = \sum_{week=1}^{52} \hat{P}$$

Fry-Equivalent Chinook Production Estimates.—The ratio of Chinook fry (<46 mm FL) to pre-smolt/smolts (>45 mm FL) passing RBDD was variable among years. Therefore, we standardized juvenile production by estimating a fry-equivalent JPI for among-year comparisons. Fry-equivalent JPI's were estimated by the summation of fry JPI and a weighted (1.7:1) pre-smolt/smolt JPI (inverse value of 59% fry-to-presmolt/smolt survival; Hallock undated). Rotary trap JPI's could then be directly compared to determine variability in production between years.

Relative Abundance.—Catch per unit volume (CPUV; Gaines and Martin 2002) was used as an index of relative abundance (RA) for Green Sturgeon and Lamprey species at RBDD.

15. $$RA_{dt} = \frac{C_{dt}}{V_{dt}}$$

RA_{dt} = relative abundance on day *d* by trap *t* (catch/acre-foot),
C_{dt} = number of fish captured on day *d* by trap *t*, and
V_{dt} = volume of water sampled on day *d* by trap *t*.

The volume of water sampled (V_{dt}) was estimated for each trap as the product of one-half the cross sectional area (wetted portion) of the cone, water velocity (ft/s) directly in front of the cone at a depth of 2-feet, cone modified (multiplied by 0.5) or not (multiplied by 1.0), and duration of sampling.

Exploratory Data Analyses.—The sampling of four runs of Chinook, *O. mykiss*, Green Sturgeon, and Lamprey occurred over 11 years and a variety of environmental conditions. Abiotic data collected or calculated throughout sample efforts included water temperature, flow, turbidity, and moon illuminosity (fraction of moon illuminated). The abiotic factors were analyzed to determine if patterns or trends existed throughout the migration periods of the various species. Additional statistical analyses were performed, when applicable, and additional methods are noted within the results section for species-specific data trends analyzed.

Results

Sampling Effort.—Annual sampling effort varied throughout the 11-year period of reporting. The reasons for less than 100% effort varied by time of year and run sampled due to numerous factors. These factors can be categorized as either intentional or unintentional decreases in effort. Intentional decreases in effort were primarily due to ESA Section 10(a)1(A) take and incidental mortality limits, the desire to decrease potential impacts to ESA listed fish or hatchery released production groups, or when staffing levels were not appropriate for the conditions encountered. Unintentional decreases in effort were due primarily to storm activity and related debris flows or conditions considered too dangerous to sample. Additionally, during the years RBDD was in operation (2002-2011), many days were not sampled due to operational requirements imposed by USBR operators (e.g., lowering or raising of the dam gates).

Annual sample effort was assigned a value of 1.0 based on sampling four traps 365 days a year. Annual sample effort values by salmonid species and run are described in Table 1. Overall, annual sample effort for all salmonids combined ranged from 0.53 to

0.91 (ȳ = 0.80, SD = 0.10) following annual juvenile salmonid brood year cycles. The lowest values corresponded to the year 2002 when sampling did not begin until mid-April of the year. The highest value corresponded to the year 2007 when flow events were mild, staffing levels were optimal, and permit restrictions did not dictate major sampling effort reductions (Table 1).

Mark-Recapture Trials.—Trap efficiency estimates were calculated by conducting mark-recapture trials (Volkhardt et al. 2007) using unmarked salmon collected from daily trap samples. Trials were conducted when trap catch values allowed the release of 1,000 fish per trial, generally, as well as when staffing and river conditions would allow. Mark-recapture trials were also employed to validate daily trap efficiency estimates by comparing actual with predicted (modeled) estimates. This was especially important during peak salmon outmigration periods.

The number of trials conducted each calendar year ranged from 0 in 2010 to 21 in 2004 (ȳ = 7.7) and totaled 85 trials between 2002 and 2013 (Table 2). Trials were conducted with four rotary traps (*N* = 74) or three traps (*N* = 11). Some trials were conducted with cones modified to sample half the volume of water (*N* = 25) or mixed (*N* = 1), but primarily unmodified and sampling full effort (*N* = 59). Trap efficiencies were tested with the RBDD gates raised (*N* = 72) and lowered (*N* = 13) during the years when RBDD was in operation (Table 2).

Trials were conducted through a variety of flow and trap effort conditions representing actual sampling conditions detected throughout various fish migration periods (Table 2). Estimates of the percentage of river water volume sampled by traps (*%Q*) ranged from 0.72 to 6.87% (ȳ = 3.10, SD = 1.32). Efficiency estimates for the 85 trials ranged from 0.34 to 5.48% (ȳ = 2.37%, SD = 0.01).

Released fish groups ranged from 340 to 5,143 individuals (ȳ = 1,598) and recaptured fish numbers ranged from 7 to 119 (ȳ = 36) per trial. Trials were conducted predominantly with fry size-class (<46 mm fork length), naturally produced fall Chinook (67%) and to a lesser extent winter Chinook (22%). Trials were conducted in some years using unmarked pre-smolt/smolts (11%) following annual Coleman National Fish Hatchery Fall Chinook production releases[5] during spring, as conditions and staffing levels allowed (Table 2).

Average fork lengths of release groups in the fry size-class had fork lengths ranging from 35.5 to 57.1 mm (ȳ = 37.2 mm). Recaptured fork lengths ranged from 34.6 to 62.4 mm (ȳ = 37.3 mm). Average fork lengths of fish released in the pre-smolt/smolt size-class ranged from 68.7 to 81.2 mm (ȳ = 75.3 mm). Recaptured fork lengths ranged from 61.3 to 80.2 mm (ȳ = 75.3 mm; Table 2). A paired t-test was performed on the average

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[5] Coleman National Fish Hatchery is located upstream of RBDD on Battle Creek a tributary to the Sacramento. Fall Chinook production fish (~12 million per year) were adipose clipped (i.e., marked) in varying proportions over the years of study between 0 and 25%. Unmarked fish were included in some efficiency trials as they could not be distinguished from naturally produced fish.

release and recaptured fish lengths for all trials and indicated no significant difference between the released and recaptured fish sizes ($P = 0.759$, $df = 83$, $t = -0.308$).

Trap Efficiency Modeling.—Between 1998 and 2000, Martin et al. (2001) developed a trap efficiency model for the RBDD rotary trapping operation by conducting 58 mark-recapture trials (one trial excluded due to zero efficiency value). These data were used as the basis of the trap efficiency model to calculate daily passage estimates. The model was further developed between 2002 and 2013 with the addition of 85 mark-recapture trials. Trap efficiency was positively correlated to (*%Q)*, with higher efficiencies occurring as the relative percentage of discharge volume sampled by rotary traps increased. Trap efficiency was inversely related to river discharge (*Q*), as river discharge increased, trap efficiency decreased.

As mark-recapture trials were conducted, the trap efficiency model was typically updated one time each year. The newest model was applied on July 1 of each year, the beginning of the annual winter Chinook juvenile brood year period. Between 2002 and 2013 nine different models were utilized. The specific dates and model parameters with *P*-values used throughout the reporting period are listed chronologically below the groups of mark-recapture trials incorporated into the models in Table 2. The net result over the 11-year period was stabilization and improvement of the trap efficiency model with the addition of 85 mark-recapture trials. Overall, the *P*-values indicated a high level of significance for the parameter *%Q* in all years ($P< 0.001$). The model's *r*-squared value dropped in the first few years and then improved greatly with the addition of numerous naturally produced fry size-class mark-recapture trials over a variety of river discharge levels (Table 2; Figure 3).

Over the 11 years' data was collected a wide range of *%Q* values were sampled (0.44 to 6.86%, $\bar{y}$ = 2.90, SD = 0.01). On 10 occasions, extremely low *%Q* values (<0.72%) were sampled outside of the range of values tested through efficiency trials (Figure 3). The net result was that trap efficiency values were extrapolated outside the range of the model on a mere 10 of 3,315 days sampled (0.3%).

Chinook Capture Fork Length Analyses.—Chinook run assignment based on length-at-date (LAD) criteria was originally developed from growth data in the Upper Sacramento River at the Tehama Colusa Fish Facility using fall Chinook production records from 1972 through 1981 (Fisher 1992). An estimate of apparent growth rate was originally developed from fall Chinook < 90 mm FL as fish migrated or were depleted from the spawning channels by this size (Fisher 1992). Johnson et al. (1992) further developed (extrapolated) the data to predict run for fish ≥ 90 mm and ≤ 250 mm FL. The data was further refined by Frank Fisher of the California Department of Fish and Game, whereby estimated growth curves were produced for all runs based on adult timing, water temperatures, and juvenile emergence timing and growth (Brown and Greene 1992). The growth curves were fitted to a table of daily growth increments (i.e., fork length at age in days) by the California Department of Water Resources in the early

1990's (Brown and Greene 1992; Greene 1992). The following fork length data encompassed fish sampled by rotary traps using the LAD tables up to 180 mm FL, as fish were rarely captured above this length (i.e., extreme outliers).

Fall Chinook sampled from brood years 2002-2012 were heavily weighted to the fry size-class category (<46mm). On average, 75.7% of all fish sampled as fall could be described as fry (SD = 6.9) with 71.0% of the fry measuring less than 40 mm FL (Figure 4a). The remaining 24.3% (SD = 6.9) were attributed to the pre-smolt/smolt category (>45 mm) with fish between 70 and 89 mm composing 71.0% of that value. Overall, fall Chinook were sampled between 30 and 134 mm annually, with trivial numbers below or above this range (Figure 4b). Fall Chinook showed little growth, on average, between December and March, followed by a significant increase in length in April, followed by more moderate and variable growth through November (Figure 4c). The growth pattern exhibited by fall Chinook appears strongly influenced by the duration of the fall Chinook spawning period and the LAD criteria. Beginning on April 1, newly emerged fry were classified as late-fall Chinook instead of fall Chinook thereby significantly increasing the median fork length of fall Chinook during the first two weeks of April.

Late-fall Chinook sampled from brood years 2002-2012 were not heavily weighted to the fry size-class category (<46mm). On average, 24.9% of all fish sampled as late-fall could be described as fry (SD = 12.8) with 96.3% of the fry measuring less than 40 mm FL (Figure 5a). The remaining 75.1% (SD = 12.8) were attributed to the pre-smolt/smolt category (>45 mm) with fish between 70 and 89 mm composing 48.3% of that value. Overall, late-fall Chinook were sampled between 26 and 180 mm annually (Figure 5b). Late-fall Chinook showed little growth, on average, between April and May, followed by a significant increase in length in June and July, followed by more moderate and variable growth between late-September and February (Figure 5c). The growth pattern exhibited by late-fall Chinook appears modestly influenced by the LAD criteria. Beginning on July 1, newly emerged fry were classified as winter Chinook instead of late-fall Chinook slightly increasing the median fork length of late-fall Chinook during the first few weeks of July. In mid-September and to a lesser extent in late-December, the overall fork length distribution for late-fall Chinook increases from one week to the next and was likely a result of decreased sampling effort due to RBDD gate operations and initial winter storms.

Winter Chinook sampled from brood years 2002-2012 were heavily weighted to the fry size-class category (<46mm). On average, 77.9% of all fish sampled as winter could be described as fry (SD = 8.8) with 92.8% of the fry measuring less than 40 mm FL (Figure 6a). The remaining 22.1% (SD = 8.8) were attributed to the pre-smolt/smolt category (>45 mm) with fish between 46 and 69 mm composing 85.3% of that value. Overall, winter Chinook were sampled between 27 and 162 mm annually (Figure 6b). Winter Chinook showed little growth, on average, between July and October, followed by a significant increase in length in mid-October, followed by more moderate growth through December. The growth pattern was then highly variable between January and

April (Figure 6c). The growth pattern exhibited by winter Chinook appears moderately influenced by the LAD criteria. Beginning on October 16, newly emerged fry were classified as spring Chinook instead of winter Chinook thereby significantly increasing the median fork length of winter Chinook during the last two weeks of October.

Spring Chinook sampled from brood years 2002-2012 were slightly weighted to the fry size-class category (<46mm). On average, 58.6% of all fish sampled as spring could be described as fry (SD = 19.6) with 90.0% of the fry measuring less than 40 mm FL (Figure 7a). The remaining 41.4% (SD = 19.6) were attributed to the pre-smolt/smolt category (>45 mm) with fish between 70 and 89 mm composing 69.2% of that value. Overall, spring Chinook were sampled between 28 and 143 mm annually (Figure 7b). Spring Chinook showed moderate growth, on average, between October and mid-December, followed by more consistent increasing growth through May (Figure 7c). Spring Chinook disappear from the catch typically by June with sporadic capture of large smolts in July of some years. The growth pattern exhibited by spring Chinook appears moderately influenced by the LAD criteria. Beginning on December 1, newly emerged fry were classified as fall Chinook instead of spring Chinook likely resulting in positive size-class bias for spring Chinook.

O. mykiss Capture Size Analyses.—Following the conventions used by Gaines and Martin (2002) size categorization for *O. mykiss* followed a slightly different pattern than Chinook and was organized by fork length as fry (<41 mm), sub-yearling (41–138 mm), and yearling (>138 mm). Moyle (2002) described Sacramento River *O. mykiss* populations as highly variable, but typically reaching 140-150 mm FL in their first year. The focus of our data reporting is age-0 and the focus of our size-class analyses was primarily < 139mm and secondarily < 200 mm for length-weight analyses.

O. mykiss sampled from calendar years 2002-2012 were heavily weighted towards the 41-80 mm size-class (79.2%; Figure 8a) which fell into the sub-yearling category (Figure 8b). On average, a modest 8.2% could be categorized as fry (Table 3). Overall, *O. mykiss* yearling and estimated age-2 fish were annually sampled at rates of 2.4% and 0.6%, respectively (Table 3). There was little variation detected within any size-class between categories, yet variance in weekly captures was high throughout the year (Figure 8c). The variable life-history strategies of *O. mykiss* resident and anadromous forms was evident from our size-class capture data. In general, newly emerged fry occurred in early-April and increased in size to early July. Thereafter, a second cohort of either resident trout or summer steelhead[6] was sampled which demonstrated a secondary growth pattern through December (Figure 8c).

O. mykiss CAMP Program Life-Stage Comparisons.— *O. mykiss* capture patterns appeared to be different than that of Chinook salmon as relatively few *O. mykiss* were captured as fry ($\bar{y}$ = 8.3%) and the majority were sampled as sub-yearlings ($\bar{y}$ = 88.7%;

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[6] Summer steelhead are believed to be extirpated since the construction of dams blocked access to headwater habitat (Moyle 2002).

Table 3; Figure 8b). Fry capture was highest in 2002 and 2006 (11.2% and 17.5%) although these years sampled the first and third fewest *O. mykiss* of the 11 years, respectively. Yearling and age-2 capture was generally low averaging only 3.0%.

Life stage classification of fry was uniform throughout all years ($\bar{y}$ = 6.8%, SD = 2.6%) and did not vary greatly in 2002 and 2006 in contrast to age classification. Parr and silvery-parr accounted for 91.5% of the *O. mykiss* handled at RBDD although there was a large difference between the two categories, 74.0% and 17.5% respectively. Annual variability in parr and silvery-parr classifications (SD = 15.5 and 16.8) seemed to change after 2005 and was likely due to a protocol change or interpretation of morphological characteristics by field staff. Juveniles showing signs of anadromy (i.e., smolts) made up only 1.6% of individuals sampled.

O. mykiss Weight-Length Analysis.—Log $_{10}$ transformed *O. mykiss* weight-length data showed a strong overall relationship between the two variables (r^2 = 0.942, Table 4). The annual slope coefficients for the 11-year period varied slightly, ranging from 2.858 to 3.052. The variability in growth was not considered significant as the 95% CI annual slope coefficients encompassed the slope coefficient of the overall mean (Table 4). Typical of most weight-length models (Pope and Kruse 2007), the variability about the regression increased with the overall length of the fish (Figure 9).

Salmonid Passage.—Passage estimates for the four runs of Chinook were calculated weekly as fry and pre-smolt/smolt passage. The sum of the weekly fry and pre-smolt/smolt passage values equal the weekly *total* passage values. Confidence intervals (CI) were calculated at the 90% level for all runs for weekly passage estimates. Weekly CI values were summed to obtain the annual CI's around the annual passage estimate (i.e., summed weekly passage estimates). Negative CI values were set to zero and result in some years CI's being asymmetrical around the annual passage estimate. Annual passage estimates (i.e., total passage estimates), by brood year, with CI's and annual effort values are presented for Chinook within Tables 5a-5d and graphically in Figures 10, 12, 14, and 16. Fry and pre-smolt/smolt Chinook passage estimates with 90% CI's summarized annually by run can be found in Appendix 1 (Tables A1-A8). Comparisons of relative variation within and between runs of Chinook were performed by calculating Coefficients of Variation (Sokal and Rohlf 1995) of passage estimates.

Fall Chinook annual passage estimates ranged between 6,627,261 and 27,736,868 juveniles for brood years 2002-2012 ($\bar{y}$ = 14,774,923, CV = 46.2%; Table 5a). On average, fall Chinook passage was composed of 74% fry and 26% pre-smolt/smolt size-class fish (SD = 10.3). Proportions as low as 56% and as high as 87% fry were detected (Table 5a). Annual effort values resulted in interpolations of between 9 and 60% of annual passage estimates ($\bar{y}$ = 28%). In general, the effect of annual effort on CI width indicated greater spread of CI's with decreasing effort (Figure 10).

On average, weekly fall passage equated to 5% of total annual fall Chinook passage between mid-January and early March (Figure 11a). Weekly passage varied considerably during this period with some weeks' passage totals accounting for >25% of annual passage values. Between BY 2002 and 2012, 75% of average annual passage occurred by the end of March, signifying January through March as the greatest period of migration. A second, albeit much diminished, mode of passage occurred between late April and May of each year due to the release of unmarked fall Chinook production fish from Coleman National Fish Hatchery. These fish could not be distinguished from wild fish due to fractional marking processes that varied over the 11-year period from 0 to 25%. Overall, fall passage was complete by the end of July each year with sporadic small pulses of smolts through November (Figure 11b).

Late-fall Chinook annual passage estimates ranged between 91,995 and 2,559,519 juveniles for brood years 2002-2012 (ȳ = 447,711, CV = 159.9%; Table 5b). On average, late-fall Chinook passage was composed of 38% fry and 62% pre-smolt/smolt size-class fish (SD = 22.5). Proportions as low as 11% and as high as 72% fry were detected (Table 5b). Annual effort values resulted in interpolations of between 9 and 56% of annual passage estimates (ȳ = 31%). The effect of annual effort on CI width indicated greater spread of CI's with decreasing effort due to hatchery fish releases, in general (Figure 12).

On average, weekly late-fall passage started abruptly and held at ≤ 5% of total annual passage between April and May (Figure 13a). Weekly passage varied considerably during this period with some weeks' passage totals accounting for >35% of annual passage values. A second, similar magnitude mode of passage occurred between July and August in most years. A third, albeit diminished, mode occurred during October and November with passage accounting for up to 35% of the annual run in some years. Between BY 2002 and 2012, 75% of average annual passage occurred by mid-September, signifying April through September as the greatest period of migration. Overall, late-fall passage was complete by the end of December each year with sporadic small pulses of smolts through February (Figure 13b).

Winter Chinook annual passage estimates ranged between 848,976 and 8,363,106 juveniles for brood years 2002-2012 (ȳ = 3,763,362, CV = 73.2%; Table 5c). On average, winter Chinook passage was composed of 80% fry and 20% pre-smolt/smolt size-class fish (SD = 11.2). Proportions as low as 53% and as high as 90% fry were detected (Table 5c). Annual effort values resulted in interpolations of between 8 and 42% of annual passage estimates (ȳ = 18%). The effect of annual effort on CI width indicated greater spread of CI's with decreasing effort due to subsampling measures during peak migration periods (i.e., take or impact reduction), in general (Figure 14).

On average, weekly winter passage increased consistently through September to a peak into early October. Weekly passage varied considerably during August through December with some weeks' passage totals accounting for >20% of annual passage values. Between BY 2002 and 2012, 75% of average annual passage occurred by mid-

October. Weekly passage between October and December indicated wide variability over the 11-year period, yet the trend showed steady decreases followed by a second increase or mode of winter passage in November and December (Figure 15a). Overall, winter passage was 99% complete by the end of December each year with sporadic pulses of smolts through March that contributed minimally to the annual total winter passage estimate (Figure 15b).

Spring Chinook annual passage estimates ranged between 158,966 and 626,925 juveniles for brood years 2002-2012 ($\bar{y}$ = 364,508, CV = 45.0%; Table 5d). On average, spring Chinook passage was composed of 54% fry and 46% pre-smolt/smolt size-class fish (SD = 20.0). Proportions as low as 24% and as high as 91% fry were detected (Table 5d). Annual effort values resulted in interpolations of between 1 and 49% of annual passage estimates ($\bar{y}$ = 29%). The effect of annual effort on CI width indicated a slightly greater spread of CI's with decreasing effort due to subsampling during winter storm events, in general (Figure 16).

On average, weekly spring passage started abruptly and held at roughly 5% of total annual passage between mid-October and mid-November (Figure 17a). Weekly passage varied somewhat during this period with some weeks' passage totals accounting for up to 20% of annual passage values. A second, increased magnitude mode of passage occurred during December in most years with a single week accounting for nearly 50% of the annual passage estimate. Between BY 2002 and 2012, 75% of average annual passage occurred by mid-April, signifying October through April as the greatest period of migration. A third mode of similar magnitude to the second mode occurred during April and May with passage accounting for up to 45% of the annual run in some years. This could be characterized as an erroneous increase in spring passage. Unmarked fall production fish exceeded the size-class for fall run and therefore fell within the spring run category using LAD criteria. Between 2007 and 2012, on average, 4.3% of the marked fall production fish fell within the spring-run size-class using LAD criteria. Assumedly, a similar proportion of the unmarked fish were added into the spring-run passage estimates as they could not be distinguished from naturally produced fish. Overall, spring Chinook passage was complete by the end of May each year (Figure 17b).

O. mykiss passage estimates were generated using trap efficiency estimates calculated using the Chinook-based trap efficiency model. Caution should be exercised when interpreting the following results as Chinook and *O. mykiss* trap efficiency values likely differ, perhaps greatly. Irrespective of the accuracy of the magnitude of passage estimates based on Chinook efficiency trials, the trends in abundance remain plausible due to the standardization of effort and catch. Unlike Chinook, *O. mykiss* were not attributed to a fry or pre-smolt/smolt category and passage estimates with 90% CI's were calculated that included all size-classes and life-stages combined.

Annual passage estimates for *O. mykiss* ranged between 56,798 and 151,694 juveniles for calendar years 2002-2012 ($\bar{y}$ = 116,272, CV = 25.7%; Table 5e). Annual effort values resulted in interpolations of between 4 and 56% of annual passage estimates (ȳ = 22%). The effect of annual effort on CI width indicated a slightly greater spread of CI's with decreasing effort, in general (Figure 18).

On average, weekly *O. mykiss* passage was low (<5% on average) from April through July of each year with some variability. In 11 years of sampling only once did passage exceed 10% of annual passage during these months. Weekly passage between July and August increased to peak values ranging from 5% to nearly 25% (Figure 19a). Between 2002 and 2012, 75% of average annual passage occurred by mid-August. Weekly passage generally declined between September and October. Overall, *O. mykiss* passage was negligible between December and the following February each year (Figure 19b).

Fry-Equivalent Chinook Production Estimates.—Juvenile Chinook passage values were standardized to *fry-equivalent* production estimates for within- and between-year comparisons. As noted above, the various runs were sampled with oftentimes considerable variability in fry to pre-smolt/smolt ratios over the 11–year sample period (Table 5a-5d). By multiplying 1.7 to all fish sampled in the pre-smolt/smolt category (>45mm) within each run, annual Chinook production above the RBDD transect could be estimated. These standardized production estimates could then be compared to adult escapement estimates calculated from the California Central Valley Chinook Population Report (Azat 2013) or carcass survey data in the case of winter Chinook (USFWS 2006-2011 and 2013). Moreover, by comparing production to the number of adult Chinook females each year (by run) and estimating fecundity data from CNFH and Livingston Stone National Fish Hatchery (LSNFH) hatchery production records, estimated recruits per female and egg-to-fry survival estimates were generated.

Fall Chinook fry-equivalent production estimates between 2002 and 2012 ranged from 7,554,574 to 30,624,209 (ȳ = 17,262,473, CV = 43.2%). Lower and upper 90% CI's were generated for each week, summed annually, and averaged between 6,670,475 and 30,707,529 (Table 6a).

Adult fall Chinook escapement estimates above RBDD (mainstem Sacramento River plus tributaries reported) estimated escapement between 12,908 and 458,772 (ȳ = 93,661) for the same years. Fall Chinook carcass survey data collected by California Department of Fish and Wildlife (CDFW) provided annual female:male sex ratio estimates averaging 0.46:0.54 (D. Killam, unpublished data). A significant relationship between estimated number of females and fry-equivalent fall Chinook production estimates was detected (r^2 = 0.53, df = 10, *P* = 0.01; Figure 20a). Recruits per female were calculated ranging from 89 to 1,515 (ȳ = 749). Assuming an average female fecundity value of 5,407, based on fall Chinook spawning records from CNFH between 2008 and 2012 (K. Brown, unpublished data), resulted in an egg-to-fry survival estimate averaging 13.9% for fall Chinook (Table 6a).

Late-fall Chinook fry-equivalent production estimates between 2002 and 2012 ranged from 116,188 to 4,041,505 ($\bar{y}$ = 669,939, CV = 169.8%). Lower and upper 90% CI's were generated for each week, summed annually, and averaged between 222,044 and 1,236,432 (Table 6b).

Adult late-fall Chinook escapement estimates above RBDD estimated escapement between 2,931 and 36,220 ($\bar{y}$ = 9,108) for the same years. Late-fall Chinook annual female:male sex ratio estimates relied on an assumption of the average ratio found for fall Chinook (i.e., 0.46:0.54). A significant relationship between estimated number of females and fry-equivalent late-fall Chinook production estimates was detected (r^2 = 0.67, df = 10, P = 0.002; Figure 20b). Recruits per female were calculated ranging from 47 to 243 ($\bar{y}$ = 131). Assuming an average female fecundity value of 4,662 based on late-fall Chinook spawning records from CNFH between 2008 and 2012 (K. Brown, unpublished data) resulted in an egg-to-fry survival estimate averaging 2.8% for late-fall Chinook (Table 6b).

Winter Chinook fry-equivalent production estimates between 2002 and 2012 ranged from 996,621 to 8,943,194 ($\bar{y}$ = 4,152,547, CV = 70.1%). Lower and upper 90% CI's were generated for each week, summed annually, and averaged between 2,265,220 and 6,124,494 (Table 6c).

Adult winter Chinook escapement estimates above RBDD (USFWS/CDFW carcass survey data; available at http://www.fws.gov/redbluff/he_reports.aspx) estimated escapement between 824 and 17,205 ($\bar{y}$ = 6,532) for the same years. Winter Chinook annual female:male sex ratio estimates were estimated during the annual carcass surveys (Table 6c). A highly significant relationship between estimated number of females and fry- equivalent winter Chinook production estimates was detected (r^2 = 0.90, df = 10, $P <$ 0.001; Figure 20c). Recruits per female were calculated ranging from 846 to 2,351 ($\bar{y}$ = 1,349). Annual female fecundity values were estimated based on winter Chinook spawning records from LSNFH between 2008 and 2012 (USFWS Annual Propagation Reports; available at http://www.fws.gov/redbluff/he_reports.aspx) and resulted in an egg-to-fry survival estimate averaging 26.4% for winter Chinook (Table 6c).

Spring Chinook fry-equivalent production estimates between 2002 and 2012 ranged from 207,793 to 747,026 ($\bar{y}$ = 471,527, CV = 40.9%). Lower and upper 90% CI's were generated for each week, summed annually, and averaged between 199,365 and 792,668 (Table 6d).

Adult spring Chinook escapement estimates above RBDD (mainstem Sacramento River plus tributaries reported) estimated escapement between 77 and 399 ($\bar{y}$ = 195) for the same years. Spring Chinook annual female:male sex ratio estimates relied on an assumption of the average ratio found for fall Chinook (i.e., 0.46:0.54). No significant relationship between estimated number of females and fry-equivalent spring Chinook production estimates was detected (r^2 = 0.00, df = 10, P = 0.971; Figure 20d). Recruits per female were calculated ranging from 1,112 to 8,592 ($\bar{y}$ = 3,122). Assuming an average female fecundity value of 5,078, based on averaging of 5 years of fall and late-fall Chinook spawning records from CNFH and 10 years of winter Chinook spawning records from LSNFH, resulted in an egg-to-fry survival estimate averaging 61.5% for spring Chinook (Table 6d).

Green Sturgeon Data.—Capture of young of the year sturgeon occurred annually between calendar years 2002 and 2012, except in 2008. Catch was highly variable, not normally distributed, and ranged between 0 and 3,701 per year (median = 193; Table 7). Sturgeon sampled by rotary traps could be positively identified as Green Sturgeon in the field *above* total length of 46 mm. At this size, lateral scutes were fully developed and could be counted to distinguish between White (*Acipenser transmontanus*) and Green Sturgeon (Moyle 2002). Of 2,912 sturgeon measured in the field, 99.14% were less than 46 mm. In all years, except 2007 and 2008, sub-samples of larval and/or juvenile sturgeon rotary trap catch (up to 50% in some years) were supplied to UC Davis for genetic research and all were determined to be Green Sturgeon (See Israel et al. 2004; Israel and May 2010). We therefore assumed all sturgeon captured in rotary traps were Green Sturgeon based on the results of genetic analyses. Moreover, Green Sturgeon were the only confirmed spawning Acipenserids sampled at or above the RBDD transect between 2008 and 2012 during sturgeon spawning surveys (Poytress et al. 2009-2013).

Green Sturgeon catch was primarily composed of recently emerged, post-exogenous feeding larvae with a 10-year median capture total length averaging 27.3 mm (SD = 0.8; Table 7). Sturgeon were sampled between 18 and 188 mm, but those sampled above 40 mm were considered outliers (N = 51; Table 7; Figure 21a).

The temporal pattern of Green Sturgeon captures occurred, on average, between May 1 and August 28 of each year. Green Sturgeon capture trends indicated annual variability, but on average 50% were sampled by the end of June each year and nearly 100% by the end of July (Figure 21b), with outliers (i.e., juveniles) captured in August, September and as late as November (e.g., 188 mm TL) in some years.

Relative abundance of Green Sturgeon was measured as catch per estimated water volume sampled (CPUV in ac-ft) through rotary trap cones and summed daily. Daily values were summed annually to produce each year's annual index of abundance. Absolute abundance estimates, via trap efficiency trials, could not be calculated due to low numbers of sturgeon sampled on a daily basis and the fragile nature of newly emerged exogenous feeding larvae.

Green Sturgeon annual CPUV was typically low and ranged from 0.0 to 20.1 fish/ac-ft ($\bar{y}$ = 2.5 fish/ac-ft, SD = 5.9). Data were positively skewed and median annual CPUV was 0.8 fish/ac-ft. Relative abundance distribution data were highly influenced by samples collected in 2011 that equated to two orders of magnitude higher than any other year's index (Figure 21c). Overall, variability in CPUV between years was relatively high as the CV was 236% for the eleven-year period (Table 7).

Lamprey Species Data.—Capture of multiple lamprey species occurred between water year (WY; October - September) 2003 and 2013. WY 2002 was excluded from analyses as less than 50% of the entire year was sampled. Lamprey species sampled included adult and juvenile Pacific Lamprey and to a much lesser extent River Lamprey (*Lampetra ayresi*), and Pacific Brook Lamprey (*Lampetra pacifica)*. Unidentified lamprey ammocoetes and Pacific Lamprey (PL) composed 99.8% of all captures, 24% and 75%, respectively. River Lamprey and Pacific Brook Lamprey combined, composed the remaining 0.2% of all captures. Annual catch, length, and relative abundance information for River and Pacific Brook Lamprey can be found in Appendix 1 (Tables A9 and A10) and are not discussed further due to very low capture rates.

Annual catch of ammocoetes was relatively stable and ranged between 385 and 1,415 individuals per year ($\bar{y}$ = 757, median = 657; Table 8a). The catch coefficient of variation for ammocoetes was 38.5%. Minimum TL of lamprey ammocoetes was 14 mm and maximum TL was 191. Over the eleven complete years sampled, the average minimum and maximum TL's were 32 and 164 mm, respectively ($\bar{y}$ =105, SD = 4.7; Figure 22a).

Annual catch of PL macropthalmia and a small fraction of adults was variable and ranged between 204 and 5,252 individuals per year ($\bar{y}$ = 2,335, median = 2,747; Table 8b). The catch coefficient of variation for PL was 75.3%. Minimum TL of PL was 72 mm and maximum TL was 834. Over the eleven years sampled, the average minimum and maximum TL's were 88 and 665 mm, respectively ($\bar{y}$ = 150, SD = 37.3; Figure 23a).

Lamprey captures occurred throughout the year between October and September. Ammocoete capture trends indicated annual variability, but on average 25% were sampled by the end of January, 50% were sampled by the end of March, 75% were sampled by the end of May and 100% by the end of September (Figure 22b). Transformed PL (macropthalmia and adult) capture trends indicated a different pattern of capture and annual variability compared to ammocoetes. On average, 5% were sampled through October, 50% were sampled through December, 75% were sampled through February, 90% by the beginning of April with a 100% by the end of September (Figure 23b).

Relative abundance of ammocoetes and PL were measured as CPUV through individual rotary trap cones and summed daily. Daily values were summed annually to produce each year's annual index of abundance. Absolute abundance estimates employing mark-recapture methods could not be calculated due to the sporadic capture of adequate numbers of juveniles (e.g., > 1,000 individuals) that would be needed for mark-recapture trials. Moreover, emphasis was placed on conducting Chinook mark-recapture trials at times of pronounced lamprey abundance.

Ammocoete annual relative abundance ranged from 3.6 to 11.7 fish/ac-ft (ȳ = 6.8 fish/ac-ft, SD = 2.6; Figure 22c). Overall, ammocoete data were normally distributed as median CPUV was 6.5 fish/ac-ft, similar to the mean value. Variability in CPUV between years was modest and the coefficient of variation was 39% for the eleven-year period (Table 8a).

PL annual relative abundance was generally higher than ammocoete relative abundance and ranged from 2.1 to 112.8 fish/ac-ft (ȳ = 41.0 fish/ac-ft, SD = 34.7; Figure 23c). Overall, PL data was slightly positively skewed and median CPUV was 34.1 fish/ac-ft. Variability in CPUV between years was moderate and the coefficient of variation was 85% for the eleven-year period (Table 8b).

Abiotic Conditions.—Tabular summaries of the abiotic conditions that were encountered during each annual capture period were summarized for each run of salmon, *O. mykiss*, Green Sturgeon and Lamprey species. Tabular summaries associated with each species annual captures are located in Tables 9a-9f and include: dates of capture, peak daily water temperature, peak daily river discharge levels and mean daily turbidity values. A series of exploratory plots comparing the above daily environmental data variables plus an index of moon illuminosity were generated for fry and pre-smolt Chinook daily passage estimates for visual analyses. Winter Chinook fry and pre-smolt/smolt plots are included in Appendix 2 (Figures A1-A23) for reference.

Annual environmental covariate data for fall Chinook salmon can be found in Table 9a. Results presented below describe data averaged over 11 brood years. Fall Chinook were sampled over a period of 250 to 273 days per year (ȳ = 264 days, SD = 7). Water temperatures ranged from 45 to 62 °F (ȳ = 55°F, SD = 0.8). Sacramento River discharge ranged from 5,605 to 72,027 CFS (ȳ = 14,844 CFS, SD = 5,442). Turbidity values ranged from 1.5 to 298.7 NTU (ȳ = 14.4 NTU, SD = 6.3).

Annual environmental covariate data for late-fall Chinook salmon can be found in Table 9b. Results presented below describe data averaged over 11 brood years. Late-fall Chinook were sampled over a period of 270 to 338 days per year (ȳ = 300 days, SD = 24). Water temperatures ranged from 46 to 62 °F (ȳ = 56°F, SD = 0.7). Sacramento River discharge ranged from 5,536 to 67,520 CFS (ȳ = 12,580 CFS, SD = 2,829). Turbidity values ranged from 1.4 to 272.0 NTU (ȳ = 11.3 NTU, SD = 6.2).

Annual environmental covariate data for winter Chinook salmon can be found in Table 9c. Results presented below describe data averaged over 11 brood years. Winter Chinook were sampled over a period of 207 to 278 days per year (ȳ = 250 days, SD = 20). Water temperatures ranged from 46 to 61 °F (ȳ = 55°F, SD = 0.8). Sacramento River discharge ranged from 5,349 to 66,800 CFS (ȳ = 11,952 CFS, SD = 3,767). Turbidity values ranged from 1.3 to 290.2 NTU (ȳ = 12.5 NTU, SD = 5.1).

Annual environmental covariate data for spring Chinook salmon can be found in Table 9d. Results presented below describe data averaged over 11 brood years. Spring Chinook were sampled over a period of 221 to 250 days per year (ȳ = 232 days, SD = 9). Water temperatures ranged from 46 to 62 °F (ȳ = 53°F, SD = 0.6). Sacramento River discharge ranged from 5,349 to 68,720 CFS (ȳ = 13,370 CFS, SD = 6,116). Turbidity values ranged from 1.4 to 305.9 NTU (ȳ = 16.0 NTU, SD = 7.0).

Annual environmental covariate data for *O. mykiss* can be found in Table 9e. Results presented below describe data averaged over 10 calendar years. *O. mykiss* were sampled over a period of 331 to 363 days per year (ȳ = 349 days, SD = 12). Water temperatures ranged from 46 to 63 °F (ȳ = 56°F, SD = 0.8). Sacramento River discharge ranged from 5,333 to 67,610 CFS (ȳ = 12,519 CFS, SD = 3,551). Turbidity values ranged from 1.4 to 263.7 NTU (ȳ = 11.4 NTU, SD = 4.1).

Annual environmental covariate data for Green Sturgeon can be found in Table 9f. Results presented below describe data averaged over 11 calendar years. Green Sturgeon were sampled over a period of 56 to 151 days per year (ȳ = 88 days, SD = 27). Water temperatures ranged from 55 to 61 °F (ȳ = 58°F, SD = 0.9). Sacramento River discharge ranged from 9,639 to 23,538 CFS (ȳ = 13,483 CFS, SD = 2,181). Turbidity values ranged from 2.4 to 93.9 NTU (ȳ = 8.5 NTU, SD = 6.9).

Due to the large amount of variability and lack of a normal distribution, all environmental covariate CPUV data analyses for Green Sturgeon were performed using natural log transformed data (Sokal and Rohlf 1995). Environmental covariates were regressed against the natural log of daily CPUV estimates for Green Sturgeon in a linear regression setting (Figure 24). Maximum daily water temperature was the only variable found to be significantly related to Green Sturgeon relative abundance, albeit the relationship explained ~5% of the variability around daily relative abundance ($r^2 = 0.045$, df = 315, $P < 0.001$).

Annual environmental covariate data for Lamprey *spp.* can be found in Table 9g. Results presented below describe data averaged over 11 water years. Lamprey were sampled over a period of 358 to 364 days per year (ȳ = 362 days, SD = 2). Water temperatures ranged from 46 to 63 °F (ȳ = 56°F, SD = 0.7). Sacramento River discharge ranged from 5,347 to 68,873 CFS (ȳ = 12,595 CFS, SD = 4,177). Turbidity values ranged from 1.2 to 306.8 NTU (ȳ = 11.9 NTU, SD = 4.4).

Due to the variability and lack of a normal distribution, all environmental covariate CPUV data analyses for Lamprey *spp.* were performed using natural log transformed data. Environmental covariates were regressed against the natural log of daily CPUV data for Lamprey *spp.* in a linear and multiple regression setting. All four independent variables appear to contribute to predicting Lamprey *spp*. relative abundance and were significantly related to abundance levels ($r^2 = 0.223$, df = 1999, $P < 0.001$). Individual variable linear regression analyses indicated turbidity, water temperature, discharge, and full moon illuminosity were correlated in descending order of magnitude (Figure 25). None of the covariates tested explained more than ~16% of the variability associated with daily CPUV data.

Discussion

Trap Efficiency Modeling.—Over the past 11 years, annual mark-recapture trials added 85 data points to the RBDD rotary trap efficiency linear regression model (Figure 3). Explanation of the variability associated with trap efficiency and *%Q*, in terms of the associated r-squared value, was reduced for the first few years and then steadily increased in more recent years. The reduction was due, in part, to more precise *%Q* calculations over the initial model when diversions from RBDD were not subtracted from daily river discharge values. Diversions were able to be removed from the total discharge (*Q*) passing the transect as these data became available in real-time starting in 2002.

The addition of a multitude of fry size-class trials over a variety of discharge levels greatly increased the accuracy of trap efficiency estimates. Fry size-class fish are the predominant size-class sampled at RBDD (i.e., fall and winter Chinook) thereby making them the best representatives for use in mark-recapture trials. The original trap efficiency model developed by Martin et al. (2001) employed primarily hatchery-raised smolts, as these fish were all that were available in large quantities and permitted for use in experiments to develop the initial model. However, hatchery fish weakly represented the primary fish size-class sampled by RBDD rotary traps. Roper and Scarnecchia (1996) and Whitton et al. (2008) found significant differences in trap efficiency when conducting paired mark-recapture trials using hatchery and wild caught fish. The most recent years of RBDD data support this concept.

While a simple linear regression model has worked well over the years for our real-time data output needs, analysis of the data within the model, other possible covariates, and other more advanced modeling techniques has been warranted. Analysis incorporating additional potential explanatory variables was conducted using a generalized additive model technique (GAM; Hastie and Tibshirani 1990). From this analysis, variables including turbidity, fish size and run, water temperature, weather condition, lunar phase, and river depth were explored in addition to *%Q*. The result was that only *%Q* and weather were found to be significant model explanatory variables ($r^2 = 0.68$; df = 141, $P < 0.01$). The weather variable needs focused testing by conducting more mark-recapture trials under a variety of weather conditions to determine the applicability or mechanism of this variable. The GAM modeling technique may be employed in the future as an improved statistical format to interpolate missed sample days.

At minimum, an update to the 142 trial linear trap efficiency model (Figure 3) needs to be implemented for future passage estimate calculations. The update will include the removal of hatchery fish trials (*N*=23) used as surrogates for natural stocks. Removal of all RBDD "gates in" mark-recapture trials (*N*=31) due to the cessation of RBDD dam operations since 2011 (NMFS 2009) is also warranted.

The loss of annual maintenance and RBDD gate lowering operations at the rotary trap sample site (Figure 1) will allow the river channel's geometry to change more frequently due to natural flow driven substrate transport mechanisms. RBDD operations of the past virtually "reset" the sample site to facilitate pumping during the gates-out period and improve fish passage at the fish ladders during the gates-in period. As the sample site's channel configuration is allowed to fluctuate in the absence of dam operations, the overall effect could be differing trap efficiency values in relation to flow compared to previous years' data. Annual mark-recapture trials will be needed to evaluate this phenomenon, which has been observed in other uncontrolled channel sampling locations (e.g., Clear Creek; Greenwald et. al. 2003). The use of a GAM model may also be of benefit in this situation as it could be constructed and employed annually to account for wide variation in annual trap efficiency values; albeit at the expense of being able to produce real-time data summaries.

A linear model that also removed the remaining pre-2002 trials (*N*=16) which estimated *%Q* in a less precise manner, would result in the most representative trap efficiency model. A post-RBDD wild Chinook model of this type would incorporate 72 mark-recapture trials with a high degree of significance (N=72, $r^2 = 0.669$, F = 141.5, $P < 0.001$) and be most representative of current sampling conditions in terms of fish size-class and environmental conditions.

Chinook Capture Size Analyses.—Overall capture of Chinook salmon by RBDD rotary traps was heavily weighted towards fry size-class less than 40mm in fork length. All four runs' greatest proportion of fish were found in this size-class, albeit in a range of proportions from 24% for late-fall (Figure 5b) to over 72% for winter run (Figure 6b). The capture size-class results fit well with the migratory strategies of 'stream' and 'ocean type' as noted in Moyle (2002) for late-fall/spring and fall/winter Chinook, respectively. The question of size selectivity or capture bias of rotary traps, a passive sampling gear (Hubert 1996), comes into question when dealing with two very different migration strategies.

A two sample t-test was performed to evaluate the potential for size-class bias by comparing fry (fall and winter Chinook) size-class trap efficiency values (*N*=43) to pre-smolt/smolt (fall) trap efficiency values (*N*=10) between similar river discharge conditions. The t-test results did not indicate any significant difference between the mean efficiency values (t = -0.398, df = 51, P = 0.624). Interestingly, the mean efficiency and standard deviation of the values were identical ($\bar{y}$ = 2.1%, SD = 0.01) between groups. We recommend further study of the relationship between pre-smolt/smolt size-class and trap efficiency to determine if differences or bias may exist between or among Chinook runs. Additional sampling effort would be needed to capture substantially more pre-smolts in the numbers required for efficiency trials in the Sacramento River to further test this potential bias. Smolting salmonids also appear to succumb to stress induced mortality at a much greater rate than fry, particularly in warmer water conditions due to relatively high respiration levels, adding to the difficulty in testing this potential bias.

O. mykiss Life-Stage and Growth.— Catch of *O. mykiss* was scattered throughout the year with multiple modes in abundance of predominately sub-yearling parr and silvery-parr occurring in early May and August. *O. mykiss* fry (<41 mm) made up 17.5% of the total *O. mykiss* catch in 2006 and was 2.4 standard deviations from the 11-year mean. In contrast, yolk-sac fry, made up only 9.4% of the *O. mykiss* catch in 2006 and varied less than 1 standard deviation from the 11-year mean (Table 3). Elevated spring discharge resulted in poor sampling conditions which reduced sampling effort, possibly scoured redds, and ultimately resulted in low overall *O. mykiss* catch in 2006. Regardless of the cause of low catch rates, it is unlikely the migration patterns of *O. mykiss* changed in 2006 and the variability in age-class distribution was likely due to our sampling effort in that year.

The small percentage of *O. mykiss* smolts that showed signs of anadromy were generally migrating during March through June which was consistent with outmigrating smolts found in Battle, Mill, and Deer Creeks (Johnson and Merrick 2012; Colby and Brown 2013). Interpretation of *O. mykiss* data collected at the RBDD was complicated as a robust resident (non-anadromous) population exists throughout the Upper Sacramento River and its' tributaries. Populations of anadromous and resident *O. mykiss* life history forms are often sympatric and may inter-breed (Zimmerman and Reeves 2000; Docker and Heath 2003), thereby reducing our abilities to separate the anadromous and non-anadromous components of this species. Donahue and Null (2013) conducted research using otolith Strontium/Calcium ratios to determine whether *O. mykiss* returning to a hatchery were progeny of anadromous or resident females. A similar analysis could be conducted using juvenile *O. mykiss* collected at the RBDD. Data from juveniles might provide incite as to whether temporal separation in spawn timing exists between anadromous and resident forms of O. mykiss coexisting within the Upper Sacramento River basin.

Linear regression equations developed using weight-length data obtained from *O. mykiss* showed a strong correlation between the two variables (r^2= 0.942). The annual slope coefficient varied slightly between 2.858 and 3.052. Carlander (1969) suggested that slopes less than 3.0 might indicate a crowded or stunted population. However, permit restrictions may have introduced bias into our results as we were unable to anesthetize and weigh fish >200 mm thereby reducing the slope of the regression compared to that of a complete analysis of the population.

Sample Effort Influence on Passage Estimates.—Sampling effort had profound effects on the precision of passage estimates and confidence intervals (Figures 10, 12, 14, 16, and 18). In general, as sampling effort decreased, variance within weekly passage estimates increased and the width of confidence intervals subsequently increased. This effect was most prominent when effort was reduced during peak periods of outmigration or for long periods of time (> 1 week) when sharp increases or decreases in fish abundance occurred. Unfortunately, sampling of outmigrant Chinook on a large river system such as the Sacramento River is invariably subject to discharge events that are insurmountable for variable periods of time.

Logistical factors including staffing and permitting restrictions can also have significant effects on the precision of estimates. For example, a comparison of BY 2002 and BY 2005 winter Chinook passage with equivalent effort values (0.64) shows less precision of BY 2002 passage estimates over BY 2005 (Table 5c). The basis of the relatively low effort in 2002 was capture restrictions prompted by ESA Section 10(a)(1)(A) NMFS permits for endangered winter Chinook. Moreover, staff levels were initially low as the program was reinstated after a nearly two-year hiatus and substantial sub-sampling measures (i.e., standardized sub-sampling of repeated weeks) had to be taken during record abundance levels. The net effect was that sampling of fry, the predominant size-class of ocean type Chinook (Moyle 2002; Figure 6a/b), was reduced in terms of the number of days each week and hours of each night sampled during the peak emigration period. The overall net effect was 20% wider CI's about the 2002 estimate (i.e., less precision) compared to BY 2005. This was due to interpolation of 45% of the fry data which comprised 90% of the 2002 annual estimate. In contrast, BY 2005 sampled 90% of the fry data which comprised 90% of the annual estimate. Effort was reduced 36% in 2005 as a result of winter storms whereby sampling ceased for 3 straight weeks due to high river discharge levels. The effect of that lost sampling time in January did little to reduce the precision of the BY 2005 estimate as it was during a period when a mere fraction of a percent of total passage for winter Chinook typically occurs (Figure 15). The impact to the BY 2005 *fall Chinook* passage estimate, on the other hand, was very wide CI's about the estimate due to the lowest effort of all 11 years during a critical time period for that run's outmigration (Table 5a, Figure 11).

In summary, the precision of passage estimates can vary widely for numerous reasons within runs and among years. Inter-annual variability in environmental conditions will always be a factor when attempting to sample a riverine environment. Making good sampling decisions with knowledge of the species of interest and riverine conditions coupled with tenacity to sample critical periods of outmigration (Volkhardt et al. 2007) are key to generating passage estimates with an acceptable level of precision. Applying effort throughout each period of interest needs to be balanced between the value of data collected, an acceptable level of precision required of the data, the cost to attain the required precision, the impact sampling may have to a particular species, and the feasibility to appropriately sample the species of interest.

Chinook Passage Variability.—Juvenile Chinook passage by one to four runs occurs every single day of the year in varying proportions at RBDD. The sources and degree of variability of juvenile Chinook passage are as diverse as the life-history and migration strategies of the runs they encompass. The magnitude of run-specific adult spawners appears to have the greatest influence on the overall magnitude of juvenile Chinook passage and associated variability.

In recent decades, fall Chinook adults consistently dominated the Upper Sacramento River spawning salmon populations (Williams 2006, Azat 2013). Throughout the past decade, we witnessed a 'collapse' of the Sacramento River fall Chinook adult population and accordingly tracked declines in juvenile passage (Figure 10). Lindley et al. (2009) analyzed the freshwater and marine components of fall Chinook outmigrants from BY 2004 and 2005 through their return as adults in 2007 and 2008. They indicated BY 2004 and 2005 juveniles encountered poor marine conditions upon ocean entry in the spring of 2005 and 2006 which resulted in the marked decline in fall Chinook adult abundance starting in 2007.

Juvenile fall Chinook had the greatest mean annual passage value (14,774,923) of the four runs sampled at RBDD (Table 5a). Fall Chinook passage also exhibited the second smallest degree of variability with a CV of 46.2%. Notably, fall Chinook annual production by the CNFH averages 12 million juveniles, a similar value to the mean passage value of unmarked fall Chinook[7]. Fall Chinook production fish from CNFH contributed heavily to the relative stability of the annual returning fall Chinook adult population (Williams 2006) and, consequently, juvenile passage estimates over the past eleven years (i.e., basis of fall Chinook population).

Temporal abundance patterns of fall Chinook indicate the primary passage of juveniles occurs between late December and March (Figure 11a/b). Over half the run passed RBDD by mid-February, yet this varied over the 11-year period by +/- one month. Fall run passage on the American River (Williams 2006), Clear Creek (Earley et al. 2013a) and Stanislaus River (Pyper and Justice 2006) in California generally subsides to low values by the end of March. This would be consistent with the ocean type migration strategy as noted by Moyle (2002). The remaining fall run smolts and subsequent 'jump' in abundance in April to May was a result of the unmarked proportion of the CNFH production releases. Reduced variability in weekly passage was observed in the final 20% of annual fall Chinook passage (Figure 11b).

Spring Chinook had the lowest average passage value of 364,000 juveniles and the lowest CV of 45% (Table 5d). The low value of spring Chinook passage at RBDD can be attributed to a relatively small number of adults spawning primarily in Battle and Clear Creeks (Figure 1). Some extant populations appear to inhabit Beegum Creek, a tributary to Cottonwood Creek (CDFG 2001), and in the mainstem Sacramento River (Killam 2009, Azat 2013). Of particular interest with respect to the accuracy of spring Chinook

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[7] Fall Chinook passages estimates do not include the marked proportion (0-25%) of CNFH production fish. Unmarked fish of hatchery origin are included in annual passage estimates and their occurrence is evidenced by increased passage values primarily in May through June of each calendar year (Figure 11b).

juvenile passage at RBDD is the annual spawn timing of adult spring Chinook and expected juvenile emergence timing. USFWS rotary trapping operations on Battle and Clear Creeks between 2003 and 2012 have not predicted emergence (i.e., through temperature unit analyses; Beacham and Murray 1990) nor sampled juvenile spring Chinook prior to November of each year. On average, the first spring Chinook juvenile migrants from Battle and Clear Creeks were sampled during the week of November 26th each year (USFWS, unpublished data). As a result, LAD criteria used to identify juvenile spring Chinook at RBDD are noticeably inaccurate as fish sampled prior to late November were not sampled upstream in primary production areas at that time of year.

Simulating a removal of all LAD spring run between October 16 and November 25 of each year sampled would result in *decreased* spring run passage estimates by 19%, on average (range 2.6 to 44.2%). The effects of removing incorrectly assigned fry annually did not indicate a statistically significant difference between annual estimates (paired *t*-test, $N = 11$, $P < 0.001$). When incorrectly assigned fry are removed, the slightly more accurate simulated spring Chinook annual passage values remain within the 90% CI of standard estimates.

Furthering the simulation by adding the weekly October through November spring Chinook estimated passage to the winter Chinook passage estimates (i.e., late spawning or emerging winter run most likely candidate; see USFWS 2013), had minimal effect on the magnitude of winter Chinook passage. The average *increase* to winter Chinook passage was a mere 2.6% (range 0.6 to 8.8%) and simulated passage remained within the 90% CI of the annual winter Chinook estimates in all years.

Winter Chinook average annual juvenile passage was the second highest of the four runs estimated at 3,763,362 (Table 5c). The CV of the annual estimates was 73.2%; higher than fall or spring, but moderately dispersed. Overall, passage in years 2002, 2003, 2005, and 2006 surpassed the highest previous value of winter Chinook passage since juvenile monitoring began in 1995 (Gaines and Martin 2002). Similar to fall Chinook, winter Chinook adult escapement and subsequent juvenile passage began a marked decline in 2007 (Figure 16). Juvenile winter Chinook have been determined to enter the ocean during March and April of each spring (Pyper et al. 2013). Overall, it is believed that juvenile winter Chinook suffered the same fate as juvenile fall Chinook with poor marine conditions upon ocean entry in the spring of 2005 and 2006. Winter Chinook juvenile cohort replacement rates dropped below 1.0 starting with BY 2007, similar to adult fall run as noted in Lindley et al. (2009). The lowest passage estimate between 2002 and 2012 for winter Chinook occurred in 2011 at 848,976. Not until 2014 will we know if adult or juvenile cohort replacement rates will improve to a value of 1.0 or greater. Winter Chinook passage estimates between BY 1999 to BY 2002 (Gaines and Poytress 2003) indicate that replacement rates can vary substantially and replacement rates of 3.0 or greater have been estimated between juvenile cohorts.

Late-fall Chinook passage averaged 447,711 juveniles for the 11-year period and exhibited the greatest amount of variability with a CV of 159.9%. Late-fall Chinook juvenile passage estimates are likely affected by LAD criteria similar to spring Chinook in terms of potential for overestimation. The variability associated with weekly late-fall passage shows a decrease in median abundance by the beginning of June each year which may be more representative of actual late-fall emergence. Additionally, as demonstrated by Figures 13 a/b, the late-fall migration starts abruptly unlike for fall and winter Chinook which follow a more bell-shaped pattern in abundance (See Figures 11a/b and 15 a/b). It was highly likely that early emergent late-fall fry were, in fact, late emerging fall Chinook. Run specific genetic monitoring (Banks et al. 2000, Banks and Jacobsen 2004) could assist in determining the magnitude of the error in run assignment.

Sampling effort during mid-April to mid-May, the early late-fall run emergent period, was also typically low in an effort to reduce impacts to CNFH fall Chinook production fish caught in rotary traps. Within trap predation of fry by CNFH production smolts could also negatively bias late-fall juvenile production estimates. Sub-sampling of portions of the day and night (≤25% of each period) were only feasible with full staffing in some years which can reduce potential bias. During all other years, multiple sample days were typically sacrificed to allow peaks in CNFH production fish to recede ultimately reducing the accuracy of late-fall passage estimates.

Fry-Equivalent Chinook Production Estimates.—Estimation and analyses of the productivity of salmon runs in the Upper Sacramento River basin can provide valuable information to a variety of interests. Management of California's complex water resources for agriculture, municipal, commercial, and ecological uses is an increasingly controversial and complex endeavor. Knowledge of the effects of manipulating water storage and river processes on the productivity of the Sacramento River fish populations can only benefit fishery and water operations managers in an attempt to balance the competing demands on the system. Reducing uncertainty associated with threatened and/or endangered fish population dynamics by employing knowledge of the abundance, migration timing, and variability of those populations over time can then inform the decision making processes guiding management of water and fishery resources into the future.

Fall Chinook fry-equivalent juvenile production indices (FEJPI; Table 6a) indicate a significant and moderate correlation with fall Chinook escapement estimates (Figure 20a). Approximately 53% of the variation associated with fall FEJPI's was attributed to the estimated number of females in the system above RBDD each year (Figure 20a). The CV of estimated fall run females was greater than 132% indicating wide dispersion of contributors to the juvenile population over the eleven-year period. Conversely, the CV of FEJPI's was relatively low valued at 43%. Furthermore, recruits per female and similarly egg-to-fry survival demonstrated moderately low average values of 749 and

13.9%, respectively, when compared to the estimated values for winter Chinook (Table 6a).

As noted in Kocik and Taylor (1987), factors limiting production are typically a combination of biotic and abiotic factors. The sources of variability relating to fall FEJPIs are directly and indirectly related to adult abundance, but abundance alone does not explain the low CV in fall run juvenile production. A simple, albeit incorrect, conclusion might be that adult escapement of fall Chinook in some years exceeds the useable spawning area of the system (Bovee 1982, Connor et al. 2001) or optimal spawning efficiency (Wales and Coots 1955). Upon closer examination of the likely origin(s) of juvenile production, the data indicate substantial variability in the distribution of fall run adults between the mainstem Sacramento River and tributaries, including Clear Creek and Battle Creek, between years. Proportions of returning adults within the mainstem and Battle Creek have demonstrated high degrees of variability (Figure 26). The overwhelming return of fall run to Battle Creek in 2002 resulted in the lowest value of fall Chinook recruits per female (*N* = 89) which was outside two standard deviations of the average (Table 6a). The number of adults returning to the CNFH clearly overwhelmed the capacity of Battle Creek to produce juveniles. Sub-optimal wetted useable spawning area (Bovee 1982), red superimposition (McNeil 1968, Heard 1978), and female stress resulting in egg retention (Neave 1953, Foerster 1968) were likely just some of the factors that reduced the overall productivity of the 2002 fall Chinook adults returning to the Upper Sacramento River.

In years when estimates of fall Chinook production were at their highest in terms of recruits/females (Table 6a), the proportions spawning in the mainstem and combined tributaries were closest to 50:50. Further examination indicates that when contributions from the Battle and Clear Creeks accounted for equal proportions (i.e., 25% each), peak values of ~1,500 recruits/females were estimated to have been produced resulting in the highest net spawning efficiency (Wales and Coots 1955). Optimal natural juvenile fall Chinook production values in the Upper Sacramento River system could result under some conditions if integration of restoration projects on Battle and Clear Creeks integrate with mitigation projects (e.g., CNFH production) for the mainstem Sacramento River. The effect of consistent hatchery fall Chinook production on Battle Creek irrespective of natural fish production in the Sacramento and Chinook-bearing tributaries should be considered for further evaluation as was noted in Williams (2006). The effects of restoration of Clear Creek appear to be providing production benefits on stream and basin wide scales. Management prerogatives and actions related to the CVP affect both factors, to varying degrees, and decisions should be prioritized to attain optimal results for both fisheries and water operations.

Late-fall Chinook FEJPIs indicated high variability (CV = 170%; Table 6b), but a strong correlation with escapement estimates (r^2 =0.67; Figure 20b). The magnitude of late-fall FEJPIs were consistently an order of magnitude less than FEJPIs of fall Chinook. One exception was 2002, which increased the CV for the eleven-year period by 100%

(Table 6b). The fall and late-fall adult Chinook escapement values of 2001 and 2002 were high compared to the other 10 years of data (Azat 2013). A large run of late spawning fall run may also have contributed to the large number of juvenile fish falling within the late-fall size-class according to LAD criteria, but the adult estimate could have suffered similar inaccuracies in run assignment. Variability in CV values of anadromous fish was described by Rothchild and Dinardo (1987) as being inversely related to the number of years included within the time series analyses. While 2002 appears to be an outlier in this data set, it is likely with more years of data collection and analyses the CV associated with late-fall production would be more commensurate with other runs of Chinook.

The stream-type migration strategy noted by Moyle (2002) and our size classification method categorized the majority of late-fall outmigrants as smolts ($\bar{y}$ = 62%) which inflated the late-fall FEJPIs greatly at times (Table 5b, Table 6b). Recruits per female and similarly egg-to-fry survival had low CVs and the lowest average values of 131 and 2.8%, respectively, in comparison to other runs (Table 6b). This was unexpected as this metric does not appear to apply well to a run that was sampled primarily as smolts ($\bar{y}$ = 62%) over eleven years. Moreover, fry-equivalent calculations based on a static fry-to-smolt survival estimate of 59% (Hallock undated) was unlikely to be an accurate constant for late-fall Chinook as it was calculated from hatchery-based fall Chinook survival data. The fact that correlations with adult escapement were determined to be significant and moderately strong was unexpected given the vagaries of sampling late-fall Chinook smolts and the use of the static 59% survival estimate inversely applied to the majority of the run sampled. Additionally, difficulties with performing carcass surveys for late-fall Chinook due to low visibility, winter flow events or logistical issues (Killam 2009 and 2012) typically result in sub-optimal sampling conditions and, assumedly, would reduce the accuracy of the adult estimate.

Overall, production of late-fall Chinook appears low and the run has been characterized by some as vulnerable to extinction (Moyle et al. 2008, Katz et al. 2012). Greater attention to the relatively low abundance levels and juvenile rearing habitat needs of this genetically distinct run (Banks et al. 2000, Garza et al. 2007, Smith et al. 2009) with its unique over-summering, relatively long freshwater residency (Randall et al. 1987) and large size-at-outmigration strategy (Zabel and Achord 2004) should be afforded. The life-history strategies of late-fall Chinook have likely allowed them to persist in the Upper Sacramento River system as they occupy a distinct ecological niche. Juvenile monitoring of this run could benefit greatly if confidence in the accuracy of run assignment of juveniles was examined using non-lethal genetic techniques (Harvey and Stroble 2013).

Comparisons between winter Chinook adults and juvenile production began early using data generated by this monitoring project. Martin et al. (2001) demonstrated a strong relationship with only 5 years of data. The annual analyses of the winter FEJPI and adult estimates continually indicated a strong relationship with the addition of each year's data (See Gaines and Poytress 2003, Poytress and Carrillo 2008, Poytress and Carrillo 2012). The analysis of the most recent 11 years of data continues to indicate a strong relationship between the two variables even as adult escapement values have varied an order of magnitude.

Winter Chinook FEJPIs indicated mild variability (CV = 67%; Table 6c) and a very strong level of significance and correlation with female adult escapement estimates (r^2 =0.90; Figure 20c). Intensive adult and juvenile monitoring for this ESA listed endangered species coupled with superlative sampling conditions, in most years, appears to have resulted in very high quality information regarding the status and trends in adult and juvenile population abundance.

Egg-to-fry survival estimates generated from annual winter Chinook data indicate a range of values between 15 and 49% (Table 6c). At first glance, this appeared counterintuitive based on the highly regulated Sacramento River system (e.g., flow and water temperatures) that typically exists during the winter Chinook spawning period. The average egg-to-fry survival estimate of 26% is considerably higher than that determined from other studies on Pacific salmonids ($\bar{y}$ = 15%; e.g., Wales and Coots 1955) but was consistent with highly regulated aquatic systems (Groot and Margolis 1991). A very low CV of 38% also appeared consistent with a regulated system. Recruits per female, similarly, indicated a low CV of 36% and the second highest average value of 1,349 (Table 6c).

Natural log transformed adult female estimates influenced juvenile production and a significant relationship was determined accounting for roughly half of the variability associated with egg-to-fry survival rates (r^2 = 0.51, *df* = 10, *P* = 0.012). Densities of winter Chinook spawners are much lower currently than in the years estimated following the completion of Shasta Dam (USFWS 2001). Completion of the re-engineered Anderson-Cottonwood Irrigation District fish ladders in 2001 resulted in greater access and subsequently a greater concentration of spawners in the uppermost reaches accessible to anadromous fish (USFWS 2006-2011). Competition for optimal spawning habitat can result in lower juvenile production if sub-optimal wetted useable spawning area (Bovee 1982), red superimposition (McNeil 1968, Heard 1978), and female stress resulting in egg retention (Neave 1953, Foerster 1968) occur to varying degrees. Low resolution carcass recovery data (e.g., reach specific) indicate an abundance of spawners utilizing the uppermost 6 river miles of the Sacramento River (USFWS 2006-2011) even as seemingly suitable habitat has been made available for approximately 20+ river miles downstream of the terminus at Keswick Dam (RM 302). Geist et al. (2002) studied physiochemical characteristics affecting redd site selection preferences by Chinook and different growth and development rates have been attributed to different segments within the same river (Wells and McNeil 1970). High resolution redd surveys or spawning area mapping employing a GIS spatial analytical framework (Earley et al. 2013b) may shed light on the variability associated with winter Chinook spawning habitat over a variety of adult abundance levels. Analyses of these types of data could result in less uncertainty over the annual specific density dependent mechanisms affecting juvenile production and provide direction for future restoration activities for winter Chinook.

Spring run Chinook FEJPIs were the lowest of all four runs monitored and indicated the lowest variability (CV = 41%; Table 6d). No relationship with female adult escapement estimates was detected (r^2 =0.00; Figure 20d) and may be attributed substantially to measurement error (Sokal and Rohlf 1995). Estimates of recruits per female averaged 3,122 and the egg-to-fry survival value averaged 61.5%. These values appear unreasonable outside of a hatchery environment and well above those found for other runs (this report) and other studies (e.g., Wales and Coots 1955, Groot and Margolis 1991). Individual annual estimates varied moderately (CV= 70.8%) and nearly half appeared highly unlikely, with some values exceeding the number of eggs deposited by spawners (Table 6d).

Spring Chinook juvenile fish production estimates at RBDD were the least accurate and currently constitute 2.1%, on average, of total annual Chinook production above RBDD. Mainstem Sacramento River spawner estimates ranged from a low of 0 to a high of 370 between 2002 and 2012. Annual indexes of spring Chinook adult abundance above RBDD during the same years constitute 2.7% of the total escapement estimated in the Sacramento River system (Azat 2013). Given the relatively sporadic and low adult abundance levels, vagaries of using LAD criteria and annual CNFH fall Chinook production releases with fractional mark rates, no relationship could be found between adult escapement and spring Chinook FEJPIs when attempting to use methods to correct for these inaccuracies. The effects of inaccurate spring run assignment did not appear to affect the FEJPIs of other runs (e.g., winter or fall run) and therefore were not considered biologically significant. Genetic monitoring of fry in the fall after emergence from tributaries where emergence and migration data is collected (e.g., Earley et al. 2013a) may allow for more accurate estimation of the contributions of this run to the Upper Sacramento River outmigrant population.

Green Sturgeon Capture Dynamics.—Rotary traps were originally constructed to sample outmigrating salmonid smolts, but have been effective in sampling a variety of downstream migrating fish (Volkhardt et al. 2007). Rotary traps sampling at RBDD have been effective at monitoring temporal and spatial trends in relative abundance of Green Sturgeon since 1995 (Gaines and Martin 2002).

Annual adult Green Sturgeon aggregations were observed behind the RBDD when gates were lowered each spring (Brown 2007). Green sturgeon larvae were captured in 2012 (Table 7), the first year the RBDD gates were not lowered as it was replaced by a permanent pumping plant (NMFS 2009). Spawning was determined to have occurred in multiple locations as far as 20 river miles upstream of RBDD (Poytress et al. 2009-2013). The location of the RBDD rotary traps has been confirmed to be within the Green

Sturgeon spawning grounds as eggs were sampled directly below the RBDD and upstream of the RBDD traps in multiple years (Poytress et al. 2009, 2010, 2012).

Total length distribution data from Green Sturgeon collections at RBDD indicate a narrow and consistent size-class of larvae (Figure 21a). These data are consistent with laboratory-based studies conducted by Kynard et al. (2005) on the behavior of early life intervals of Klamath River Green Sturgeon. Their study determined that larvae migrated during two distinct periods (i.e., two-step migration). The first migration of newly exogenous feeding larvae was determined to be an initial dispersion from production areas. The second migration (of juveniles) to overwintering areas occurred in the fall some 180 days after hatching, on average. Our rotary trap data suggest we are sampling exclusively the initial redistribution of larvae from egg incubation and hatching areas.

Benthic D-net sampling conducted by Poytress et al. (2010-2011) targeted the lowest portion of the water column (inverse of rotary traps) and consistently captured Green Sturgeon larvae of the same size-class and temporal distribution pattern as rotary traps. D-net samples were collected between May and early-August (See Figure 21b for corresponding RST data only) downstream of spawning areas in years 2008-2011; even as no larvae were collected by rotary traps in 2008. Larvae were sampled by both methods primarily in the thalweg and in river velocities >/= 1.3 ft/sec[8]. Conversely, zero *juveniles* were collected with benthic D-nets in a pilot study (Poytress et al. 2013) targeting this life-stage and habitat type in the benthos during the fall period. Rotary traps have collected a few sporadic juveniles (e.g., outliers; Figure 21a) over the entire sample record of the project. These data indicate that Green Sturgeon juveniles are no longer utilizing our sampling region or more likely using a different habitat type (Hayes et al. 1996). Accordingly, rotary traps appear to be a relatively ineffective gear type for sampling the secondary juvenile sturgeon migration.

Protections afforded to ESA listed southern distinct population segment of Green Sturgeon (since 2006), limited quantities of larvae, and the small size at capture have not allowed their drift distances (Auer and Baker 2002), rates (Braaten et al. 2008), or rotary trap efficiencies to be calculated for the initial dispersion migration of Sacramento River Green Sturgeon at RBDD. Relative abundance indices for Green Sturgeon were highly variable, typically low valued at <1.0 fish/ac-ft sampled (Table 7), and contained one extraordinarily strong year-class (Figure 21c). As noted by Allen and Hightower (2010), variations in recruitment by orders of magnitude between years is common among fish stocks. Moreover, strong and weak year classes greatly influence adult fish populations. Green sturgeon relative abundance indices should not be interpreted as recruitment to the adult population, but should be viewed as a production metric influencing recruitment (e.g., age-0 year class strength). Alternately,

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[8] Rotary traps generally require a minimum water velocity of 1.2 ft/sec to operate properly. D-nets sampled velocities ranging from 1.3 – 6.6 ft/sec. RST' sampled velocities ranging from 1.3 – 6.3 ft/sec.

Green Sturgeon larvae relative abundance indices could be viewed as an indirect metric for adult spawning population densities *upstream* of RBDD if genetic monitoring were conducted consistently (Israel and May 2010).

Lamprey Capture Dynamics.— Similar to Green Sturgeon, rotary trap sampling for Chinook salmon has provided the additional benefit of capturing out-migrating lamprey ammocoetes and juveniles. Greater attention to this ancestor of the earliest vertebrates (Moyle 2002) has recently been paid by the USFWS since it was petitioned for listing under the ESA in 2003 (Nawa et al. 2003). Although not listed due to inadequate data on the species' range and threats, the USFWS has engaged in a strategy to collaboratively conserve and restore Pacific Lamprey throughout their native range. Through the formation and development of the Pacific Lamprey Conservation Initiative, an assessment of Lamprey populations in California has recently been completed (Goodman and Reid 2012). The assessment noted that Lamprey species had been extirpated from at least 55% of their historical habitat north of Point Conception, CA by 1985. Long-term monitoring data sets including the RBDD rotary trap data, utilizing temporal and spatial distribution patterns as well as size-class and relative abundance levels of lamprey, can aid in the assessment and conservation of this ecologically vital species (Close et al. 2002).

Variability in annual size-class total length distributions was typically minor for both lamprey life stages sampled (Figure 22a and Figure 23a). Ammocoetes were slightly smaller than macropthalmia and slightly more variable in their annual average length distributions valued at 110 mm TL (CV= 4.6%; Table 8a). Pacific Lamprey macropthalmia were the dominant life stage sampled and the median size at capture was consistently near 125 mm TL (CV= 1.6%; Table 8b). Adults, typically noted as outliers, were encountered in much lower frequencies and were considered upstream migrants inadvertently captured when the RBDD gates were lowered as they sought upstream passage around the partial migration barrier.

Temporal distribution patterns indicated that ammocoetes and macropthalmia migrate past RBDD year-round. Ammocoetes, on average, were sampled regularly throughout the year (Figure 22b), whereas macropthalmia moved, en masse, episodically between November and March (Figure 23b). These data are consistent with studies of macropthalmia in the Columbia River system as noted by Close et al. (1995) and Kostow (2002).

Relative abundance indices of ammocoetes (Figure 22c) varied little between years and little overall when compared with macropthalmia (Figure 23c). Macropthalmia abundance indices varied considerably between years (Table 8b). On average, macropthalmia relative abundance was six times that of ammocoetes indicating metamorphosis and redistribution to different habitats from those used for rearing by ammocoetes (Goodman and Reid 2012). Differences in the relative abundance CV's of the two life stages likely indicates differences in catchability (Hubert and Fabrizio 2007) or habitat use (Hayes et al. 1996), variable migration trigger effects, or variability in sampling effort that often occurred during periods of macropthalmia migration.

Water Temperature and Juvenile Fish Dynamics.—Slight variation within and among salmonid runs (including *O. mykiss*) and years was noted for water temperatures found at RBDD (Tables 9a-e). Nonetheless, Upper Sacramento River salmonids were subjected to a relatively wide 20 degree range of water temperatures. Temperatures were recorded between 44 and 64 degrees with the average being 55 degrees each year. As summarized in Vogel and Marine (1991), the range of temperatures experienced by Chinook fry and pre-smolt/smolts in the last 11 years of passage at RBDD have been within the optimal range of thermal tolerances for survival.

Sacramento River water temperatures below Shasta/Keswick dams can be managed at certain times of the year under some conditions through discharge management to provide selective withdrawal at submerged intakes (USBR 1991 & 1994, Vermeyen 1997). Ambient air temperatures typically regulate river water temperatures during winter and early spring periods while storage and flood control operations are preeminent. The water temperatures recorded during the last 11 years appear to have been favorable for extant spring run spawners, and more so for fall and late-fall run Chinook and *O. mykiss* spawner and outmigrant populations.

The most vulnerable Chinook run to temperature management operations conducted by the USBR is winter Chinook (NMFS 2009). Temperature management of the Sacramento River via Shasta/Keswick releases by the USBR for winter Chinook appeared to be effective during the last 11 years as evidenced by the relatively favorable and stable egg-to-fry survival estimates (Table 6c). Moreover, temperature management of the upper 50 river miles of the Sacramento River aimed at winter Chinook resulted in benefits to over-summering late-fall Chinook pre-smolts and a relatively small proportion of fall Chinook smolts.

Temperature management during the summertime aimed at winter Chinook may have indirectly favored the resident form of *O. mykiss*. As noted by Lieberman et al. (2001), altering the thermal regime and food web structure by way of temperature management likely affects the proportion of anadromous to resident forms in large rivers. Lamprey species have likely benefitted from temperature management as temperatures for early life stages of lamprey in the mainstem Sacramento River appear to have been, on average, optimal (Meeuwig et al. 2005) in the last 11 years (Table 9g).

Green Sturgeon have likely benefitted from temperature management efforts aimed at winter Chinook spawning and production, albeit less comprehensively. Van Ennennaam et al. (2005) determined Green Sturgeon egg development temperatures to be optimal between 57.0 and 63.5° F. Mayfield and Cech (2004) determined optimal temperatures for larval development to be between 59.0 and 66.2°F. Temperatures recorded at RBDD during larval capture periods averaged 58.3°F and were generally within sub-optimal (lower end) to optimal ranges (Table 9f). A weak negative relationship between Green Sturgeon CPUV and water temperatures was detected in our analysis indicating greater capture rates at lower water temperatures (Figure 24d). The slightly sub-optimal temperatures might result in larvae migrating from incubation areas prematurely. Conversely, the optimal thermal environment of the lab-based migration data from Kynard et al. (2005) resulted in very similar migration timing between the lab and larval captures in rotary traps in terms of days post hatch (Poytress et al. 2013). Sacramento River Green Sturgeon larvae appear to be following their natural life-history migration patterns as opposed to being coerced from their incubation areas due to sub-optimal water temperatures at RBDD. This may not be true for larvae migrating some 20 miles upstream where the effects of temperature management may have a more pronounced negative effect on Green Sturgeon larvae (Poytress et al. 2013). Temperature management for Chinook may also have the indirect negative effect of redirecting the spawning habitat of Green Sturgeon adults by 20 river miles. A habitat comparison study on the relative value of the upper 20 river miles of the Sacramento River versus 20 lower river miles of habitat currently benefitting Green Sturgeon adult spawners and eggs from temperature management efforts should be conducted.

River Discharge, Turbidity, and Juvenile Fish Dynamics.—Volkhardt et al. (2007) stated that "flow" (i.e., discharge) was a dominant factor in juvenile trapping operations. Trapping efficiency and migration rates are affected by flow and the RBDD rotary trap passage data reflect these statements well. Exploratory plots demonstrating fry (Appendix 2, Figures A1-A11) and pre-smolt/smolt winter Chinook passage (Appendix 2, Figures A12-A23) were produced to illustrate the effects of environmental variables on fish migration. Turbidity was plotted, but not included in the final plots presented as the effects could not be deciphered from discharge at the daily scale of analyses.

The effects of river discharge on turbidity and resultant fish passage are complex in the Upper Sacramento River where ocean and stream-type Chinook of various size-classes (i.e., runs, life stages and ages) migrate daily throughout the year. Decreases in discharge in the Shasta/Keswick dam regulated Sacramento River, typical of late summer to early winter periods, appear to coincide with relatively clear water conditions and low turbidity (e.g., ~ 1.5 NTU) at RBDD. Fall or early winter freshets and winter rain-driven storm events result in highly variable increases in discharge levels and turbidity measures in terms of the magnitude and duration depending upon the source(s) of run-off.

A course scale analyses of fish passage and river discharge and turbidity measurements during storm events typically indicates a pattern that fish passage increases with simultaneous increases in both variables. Inspection of Chinook passage on a daily time step typically demonstrate a reduction in fish passage a day prior to a storm or rain-event during periods of stable river discharge. As storms produced increases in run-off or discharge from tributary inputs outside of the Shasta/Keswick dam complex, mean daily turbidity typically increased and fish passage began to increase. When storm related increases in discharge diminished, turbidity diminished, but Chinook passage often increased greatly for 24-72 hours after the peak flow event.

One problem confounding the results of storm and fish passage observations and analyses was that sampling during large storm run-off/discharge events often ceased due to safety concerns, concerns for fish impacts or simply due to the inability to sample the river when woody debris stop rotary traps from operating properly. In some years, storm events resulted in discharge levels too great to sample effectively or damaged traps which resulted in numerous days or weeks un-sampled afterwards. The results are typically negative bias in passage estimates if days following the peak discharge or concurrent turbidity events are un-sampled. Alternately, the direction of bias can be positive depending on time of year, interpolation methods, sample effort during extended storm periods, or fish developmental stage.

A fine scale, hourly analysis of fish passage, river discharge and turbidity during storm events indicated a more intricate relationship between the variables. As a comparison, two separate storm events (December 2005 and November 2012) were analyzed (Figure 27a/b). In 2005, 24-hour samples were conducted prior to and after the peak flow period which was missed due to an inability to sample the river as it more than quintupled in discharge (i.e., 7,000 CFS to ~35,000 CFS). During this storm event, sampling was conducted following the peak of river discharge as river stage decreased, but while turbidity continued to peak (Figure 27a). The planned 24-hour sample had to be cut short due to the huge influx of fry and smolt passage that occurred during the turbidity increase (i.e., from 10’s to 1,000’s per hour) and the need to reduce the potential impact to listed winter Chinook.

During a November 2012 storm event, a different strategy was employed to collect data more effectively throughout the storm period. For this event, we randomly sampled portions of the day and night in an attempt to manage the huge influx of fish anticipated to occur during the year’s first storm event. Between 11/17/12 and 11/23/12, the project was able to collect 7-randomly selected samples that occurred throughout the first major river stage increase (Figure 27b). Samples were collected during increases and decreases in river stage. Samples were also collected prior to, during, and following a substantial increase in turbidity that lagged behind the initial stage increase by nearly 12 hours (Figure 27b). Fry and pre-smolt/smolt Chinook and juvenile lamprey fish passage increased exponentially. The peak period of fish capture occurred following the peak in river stage and during the increase and peak periods of turbidity measurements taken at RBDD. Capture rates subsided in the following days, but then increased greatly during the night-time period at the beginning of the next stage increase (Figure 27b).

Overall, it appears that flow and turbidity are important drivers for fish passage. The RBDD rotary trap data indicate that increased turbidity often results in greater fish passage than increases in river discharge or stage alone which often occur as part of water management operations at Shasta Dam. The two variables generally increase sequentially with discharge increases followed by turbidity increases (Figure 27a/b). Fish passage increases often coincide with the increase in turbidity which can often be sampled more effectively than increases in river discharge and may result in positive bias of juvenile fish passage estimates if the peak turbidity event is sampled compared to the peak flow event.

The importance of the first storm event of the fall or winter period cannot be overstated. Chinook smolt and juvenile lamprey passage increased exponentially and fry passage can be significant if first storms occur as fall Chinook begin to emerge. Fishery and water operations managers should be aware of the importance of the first Sacramento River stage increases following the summer and fall Sacramento River flow regulation period. The redistribution of winter and over-summering fall and late-fall Chinook smolts, or more generally, all anadromous juvenile fish[9] migrating from the Upper Sacramento River to the lower river and Sacramento San-Joaquin Delta with the first storm events of each water year should be incorporated into management plans for Delta operations.

Moon Illuminosity and Juvenile Fish Dynamics.—As noted in Hubert and Fabrizio (2007), species and life stages within species exhibit differing behaviors and therefore catchability in response to light levels. Gaines and Martin (2002) determined that Chinook passage occurred primarily during nocturnal periods except when turbidity levels and discharge increased with storm events. Further analyses of the effects of moon phase and ambient light levels in a statistical framework may be warranted for Chinook salmon as trends were detected based on observations. Rotary trap passage data indicated winter Chinook fry exhibit decreased nocturnal passage levels during and around the full moon phase in the fall (Appendix 3, Figures A1-A11). Pre-smolt/smolt winter Chinook appeared less influenced by night-time light levels and much more influenced by changes in discharge levels (Appendix 3, Figures A12-A23). A similar phenomenon was noted by Reimers (1971) for juvenile fall Chinook in Edson Creek, Oregon. Alternately, more data concerning night time cloud cover may further clarify the behavior associated with moon illuminosity as pre-smolt/smolts were more likely to encounter unclear night time weather between late October and December each year.

Spring, fall and late-fall Chinook fry exhibited varying degrees of decreased passage during full moon periods, albeit storms and related hydrologic influx dominated peak migration periods. *O. mykiss* relative abundance was not analyzed with respect to moon illuminosity. Lamprey CPUV regression analyses indicated a significant, but nearly imperceptible relationship (Figure 25a) likely due to the fact that lamprey are captured throughout the year under nearly all conditions. Green Sturgeon regression analysis

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[9] Juvenile Green Sturgeon have been captured sporadically during the first flow events along with large numbers of Pacific Lamprey juveniles and ammocoetes.

indicated no significant linear relationship between moon illuminosity and relative abundance (Figure 24a). Migration of age-0 Green Sturgeon larvae has been determined to occur during nocturnal hours (Kynard et al. 2005) primarily between 21:00 and 02:00 using D-nets (Poytress et al. 2011) and was presumed to be similar for rotary traps as periodic diel sampling events have not collected sturgeon during daytime sample periods.

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Tables

Table 1. Summary of annual RBDD rotary trap sample effort by run and species for the period April 2002 through September 2013, by brood year (BY).

BY	Fall	Late-Fall	Winter	Spring	*O. mykiss*
2002	0.76	0.57	0.64	0.75	0.53
2003	0.81	0.76	0.81	0.81	0.76
2004	0.85	0.88	0.84	0.85	0.83
2005	0.56	0.73	0.64	0.57	0.83
2006	0.90	0.70	0.83	0.89	0.59
2007	0.88	0.90	0.89	0.89	0.91
2008	0.79	0.89	0.87	0.85	0.89
2009	0.84	0.72	0.75	0.79	0.76
2010	0.75	0.86	0.81	0.77	0.85
2011	0.87	0.77	0.82	0.86	0.76
2012	0.85	0.89	0.89	0.86	0.86
Min	0.56	0.57	0.64	0.57	0.53
Max	0.90	0.90	0.89	0.89	0.91
Mean	0.81	0.79	0.80	0.81	0.78
SD	0.094	0.104	0.088	0.091	0.122
CV	11.7%	13.2%	10.9%	11.3%	15.6%

Table 2. Summary of mark-recapture experiments conducted by RBDD rotary trap project between 2002 and 2013. Summaries include trap effort data, fish release and recapture group sizes (*N*) and mean fork lengths (FL), percentage of river discharge sampled (%Q) and estimated trap efficiency for each trial (%TE). Model data below each trial period indicate dates model was employed, total trials incorporated into model and linear regression values of slope, intercept, p-value and coeeficient of determination.

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
6/26/2002	Fall[1]	4	Yes	Lowered	805	68.7	8	61.3	1.58	0.99
8/6/2002	Fall[1]	4	Yes	Lowered	743	69.7	16	80.2	1.66	2.15
8/20/2002	Fall[1]	3	Yes	Lowered	340	76.5	7	77.7	1.41	2.06

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2002 -	6/30/2003	61	0.00792	0.00003205	<0.0001	0.394

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/28/2003	Fall	4	Yes	Raised	5,143	36.8	33	37.0	0.75	0.64
2/5/2003	Fall	4	Yes	Raised	2,942	36.7	10	37.9	1.36	0.34
2/10/2003	Fall	4	Yes	Raised	3,106	37.8	29	37.9	1.59	0.93
2/21/2003	Fall	3	Yes	Raised	3,256	37.4	15	37.3	0.72	0.46
2/26/2003	Fall	4	Yes	Raised	2,019	37.0	22	37.2	1.14	1.09
3/1/2003	Fall	4	No	Raised	1,456	37.0	31	37.0	3.31	2.13
3/4/2003	Fall	4	No	Raised	1,168	37.1	28	37.4	3.76	2.40
3/7/2003	Fall	4	No	Raised	1,053	37.4	22	36.6	3.58	2.09
3/20/2003	Fall	3	No	Raised	1,067	38.2	17	38.3	2.83	1.59
9/2/2003	Winter	4	No	Lowered	1,119	37.1	14	36.1	2.03	1.25
9/5/2003	Winter	3	No	Lowered	1,283	36.7	26	37.2	2.52	2.03
9/8/2003	Winter	3	No	Lowered	1,197	37.3	30	37.1	2.57	2.51
9/23/2003	Winter	3	No	Raised	1,012	35.5	18	35.6	2.20	1.78

9/27/2003	Winter	4	No	Raised	1,017	36.9	28	36.6	2.93	2.75
10/1/2003	Winter	4	No	Raised	1,064	37.6	20	36.7	3.09	1.88
10/6/2003	Winter	4	No	Raised	999	37.2	22	36.8	2.82	2.20
10/10/2003	Winter	4	No	Raised	1,017	38.1	16	38.3	3.06	1.57
10/15/2003	Winter	4	No	Raised	1,209	38.0	26	37.6	2.98	2.15

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2003 -	6/30/2004	79	0.00752	0.00046251	<0.0001	0.426

Date	Run	# Traps Sampling	Traps Modified	RBDD Gates	Release Group *N*	Release Group FL (mm)	Recapture Group *N*	Recapture Group FL (mm)	%Q	%TE
1/18/2004	Fall	4	Yes	Raised	2,074	37.1	26	37.1	1.52	1.25
1/24/2004	Fall	4	Yes	Raised	2,018	38.4	36	37.4	1.79	1.78
1/31/2004	Fall	4	Yes	Raised	2,024	37.7	33	37.6	1.61	1.63
2/6/2004	Fall	4	Yes	Raised	1,999	37.9	31	38.0	1.61	1.55
2/9/2004	Fall	4	Yes	Raised	2,017	37.8	27	37.0	1.69	1.34
2/13/2004	Fall	4	Yes	Raised	2,009	37.2	31	38.3	1.87	1.54
3/14/2004	Fall	3	No	Raised	1,401	38.3	18	39.6	1.98	1.28
3/23/2004	Fall	3	No	Raised	815	38.8	15	39.1	2.50	1.84
4/28/2004	Fall[1]	4	Yes	Raised	1,304	72.9	33	71.7	1.94	2.53
5/4/2004	Fall[1]	4	No	Raised	814	75.5	18	75.1	3.35	2.21
5/18/2004	Fall[1]	4	No	Lowered	867	80.2	10	75.1	3.20	1.15
5/26/2004	Fall[1]	4	No	Lowered	1,096	81.2	27	80.2	2.83	2.46
6/2/2004	Fall[1]	4	No	Lowered	888	76.2	28	77.2	2.77	3.15
6/15/2004	Fall[1]	4	No	Lowered	691	76.4	12	79.1	2.17	1.74
8/31/2004	Winter	4	No	Lowered	1,096	36.5	41	36.0	3.00	3.74
9/3/2004	Winter	4	No	Lowered	1,153	36.6	50	35.6	3.23	4.34
9/17/2004	Winter	4	No	Raised	1,023	36.0	14	35.4	2.52	1.37

9/20/2004	Winter	4	No	Raised	1,017	35.8	21	35.4	2.48	2.06
9/23/2004	Winter	4	No	Raised	2,006	36.0	31	35.1	2.62	1.55
9/27/2004	Winter	4	No	Raised	1,918	36.1	36	36.1	2.77	1.88
10/1/2004	Winter	4	No	Raised	1,682	36.4	24	36.0	3.11	1.43
Model	Employed	#Trials	Slope	Intercept	*P*	R^2				
7/1/2004 -	6/30/2006	99	0.007464	0.00087452	<0.0001	0.385				

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/23/2005	Fall	4	No	Raised	1,283	36.6	41	37.2	4.21	3.20
2/1/2005	Fall	3	Yes	Raised	1,971	36.6	31	36.0	1.35	1.57
2/10/2005	Fall	4	No	Raised	1,763	36.6	46	36.7	4.06	2.61
3/10/2005	Fall	4	No	Raised	1,216	36.6	27	36.5	3.93	2.22
3/13/2005	Fall	4	No	Raised	1,328	36.3	43	35.6	4.06	3.24
4/1/2005	Fall	4	No	Raised	1,949	57.1	50	62.3	3.49	2.57
9/11/2005	Winter	4	No	Lowered	1,437	35.6	14	38.9	2.22	0.97
10/4/2005	Winter	4	No	Raised	1,587	35.9	14	36.1	1.83	0.88
10/13/2005	Winter	4	No	Raised	1,577	35.7	21	36.6	2.33	1.33
2/15/2006	Fall	4	No	Raised	1,610	37.4	33	36.6	3.19	2.05
2/23/2006	Fall	4	No	Raised	1,503	37.2	38	36.6	2.68	2.53
1/21/2007	Fall	4	No	Raised	1,520	0.0	33	37.8	4.02	2.17
1/28/2007	Fall	4	Yes	Raised	1,987	37.6	18	37.8	3.65	0.91
2/5/2007	Fall	3	Yes	Raised	2,909	37.5	29	37.3	1.62	1.00
2/16/2007	Fall	4	No	Raised	1,782	37.9	34	38.5	3.51	1.91
3/2/2007	Fall	4	No	Raised	1,591	38.5	54	38.6	3.68	3.39
3/15/2007	Fall	4	No	Raised	953	37.6	26	37.6	4.29	2.73
3/20/2007	Fall	4	No	Raised	835	37.6	23	38.8	4.18	2.75

3/24/2007	Fall	4	No	Raised	944	37.7	23	38.0	4.24	2.44

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2006 -	6/30/2007	118	0.006653	0.00240145	<0.0001	0.420

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/23/2008	Fall	4	No	Raised	2,234	38.4	50	38.2	3.99	2.24
2/7/2008	Fall	4	Yes	Raised	2,324	38.1	60	37.9	2.19	2.58
2/14/2008	Fall	4	Mixed	Raised	1,993	38.4	83	38.8	3.40	4.16
2/20/2008	Fall	4	No	Raised	1,703	37.2	48	36.8	5.29	2.82
2/28/2008	Fall	3	No	Raised	2,080	37.6	63	38.3	3.45	3.03

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2007 -	6/30/2008	123	0.00645	0.00303101	<0.0001	0.414

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/23/2009	Fall	4	No	Raised	1,923	36.1	54	37.1	4.53	2.81
2/5/2009	Fall	4	No	Raised	1,868	36.8	58	37.4	4.65	3.10

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2008 -	6/30/2010	125	0.006332	0.00328530	<0.0001	0.425

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/20/2011	Fall	4	No	Raised	1,834	36.9	79	35.9	3.92	4.31
1/26/2011	Fall	4	No	Raised	1,989	37.6	109	36.0	4.56	5.48
2/1/2011	Fall	4	No	Raised	1,593	36.4	61	36.0	5.04	3.83

2/11/2011	Fall	4	No	Raised	1,582	35.7	81	37.4	5.34	5.12

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2010 -	6/30/2012	129	0.007297	0.00123101	<0.0001	0.493

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/30/2012	Fall	4	No	Raised	1,319	36.3	46	36.1	4.08	3.49
2/4/2012	Fall	4	No	Raised	1,146	35.8	51	35.4	5.52	4.45
2/16/2012	Fall	4	No	Raised	1,465	35.7	73	35.0	5.36	4.98
2/28/2012	Fall	4	No	Raised	1,228	35.5	57	34.6	5.40	4.64

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2012 -	6/30/2012	133	0.007676	0.00037735	<0.0001	0.561

		# Traps	Traps		Release Group		Recapture Group			
Date	Run	Sampling	Modified	RBDD Gates	*N*	FL (mm)	*N*	FL (mm)	%Q	%TE
1/16/2013	Fall	4	Yes	Raised	1,991	35.6	72	35.8	2.56	3.62
1/23/2013	Fall	4	Yes	Raised	1,965	35.9	39	35.3	2.61	1.98
1/30/2013	Fall	4	Yes	Raised	1,981	36.3	44	35.6	2.57	2.22
2/3/2013	Fall	4	Yes	Raised	1,998	36.5	42	36.1	2.69	2.10
2/13/2013	Fall	4	Yes	Raised	2,079	36.3	48	36.2	2.62	2.31
2/18/2013	Fall	4	Yes	Raised	2,156	36.1	35	36.8	2.89	1.62
2/22/2013	Fall	4	No	Raised	2,439	36.7	119	36.6	6.52	4.88
2/26/2013	Fall	4	No	Raised	1,400	36.1	65	37.3	6.87	4.64
3/3/2013	Fall	4	No	Raised	899	36.5	37	36.9	6.71	4.12

Model	Employed	#Trials	Slope	Intercept	*P*	R^2
7/1/2013 -	9/30/2013	142	0.007255	0.00150868	<0.0001	0.587

[1] Denotes Coleman National Fish Hatchery Fall Chinook production fish used during trial.

Table 3. Annual capture fork length summary of *O. mykiss* by age and life-stage classification from the RBDD rotary trap project between April 2002 through December 2012 by calendar year (CY).

Age Classification (%)				
CY	Fry <41 mm	Sub-Yearling 41-138 mm	Yearling 139-280 mm	2+ >280 mm
2002	11.2	86.7	1.6	0.5
2003	8.1	89.5	2.3	0.0
2004	9.8	89.7	0.5	0.0
2005	3.5	93.2	3.1	0.2
2006	17.5	75.3	5.6	1.5
2007	6.5	91.2	1.7	0.6
2008	6.3	92.3	0.9	0.5
2009	9.0	87.7	2.1	1.2
2010	7.7	89.8	1.7	0.8
2011	4.6	89.7	5.0	0.6
2012	6.6	90.0	2.3	1.1
Mean	8.3	88.7	2.4	0.6
SD	3.8	4.8	1.6	0.5

Life Stage Classification (%)					
CY	Yolk-sac Fry	Fry	Parr	Silvery-parr	Smolt
2002	0.0	6.3	54.4	37.2	2.1
2003	0.0	5.6	57.7	34.9	1.8
2004	0.0	4.6	60.2	34.7	0.5
2005	0.0	2.8	48.7	45.6	2.9
2006	0.2	9.2	78.9	9.2	2.4
2007	0.1	8.7	85.3	5.3	0.6
2008	0.1	8.2	79.4	12.0	0.4
2009	0.0	10.7	82.8	5.1	1.4
2010	0.3	9.7	87.4	1.7	1.0
2011	0.1	3.5	90.9	2.8	2.7
2012	0.2	5.9	88.2	4.2	1.5
Mean	0.1	6.8	74.0	17.5	1.6
SD	0.1	2.6	15.5	16.8	0.9

Table 4. Annual linear regression equations with 95% confidence intervals (CI) for Log_{10} transformed juvenile (80-200 mm) *O. mykiss* weight-length data sampled at the RBDD rotary traps from April 2002 through December 2012 by calendar year (CY).

CY	Weight-Length Equation	R^2	Slope	
			Lower 95% CI	Upper 95% CI
2002	Log_{10}(weight)=2.843(Log_{10}FL)-4.616	0.903	2.648	3.039
2003	Log_{10}(weight)=2.968(Log_{10}FL)-4.886	0.968	2.885	3.052
2004	Log_{10}(weight)=3.005(Log_{10}FL)-4.941	0.952	2.879	3.132
2005	Log_{10}(weight)=3.03(Log_{10}FL)-5.009	0.952	2.929	3.132
2006	Log_{10}(weight)=3.052(Log_{10}FL)-5.085	0.917	2.811	3.293
2007	Log_{10}(weight)=2.961(Log_{10}FL)-4.864	0.947	2.853	3.069
2008	Log_{10}(weight)=2.939(Log_{10}FL)-4.819	0.942	2.833	3.044
2009	Log_{10}(weight)=3.017(Log_{10}FL)-4.981	0.974	2.922	3.112
2010	Log_{10}(weight)=2.977(Log_{10}FL)-4.911	0.934	2.836	3.118
2011	Log_{10}(weight)=2.911(Log_{10}FL)-4.778	0.939	2.743	3.078
2012	Log_{10}(weight)=2.858(Log_{10}FL)-4.662	0.903	2.746	2.970
Mean	Log_{10}(weight)=2.946(Log_{10}FL)-4.840	0.942	2.913	2.979

Table 5a. RBDD rotary trap fall Chinook total annual effort and passage estimates (sum of weekly values), lower and upper 90% confidence intervals (CI), ratio of fry to pre-smolt/smolt passage and ratio of estimated passage (Est) and interpolated passage (Interp) for brood year (BY) 2002-2012.

BY	Effort	Total	Low 90%CI	Up 90% CI	Fry	Smolt	Est	Interp
2002	0.76	17,038,417	857,106	47,315,257	0.86	0.14	0.54	0.46
2003	0.81	27,736,868	8,839,840	50,653,446	0.85	0.15	0.74	0.26
2004	0.85	14,108,238	5,079,300	24,967,671	0.56	0.44	0.70	0.30
2005	0.56	18,210,294	3,500,275	39,096,017	0.64	0.36	0.40	0.60
2006	0.90	16,107,651	6,522,666	26,414,402	0.63	0.37	0.85	0.15
2007	0.88	12,131,603	6,130,892	18,170,520	0.79	0.21	0.84	0.16
2008	0.79	9,115,547	4,381,560	13,849,709	0.73	0.27	0.81	0.19
2009	0.84	8,532,377	3,064,273	14,052,588	0.81	0.19	0.56	0.44
2010	0.75	8,842,481	4,727,816	13,252,907	0.71	0.29	0.79	0.21
2011	0.87	6,271,261	3,431,940	9,125,109	0.71	0.29	0.82	0.18
2012	0.85	24,429,420	16,028,521	33,112,943	0.87	0.13	0.91	0.09
Mean	0.81	14,774,923			0.74	0.26	0.72	0.28
SD	0.09	6,825,382			0.10	0.10	0.16	0.16
CV	11.7%	46.2%			13.9%	40.3%	22.0%	57.4%

Table 5b. RBDD rotary trap late-fall Chinook total annual effort and passage estimates (sum of weekly values), lower and upper 90% confidence intervals (CI), ratio of fry to pre-smolt/smolt passage and ratio of estimated passage (Est) and interpolated passage (Interp) for brood year (BY) 2002-2012.

BY	Effort	Total	Low 90%CI	Up 90% CI	Fry	Smolt	Est	Interp
2002	0.57	2,559,519	659,986	4,953,910	0.17	0.83	0.52	0.48
2003	0.76	346,058	78,407	911,270	0.57	0.43	0.56	0.44
2004	0.88	147,160	74,930	220,231	0.17	0.83	0.91	0.09
2005	0.73	143,362	41,800	333,415	0.35	0.65	0.71	0.29
2006	0.70	460,268	125,197	902,089	0.62	0.38	0.44	0.56
2007	0.90	535,619	271,079	800,447	0.27	0.73	0.86	0.14
2008	0.89	91,995	46,660	138,310	0.11	0.89	0.89	0.11
2009	0.72	219,824	97,294	342,652	0.13	0.87	0.73	0.27
2010	0.86	183,439	61,775	305,937	0.62	0.38	0.61	0.39
2011	0.77	97,040	28,738	165,997	0.72	0.28	0.53	0.47
2012	0.89	140,534	42,673	249,500	0.48	0.52	0.80	0.20
Mean	0.79	447,711			0.38	0.62	0.69	0.31
SD	0.10	715,999			0.23	0.23	0.16	0.16
CV	13.2%	159.9%			58.8%	36.5%	23.8%	52.5%

Table 5c. RBDD rotary trap winter Chinook total annual effort and passage estimates (sum of weekly values), lower and upper 90% confidence intervals (CI), ratio of fry to pre-smolt/smolt passage and ratio of estimated passage (Est) and interpolated passage (Interp) for brood year (BY) 2002-2012.

BY	Effort	Total	Low 90%CI	Up 90% CI	Fry	Smolt	Est	Interp
2002	0.64	7,119,041	2,541,407	12,353,367	0.90	0.10	0.58	0.42
2003	0.81	5,221,016	3,202,609	7,260,798	0.85	0.15	0.86	0.14
2004	0.84	3,434,683	1,998,468	4,874,794	0.90	0.10	0.82	0.18
2005	0.64	8,363,106	4,558,069	12,277,233	0.90	0.10	0.89	0.11
2006	0.83	6,687,079	3,801,539	9,575,937	0.87	0.13	0.76	0.24
2007	0.89	1,440,563	931,113	1,953,688	0.80	0.20	0.92	0.08
2008	0.87	1,244,990	776,634	1,714,013	0.85	0.15	0.77	0.23
2009	0.75	4,402,322	2,495,734	6,311,739	0.81	0.19	0.74	0.26
2010	0.81	1,285,389	817,207	1,756,987	0.68	0.32	0.92	0.08
2011	0.82	848,976	576,177	1,122,022	0.75	0.25	0.88	0.12
2012	0.89	1,349,819	904,552	1,795,106	0.53	0.47	0.92	0.08
Mean	0.80	3,763,362			0.80	0.20	0.82	0.18
SD	0.09	2,753,256			0.11	0.11	0.11	0.11
CV	10.9%	73.2%			13.9%	57.5%	12.8%	59.6%

Table 5d. RBDD rotary trap spring Chinook total annual effort and passage estimates (sum of weekly values), lower and upper 90% confidence intervals (CI), ratio of fry to pre-smolt/smolt passage and ratio of estimated passage (Est) and interpolated passage (Interp) for brood year (BY) 2002-2012.

BY	Effort	Total	Low 90%CI	Up 90% CI	Fry	Smolt	Est	Interp
2002	0.75	277,477	110,951	494,590	0.57	0.43	0.59	0.41
2003	0.81	626,915	249,225	1,053,421	0.80	0.20	0.67	0.33
2004	0.85	430,951	174,174	710,419	0.36	0.64	0.78	0.22
2005	0.57	616,040	131,328	1,382,036	0.69	0.30	0.58	0.42
2006	0.89	421,436	239,470	603,952	0.41	0.59	0.80	0.20
2007	0.89	369,536	229,766	510,868	0.91	0.09	0.99	0.01
2008	0.85	164,673	66,515	262,959	0.24	0.76	0.62	0.38
2009	0.79	438,405	176,952	700,959	0.50	0.50	0.51	0.49
2010	0.77	158,966	62,563	261,105	0.56	0.44	0.67	0.33
2011	0.86	184,290	101,443	272,769	0.48	0.52	0.85	0.15
2012	0.86	320,897	173,312	469,137	0.42	0.58	0.74	0.26
Mean	0.81	364,508			0.54	0.46	0.71	0.29
SD	0.09	164,135			0.20	0.20	0.14	0.14
CV	11.3%	45.0%			36.4%	43.0%	19.7%	47.6%

Table 5e. RBDD rotary trap *O. mykiss* total annual effort and passage estimates (sum of weekly values), lower and upper 90% confidence intervals (CI), and ratio of estimated passage (Est) and interpolated passage (Interp) for calendar year (CY) 2002-2012.

CY	Effort	Total	Low 90%CI	Up 90% CI	Est	Interp
2002[1]	0.53	124,436	27,224	244,701	0.53	0.47
2003	0.76	139,008	54,885	243,927	0.78	0.22
2004	0.83	151,694	86,857	218,132	0.95	0.05
2005	0.83	85,614	32,251	152,568	0.76	0.24
2006	0.59	83,801	20,603	169,712	0.44	0.56
2007	0.91	139,424	73,827	205,647	0.89	0.11
2008	0.89	131,013	69,331	193,584	0.88	0.12
2009	0.76	129,581	62,350	197,795	0.83	0.17
2010	0.85	100,997	47,050	155,692	0.74	0.26
2011	0.76	56,798	23,494	89,369	0.76	0.24
2012	0.86	136,621	78,804	194,892	0.96	0.04
Mean	0.78	116,272			0.78	0.22
SD	0.12	29,912			0.16	0.16
CV	15.6%	25.7%			20.9%	72.2%

[1] Incomplete year; sampling began in April 2002.

Table 6a. Fall Chinook fry-equivalent production estimates, lower and upper 90% confidence intervals (CI), estimates of adults upstream of RBDD (Adult Estimate), estimated female to male sex ratios, estimated females, estimates of female fecundity, calculated juveniles per estimated female (recruits per female) and egg-to-fry survival estimates (ETF) by brood year (BY) for Chinook sampled at RBDD rotary traps between December 2002 and September 2013.

BY	FRY EQ Passage	Lower 90% CI	Upper 90% CI	Adult Estimate	Sex Ratio (F: M)[1]		Estimated Females	Fecundity[2]	Recruits per Female	ETF
2002	18,683,720	1,216,244	51,024,926	458,772	*0.46*	*0.54*	211,035	5,407	89	1.6%
2003	30,624,209	10,162,712	55,109,506	140,724	0.57	0.44	79,509	5,407	385	7.1%
2004	18,421,457	6,224,790	33,728,746	64,276	0.48	0.52	31,045	5,407	593	11.0%
2005	22,739,315	4,235,720	49,182,045	80,294	0.47	0.53	37,738	5,407	603	11.1%
2006	20,276,322	8,670,090	32,604,760	78,692	0.54	0.46	42,730	5,407	475	8.8%
2007	13,907,856	7,041,759	20,838,463	31,592	0.54	0.46	16,996	5,407	818	15.1%
2008	10,817,397	5,117,059	16,517,847	36,104	0.46	0.54	16,644	5,407	650	12.0%
2009	9,674,829	3,678,373	15,723,368	12,908	0.51	0.49	6,531	5,407	1,481	27.4%
2010	10,620,144	5,637,617	15,895,197	29,321	0.24	0.76	7,008	5,407	1,515	28.0%
2011	7,554,574	4,171,332	10,960,125	31,931	0.29	0.71	9,260	5,407	816	15.1%
2012	26,567,379	17,219,525	36,197,837	65,664	0.50	0.50	32,635	5,407	814	15.1%
Mean	17,262,473	6,670,475	30,707,529	93,662	0.46	0.54	44,648		749	13.9%
CV	43.2%	64.0%	51.7%	134.7%			132.4%		57.2%	57.2%

[1] Sex ratios based on RBDD fish ladder data between 2003 and 2007 and CNFH data between 2008 and 2012. Average, in italics, input for 2002 due to lack of available data.

[2] Female fecundity estimates based on average values from CNFH fall Chinook spawning data collected between 2008 and 2012.

Table 6b. Late-fall Chinook fry-equivalent production estimates, lower and upper 90% confidence intervals (CI), estimates of adults upstream of RBDD (Adult Estimate), estimated female to male sex ratios, estimated females, estimates of female fecundity, calculated juveniles per estimated female, and egg-to-fry survival estimates (ETF) by brood year (BY) for Chinook sampled at RBDD rotary traps between April 2002 and March 2013.

BY	FRY EQ Passage	Lower 90% CI	Upper 90% CI	Adult Estimate	Sex Ratio (F: M)[1]		Estimated Females	Fecundity[2]	Recruits per Female	ETF
2002	4,041,505	1,063,720	7,808,619	36,220	0.46	0.54	16,661	4,662	243	5.2%
2003	451,230	133,225	1,067,819	5,513	0.46	0.54	2,536	4,662	178	3.8%
2004	233,106	124,245	342,837	8,924	0.46	0.54	4,105	4,662	57	1.2%
2005	209,066	70,548	441,133	9,610	0.46	0.54	4,421	4,662	47	1.0%
2006	582,956	186,984	1,086,699	7,770	0.46	0.54	3,574	4,662	163	3.5%
2007	809,272	426,272	1,192,625	13,939	0.46	0.54	6,412	4,662	126	2.7%
2008	149,049	80,500	218,597	3,747	0.46	0.54	1,724	4,662	86	1.9%
2009	353,003	159,726	546,546	3,792	0.46	0.54	1,744	4,662	202	4.3%
2010	232,279	89,343	376,286	3,961	0.46	0.54	1,822	4,662	127	2.7%
2011	116,188	38,688	194,400	3,777	0.46	0.54	1,737	4,662	67	1.4%
2012	191,672	69,229	325,189	2,931	0.46	0.54	1,348	4,662	142	3.0%
Mean	669,939	222,044	1,236,432	9,108			4,190		131	2.8%
CV	169.8%	134.4%	178.7%	105.5%			105.5%		48.1%	48.1%

[1] Sex ratio value of (0.46:0.54) is equivalent to the average ratio for fall Chinook between 2003 and 2012 used in Table 6a.

[2] Female fecundity estimates based on average values from CNFH late-fall Chinook spawning data collected between 2008 and 2012.

Table 6c. Winter Chinook fry-equivalent production estimates, lower and upper 90% confidence intervals (CI), estimates of adults upstream of RBDD (Adult Estimate), estimated female to male sex ratios, estimated females, estimates of female fecundity, calculated juveniles per estimated female (recruits per female) and egg-to-fry survival estimates (ETF) by brood year (BY) for Chinook sampled at RBDD rotary traps between July 2002 and June 2013.

BY	FRY EQ Passage	Lower 90% CI	Upper 90% CI	Adult Estimate	Sex Ratio (F: M)[1]		Estimated Females	Fecundity[2]	Recruits per Female	ETF
2002	7,635,469	2,811,132	13,144,325	7337	0.77	0.23	5,670	4,923	1,347	27.4%
2003	5,781,519	3,525,098	8,073,129	8133	0.64	0.36	5,179	4,854	1,116	23.0%
2004	3,677,989	2,129,297	5,232,037	8635	0.37	0.63	3,185	5,515	1,155	20.9%
2005	8,943,194	4,791,726	13,277,637	15730	0.56	0.44	8,807	5,500	1,015	18.5%
2006	7,298,838	4,150,323	10,453,765	17205	0.50	0.50	8,626	5,484	846	15.4%
2007	1,637,804	1,062,780	2,218,745	2488	0.61	0.39	1,517	5,112	1,080	21.1%
2008	1,371,739	858,933	1,885,141	2850	0.51	0.49	1,443	5,424	951	17.5%
2009	4,972,954	2,790,092	7,160,098	4537	0.60	0.40	2,702	5,519	1,840	33.3%
2010	1,572,628	969,016	2,181,572	1533	0.53	0.47	813	5,161	1,934	37.5%
2011	996,621	671,779	1,321,708	824	0.51	0.49	424	4,832	2,351	48.6%
2012	1,789,259	1,157,240	2,421,277	2581	0.58	0.42	1,491	4,518	1,200	26.6%
Mean	4,152,547	2,265,220	6,124,494	6,532	0.56	0.44	3,623	5,167	1,349	26.4%
CV	70.1%	64.0%	74.9%	85.7%	17.9%	22.9%	83.4%	6.7%	35.5%	37.9%

[1] Annual sex ratio values based on annual carcass survey estimates of female recoveries.

[2] Female fecundity estimates based on annual values from LSNFH winter Chinook spawning data collected between 2002 and 2012.

Table 6d. Spring Chinook fry-equivalent production estimates, lower and upper 90% confidence intervals (CI), estimates of adults upstream of RBDD (Adult Estimate), estimated female to male sex ratios, estimated females, estimates of female fecundity, calculated juveniles per estimated female (recruits per female) and egg-to-fry survival estimates (ETF) by brood year (BY) for Chinook sampled at RBDD rotary traps between October 16, 2002 and September 30, 2013.

BY	FRY EQ Passage	Lower 90% CI	Upper 90% CI	Adult Estimate	Sex Ratio (F: M)[1]		Estimated Females	Fecundity[2]	Recruits per Female	ETF
2002	360,352	142,134	657,043	608	0.46	0.54	280	5,078	1,288	25.4%
2003	714,086	293,095	1,187,827	319	0.46	0.54	147	5,078	4,866	95.8%
2004	624,079	255,886	1,029,162	575	0.46	0.54	265	5,078	2,359	46.5%
2005	747,026	146,488	1,695,236	189	0.46	0.54	87	5,078	8,592	169.2%
2006	594,511	328,845	860,757	353	0.46	0.54	162	5,078	3,661	72.1%
2007	392,451	242,563	544,184	767	0.46	0.54	353	5,078	1,112	21.9%
2008	251,795	96,737	406,863	305	0.46	0.54	140	5,078	1,795	35.3%
2009	591,549	238,710	945,904	314	0.46	0.54	144	5,078	4,095	80.7%
2010	207,793	80,320	344,475	208	0.46	0.54	96	5,078	2,172	42.8%
2011	251,444	130,051	382,077	167	0.46	0.54	77	5,078	3,273	64.5%
2012	451,705	238,187	665,825	868	0.46	0.54	399	5,078	1,131	22.3%
Mean	471,527	199,365	792,668	425			195		3,122	61.5%
CV	40.9%	41.7%	51.5%	56.8%			56.8%		70.8%	70.8%

[1] Sex ratio value of (0.46:0.54) is equivalent to the average ratio for fall Chinook between 2003 and 2012 used in Table 6a.

[2] Female fecundity estimates based on average of winter, fall, and late-fall hatchery data provided by CNFH and LSNFH; Table 6a-6c above.

Table 7. Green Sturgeon annual capture, catch per unit volume (CPUV) and total length summaries for sturgeon captured by RBDD rotary traps between calendar year (CY) 2002 and 2012.

CY	Captures	CPUV fish/ac-ft	Min TL (mm)	Max TL (mm)	Mean (mm)	Median (mm)
2002	35	0.3	23	52	28.8	27.5
2003	360	1.9	22	188	27.8	27
2004	266	1.0	21	58	30.5	29
2005	271	1.1	24	65	28.9	27
2006	193	0.8	21	79	30.5	28
2007	19	0.1	25	49	29.6	27
2008	0	0.0	-	-	-	-
2009	32	0.2	24	47	28.0	26
2010	70	0.5	20	36	27.1	27
2011	3701	20.1	18	86	27.4	27
2012	288	1.4	21	41	27.2	27
Ave	475.9	2.5	21.9	70.1	28.6	27.3
SD	1077.4	5.9	2.1	44.4	1.3	0.8
CV	226.4%	236.3%	9.7%	63.3%	4.5%	2.9%

Table 8a. Unidentified Lamprey ammocoetes annual capture, catch per unit volume (CPUV) and total length summaries for ammocoetes captured by RBDD rotary traps between water year (WY) 2003 and 2013.

WY	Captures	CPUV Fish/ac-ft	Min TL (mm)	Max TL (mm)	Mean (mm)	Median (mm)
2003	908	7.30	14	144	98	100
2004	925	6.80	27	191	105	108
2005	1415	11.65	22	159	104	108
2006	657	4.45	52	186	112	115
2007	556	5.16	29	155	105	111
2008	385	3.64	41	146	101	108
2009	593	5.53	41	150	106	112
2010	935	11.45	45	166	111	114
2011	859	7.07	30	186	111	117
2012	455	5.11	27	155	100	104
2013	632	6.45	25	160	103	107
Mean	756.4	6.8	32.1	163.5	105.1	109.5
SD	291.3	2.6	11.3	16.8	4.7	5.0
CV	38.5%	38.5%	35.1%	10.3%	4.5%	4.6%

Table 8b. Pacific Lamprey macrothalmia and adult annual capture, catch per unit volume (CPUV) and total length summaries for macrothalmia captured by RBDD rotary traps between water year (WY) 2003 and 2013.

WY	Captures	CPUV Fish/ac-ft	Min TL (mm)	Max TL (mm)	Mean (mm)	Median (mm)
2003	204	2.16	100	693	261	131
2004	478	3.91	96	630	149	125
2005	4645	45.00	72	665	137	126
2006	417	5.62	98	700	136	125
2007	3107	34.08	96	660	150	128
2008	5252	40.29	78	580	139	128
2009	2938	81.24	91	834	132	124
2010	699	32.30	80	819	136	125
2011	2747	68.18	92	620	140	129
2012	3464	112.76	86	500	136	127
2013	1734	25.63	88	617	131	127
Mean	2335.0	41.0	88.8	665.3	149.7	126.8
SD	1759.4	34.7	9.0	97.1	37.3	2.1
CV	75.3%	84.5%	10.2%	14.6%	24.9%	1.6%

Table 9a. Summary of fall Chinook abiotic sample conditions at RBDD rotary traps during dates of capture by brood year (BY).

	Dates of Capture			H_20 Temperature (^oF)			Discharge (CFS)			Turbidity (NTU)		
BY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002	4-Dec	30-Aug	269	47	61	55	6,390	86,500	17,471	0.5	240.2	19.6
2003	9-Dec	15-Aug	250	46	62	55	7,380	92,800	18,707	2.0	413.5	21.8
2004	8-Dec	29-Aug	264	46	63	56	5,390	76,200	13,315	1.9	626.5	24.6
2005	3-Dec	29-Aug	269	47	61	53	6,450	118,000	27,279	1.6	731.7	22.5
2006	10-Dec	26-Aug	259	46	62	55	6,030	45,400	10,628	1.6	90.0	8.0
2007	7-Dec	2-Sep	270	44	62	55	5,210	44,600	10,127	1.5	233.3	11.1
2008	5-Dec	4-Sep	273	45	64	56	4,160	33,000	9,297	2.1	129.8	12.0
2009	10-Dec	21-Aug	254	45	61	54	5,260	95,100	17,531	1.3	162.6	10.3
2010	7-Dec	29-Aug	265	45	61	54	5,260	95,100	17,331	1.3	162.6	10.2
2011	10-Dec	2-Sep	267	45	65	55	4,800	35,200	10,281	1.4	180.6	8.8
2012	2-Dec	23-Aug	264	44	64	56	5,330	70,400	11,323	1.5	315.5	9.9
Mean	7-Dec	27-Aug	264	45	62	55	5,605	72,027	14,844	1.5	298.7	14.4
SD			7	1.1	1.4	0.8	890	28,600	5,442	0.4	209.6	6.3
CV			3%	2%	2%	1%	16%	40%	37%	28%	70%	44%

Table 9b. Summary of late-fall Chinook abiotic sample conditions at RBDD rotary traps during dates of capture by brood year (BY).

	Dates of Capture			H_20 Temperature (^{o}F)			Discharge (CFS)			Turbidity (NTU)		
BY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002	19-Apr	14-Jan	270	47	62	57	6,176	86,500	12,981	0.4	59.7	11.3
2003	3-Apr	6-Mar	338	46	61	55	6,310	92,800	16,650	0.9	413.5	20.9
2004	2-Apr	21-Jan	294	46	62	57	5,170	57,000	10,983	1.4	470.0	8.0
2005	2-Apr	22-Jan	295	48	63	57	6,050	118,000	17,431	1.6	731.7	24.4
2006	1-Apr	13-Jan	287	46	61	55	6,610	80,900	15,374	2.0	178.0	8.8
2007	4-Apr	9-Jan	280	46	62	57	5,490	38,600	10,035	1.3	198.0	5.7
2008	2-Apr	2-Mar	334	45	64	56	4,160	33,000	8,775	1.5	129.8	6.9
2009	3-Apr	1-Mar	332	46	64	57	3,920	60,400	9,855	1.9	250.6	14.2
2010	1-Apr	12-Jan	286	47	62	56	5,900	50,600	11,831	1.1	220.3	7.3
2011	1-Apr	27-Jan	301	45	61	55	5,570	57,400	11,888	2.0	68.5	5.5
2012	2-Apr	11-Jan	284	46	62	56	5,536	67,520	12,580	1.4	272.0	11.3
Mean	4-Apr	29-Jan	300	46	62	56	5,536	67,520	12,580	1.4	272.0	11.3
SD			24	0.9	1.0	0.7	849	25,109	2,829	0.5	198.7	6.2
CV			8%	2%	2%	1%	15%	37%	22%	34%	73%	55%

Table 9c. Summary of winter Chinook abiotic sample conditions at RBDD rotary traps during dates of capture by brood year (BY).

	Dates of Capture			H_20 Temperature (^oF)			Discharge (CFS)			Turbidity (NTU)		
BY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002	4-Jul	8-Apr	278	47	61	55	6,176	86,500	14,081	0.4	240.2	13.5
2003	16-Jul	17-Mar	245	46	61	54	6,310	92,800	16,809	0.9	413.5	22.8
2004	22-Jul	25-Mar	246	46	62	55	5,170	57,000	9,817	1.4	470.0	12.1
2005	25-Jul	17-Feb	207	48	61	55	6,450	118,000	19,174	1.6	731.7	19.7
2006	16-Jul	10-Mar	237	46	59	54	6,030	45,400	9,788	1.6	90.0	7.2
2007	18-Jul	4-Apr	261	44	62	54	5,210	44,600	9,318	1.3	233.3	11.3
2008	30-Jul	24-Apr	268	45	64	55	4,160	33,000	7,647	1.5	129.8	8.2
2009	26-Jul	30-Mar	247	46	64	55	3,920	60,400	9,303	1.9	250.6	15.0
2010	18-Jul	7-Apr	263	45	61	54	5,260	95,100	14,941	1.1	162.6	8.6
2011	12-Aug	31-Mar	232	45	60	53	4,800	35,200	8,646	1.7	180.6	7.0
2012	23-Jul	19-Apr	270	46	61	55	5,349	66,800	11,952	1.3	290.2	12.5
Mean	22-Jul	28-Mar	250	46	61	55	5,349	66,800	11,952	1.3	290.2	12.5
SD			20	1.1	1.5	0.8	843	27,776	3,767	0.4	185.4	5.1
CV			8%	2%	2%	1%	16%	42%	32%	31%	64%	41%

Table 9d. Summary of spring Chinook abiotic sample conditions at RBDD rotary traps during dates of capture by brood year (BY).

	Dates of Capture			$H_2$0 Temperature (^{o}F)			Discharge (CFS)			Turbidity (NTU)		
BY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002	16-Oct	29-May	225	47	61	54	6,176	86,500	16,877	0.4	240.2	19.1
2003	16-Oct	11-Jun	239	46	62	54	6,310	92,800	17,267	0.9	413.5	23.0
2004	16-Oct	3-Jun	230	46	63	54	5,170	76,200	11,612	1.4	626.5	27.6
2005	16-Oct	3-Jun	230	47	61	52	6,450	118,000	28,158	1.6	731.7	25.3
2006	16-Oct	26-May	222	46	62	53	6,030	45,400	8,630	1.6	90.0	8.3
2007	16-Oct	12-Jun	240	44	61	53	5,210	44,600	8,823	1.3	233.3	11.4
2008	16-Oct	7-Jun	234	45	64	54	4,160	33,000	7,841	1.7	129.8	10.1
2009	16-Oct	25-May	221	46	62	54	3,920	60,400	9,495	1.9	250.6	17.1
2010	16-Oct	12-Jun	239	45	61	53	5,260	95,100	16,656	1.3	162.6	9.9
2011	16-Oct	27-May	224	45	65	53	4,800	35,200	8,344	1.7	180.6	8.8
2012	16-Oct	23-Jun	250	46	62	53	5,349	68,720	13,370	1.4	305.9	16.0
Mean	16-Oct	4-Jun	232	46	62	53	5,349	68,720	13,370	1.4	305.9	16.0
SD			9	1.0	1.4	0.6	843	27,696	6,116	0.4	205.5	7.0
CV			4%	2%	2%	1%	16%	40%	46%	30%	67%	43%

Table 9e. Summary of *O. mykiss* abiotic sample conditions at RBDD rotary traps during dates of capture by calendar year (CY).

	Dates of Capture			H_20 Temperature (^{o}F)			Discharge (CFS)			Turbidity (NTU)		
CY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002[1]	-	-	-	-	-	-	-	-	-	-	-	-
2003	19-Jan	30-Dec	345	46	61	56	6,310	56,800	13,677	0.9	240.2	16.4
2004	6-Jan	17-Dec	346	46	62	56	5,170	92,800	14,613	1.4	413.5	9.3
2005	1-Jan	29-Dec	362	46	63	56	5,890	94,700	12,661	1.6	626.5	20.1
2006	3-Jan	30-Dec	361	47	61	54	6,610	82,900	20,803	2.0	190.5	11.4
2007	16-Jan	27-Dec	345	46	62	56	5,510	45,400	9,596	1.3	74.5	6.4
2008	6-Jan	28-Dec	357	44	64	56	4,610	44,600	9,478	1.5	233.3	9.0
2009	12-Jan	25-Dec	347	45	64	57	4,020	33,000	8,775	1.9	129.8	10.3
2010	15-Jan	12-Dec	331	47	62	56	5,150	60,400	11,194	1.1	250.6	12.4
2011	1-Jan	30-Dec	363	45	61	55	5,260	95,100	13,833	1.3	162.6	7.2
2012	17-Jan	14-Dec	332	45	65	56	4,800	70,400	10,557	1.2	315.5	11.0
Mean	10-Jan	23-Dec	349	46	63	56	5,333	67,610	12,519	1.4	263.7	11.4
SD			12	0.9	1.3	0.8	783	22,986	3,551	0.3	159.1	4.1
CV			3%	2%	2%	1%	15%	34%	28%	24%	60%	37%

[1] Sampling did not begin until mid-April of 2002 and this year not included in analyses.

Table 9f. Summary of Green Sturgeon abiotic sample conditions at RBDD rotary traps during dates of capture by calendar year (CY).

	Dates of Capture			H_20 Temperature (^oF)			Discharge (CFS)			Turbidity (NTU)		
CY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2002	7-May	16-Jul	70	55	60	58	9,317	15,680	13,038	0.9	16.3	3.5
2003	13-Jun	11-Nov	151	52	61	58	6,950	16,000	10,802	0.9	48.6	6.5
2004	4-May	29-Jul	86	55	60	58	9,560	16,700	14,210	3.0	18.3	4.9
2005	7-May	13-Aug	98	54	61	58	10,200	76,200	18,614	2.3	626.5	26.4
2006	10-Jun	25-Aug	76	56	59	57	12,800	15,600	14,579	3.4	13.9	5.7
2007	11-May	24-Jul	74	55	61	58	9,790	17,000	12,905	1.7	50.4	4.5
2008	-	-	0	-	-	-	-	-	-	-	-	-
2009	11-May	16-Jul	66	58	64	61	9,460	13,700	11,226	4.1	34.4	13.5
2010	26-May	29-Aug	95	55	61	58	9,150	18,300	13,143	1.6	22.0	5.4
2011	16-May	27-Aug	103	52	61	58	10,400	24,800	14,059	3.6	23.5	6.8
2012	1-May	26-Jun	56	55	61	58	8,763	21,398	12,258	2.2	85.4	7.7
Mean	17-May	12-Aug	88	55	61	58	9,639	23,538	13,483	2.4	93.9	8.5
SD			27	1.7	1.2	0.9	1,464	18,782	2,181	1.1	188.4	6.9
CV			31%	3%	2%	2%	15%	80%	16%	47%	201%	81%

Table 9g. Summary of Lamprey *spp.* abiotic sample conditions at RBDD rotary traps during dates of capture by water year (WY).

	Dates of Capture			$H_2$0 Temperature (^{o}F)			Discharge (CFS)			Turbidity (NTU)		
WY	Initial	Final	Days	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
2003	1-Oct	27-Sep	361	47	61	56	6,176	86,500	15,033	0.4	240.2	15.1
2004	1-Oct	29-Sep	364	46	62	55	6,310	92,800	15,528	0.9	413.5	16.3
2005	2-Oct	29-Sep	362	46	63	56	5,170	76,200	11,800	1.4	626.5	18.6
2006	1-Oct	29-Sep	363	47	61	54	6,450	118,000	22,724	1.6	731.7	17.9
2007	1-Oct	29-Sep	363	46	62	55	6,030	45,400	9,832	1.6	90.0	7.3
2008	1-Oct	29-Sep	364	44	63	56	5,210	44,600	9,342	1.3	233.3	8.8
2009	1-Oct	29-Sep	363	45	64	57	4,160	33,000	8,791	1.6	129.8	10.5
2010	1-Oct	30-Sep	364	46	62	56	3,920	60,400	10,241	1.1	250.6	12.1
2011	3-Oct	30-Sep	362	45	61	55	5,260	95,100	15,022	1.3	162.6	8.4
2012	3-Oct	27-Sep	360	45	65	55	4,800	35,200	9,753	1.2	180.6	7.1
2013	5-Oct	28-Sep	358	44	64	56	5,330	70,400	10,479	1.1	315.5	8.5
Mean	2-Oct	29-Sep	362	46	63	56	5,347	68,873	12,595	1.2	306.8	11.9
SD			2	1.1	1.3	0.7	843	27,701	4,177	0.3	205.5	4.4
CV			1%	2%	2%	1%	16%	40%	33%	29%	67%	37%

Figures

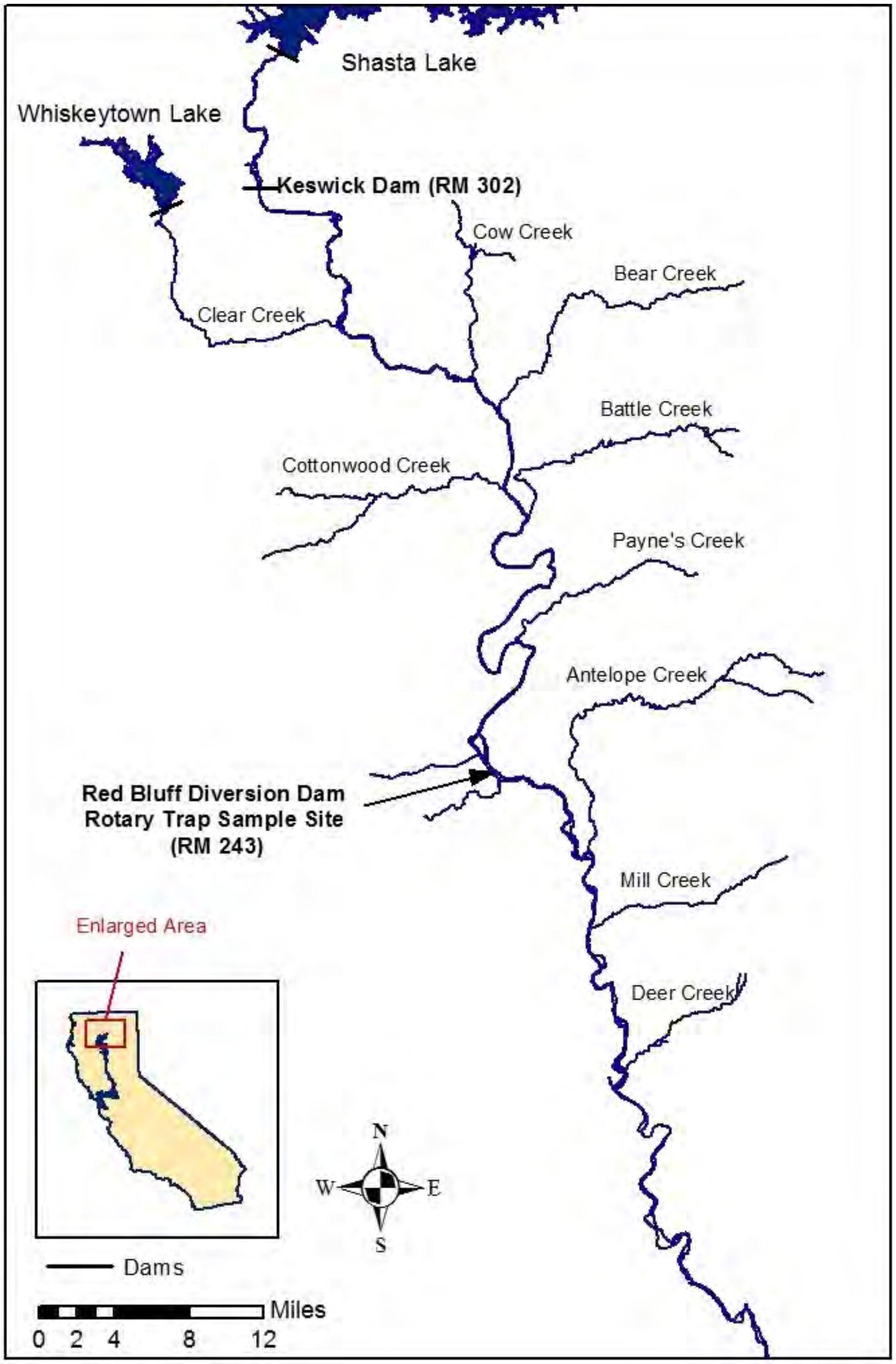


Figure 1. Location of Red Bluff Diversion Dam rotary trap sample site on the Sacramento River, California (RM 243).

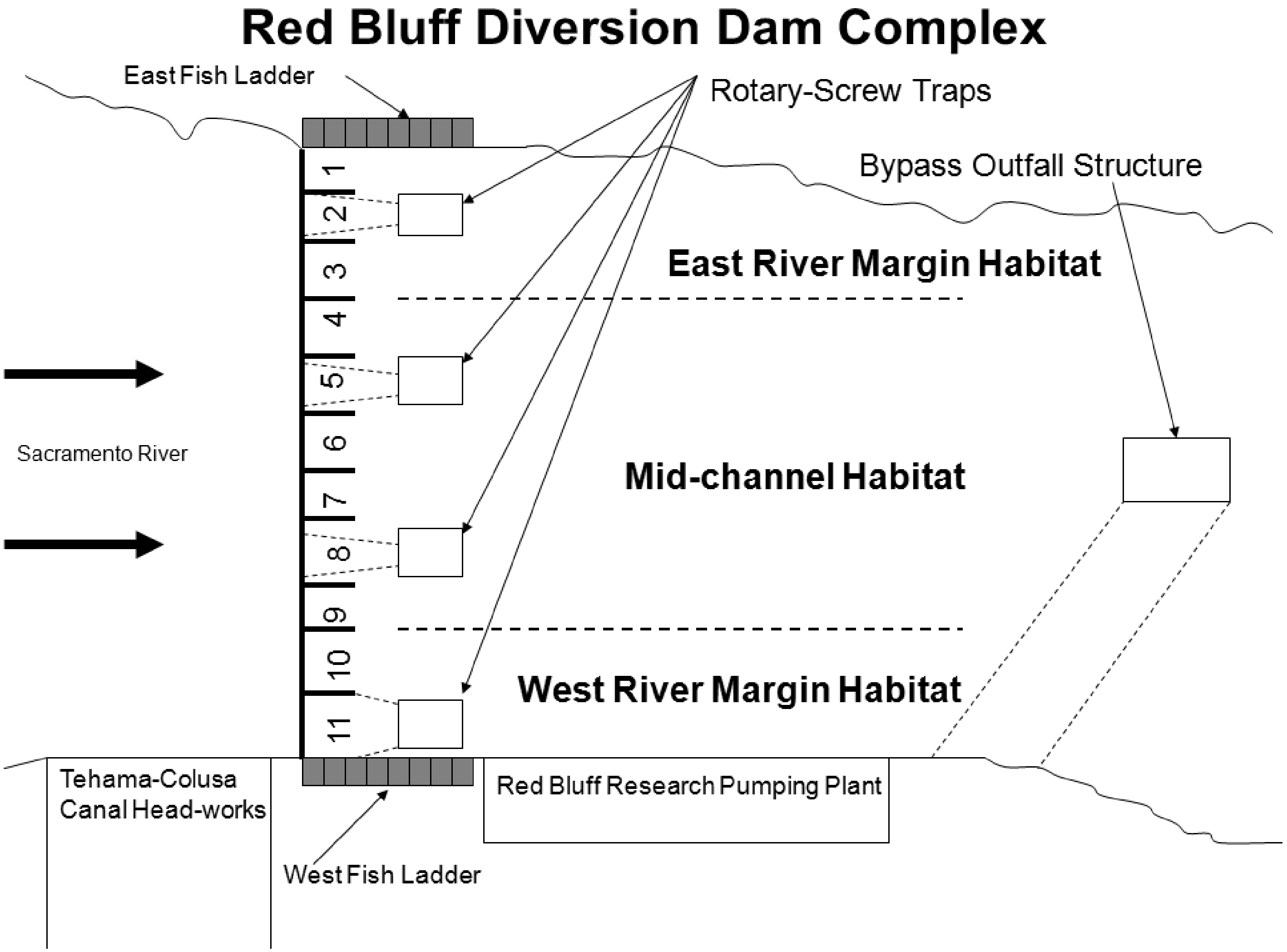


Figure 2. Rotary-screw trap sampling transect at Red Bluff Diversion Dam Site (RM 243) on the Sacramento River, California.

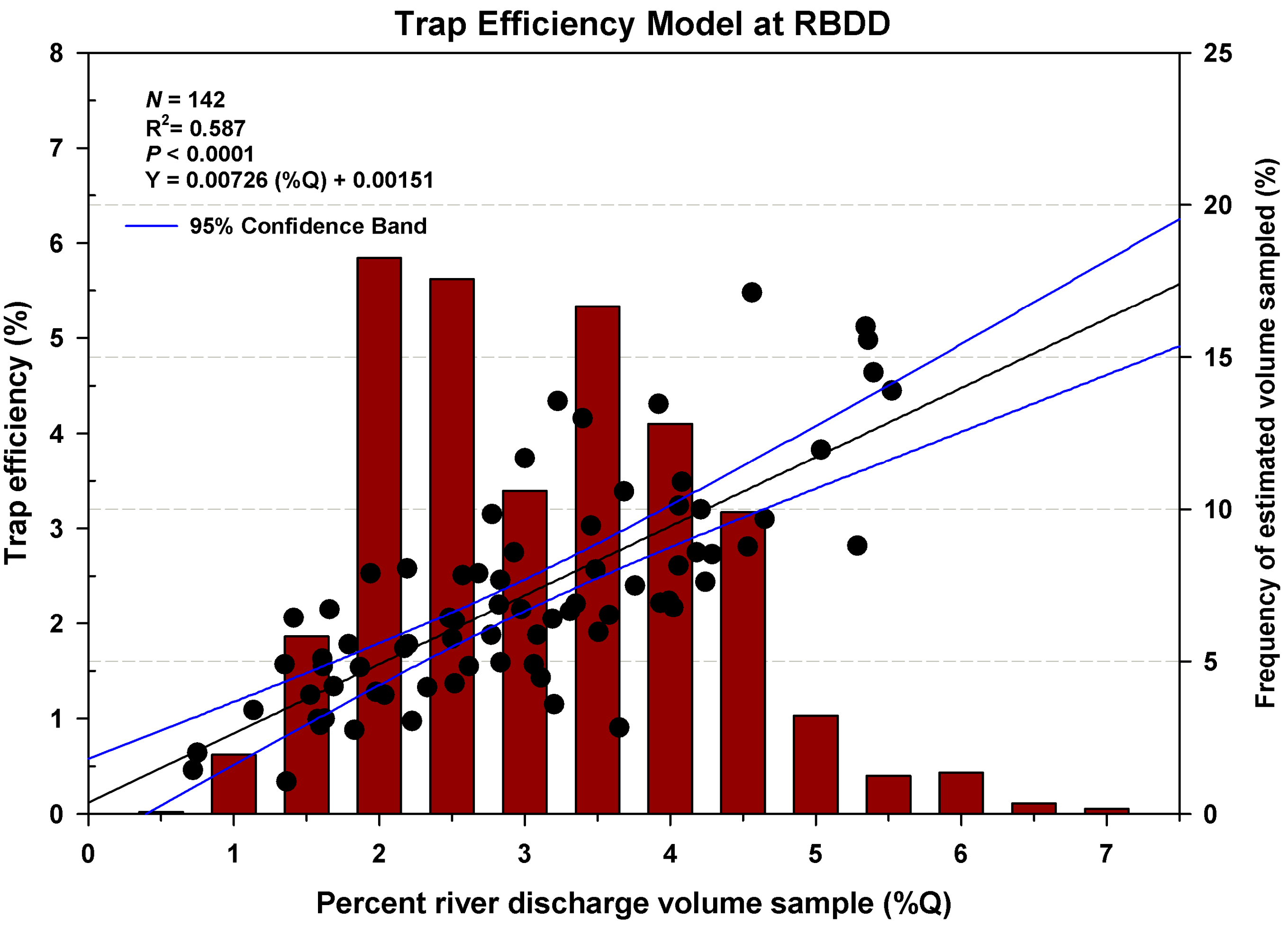


Figure 3. Trap efficiency model for combined 8-ft diameter rotary traps at Red Bluff Diversion Dam (RM 243), Sacramento River, CA. Mark-recapture trials (*N* = 142) were used to estimate trap efficiencies. Histogram indicates percentage of time traps sampled various levels (half percent bins) of river discharge between April 2002 and September 2013.

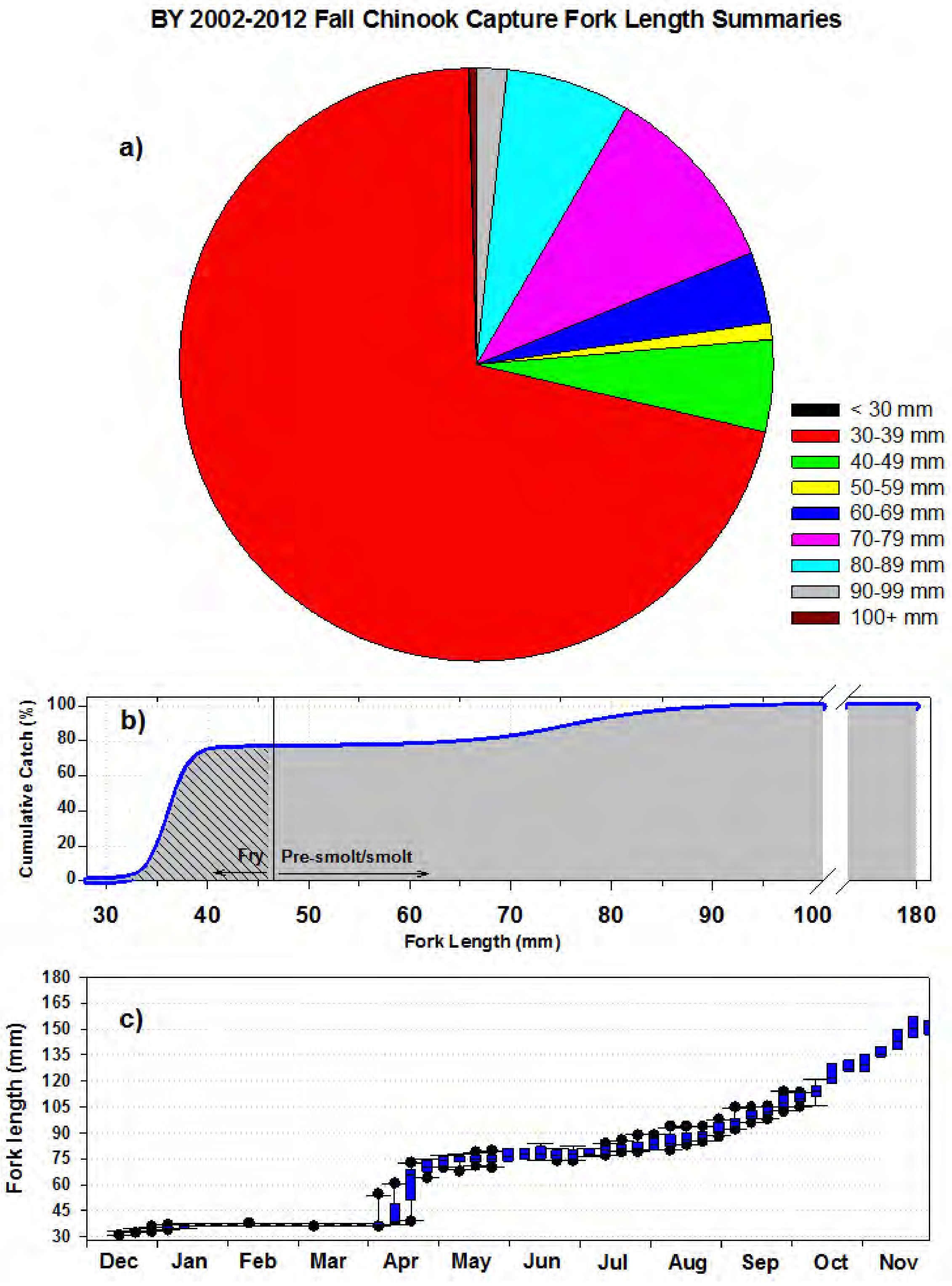


Figure 4. Fall Chinook fork length (a) capture proportions, (b) cumulative capture size curve, and (c) average weekly median boxplots for fall Chinook sampled by rotary traps at RBDD between December 2002 and September 2013.

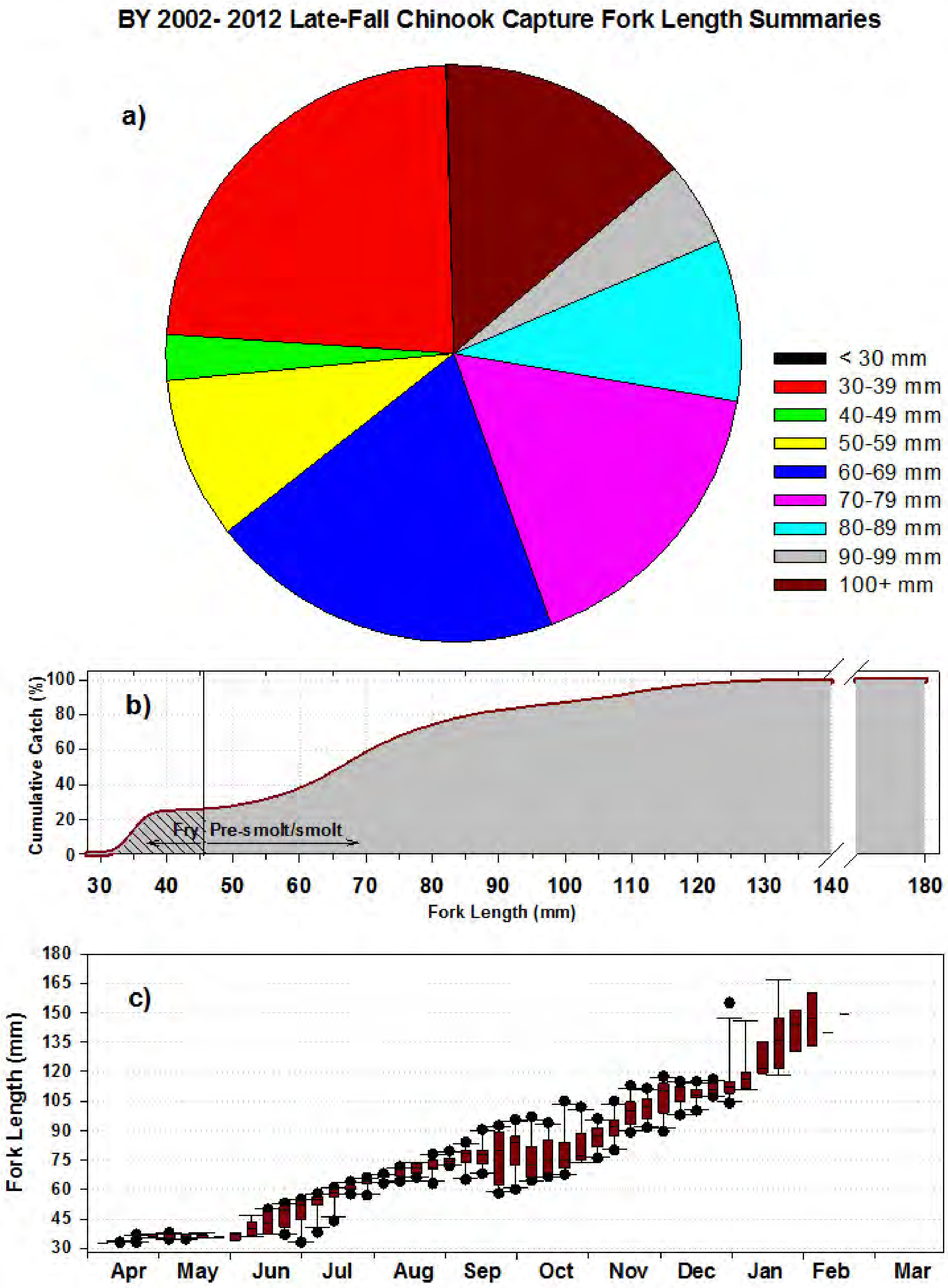


Figure 5. Late-fall Chinook fork length (a) capture proportions, (b) cumulative capture size curve, and (c) average weekly median boxplots for late-fall Chinook sampled by rotary traps at RBDD between April 2002 and March 2013.

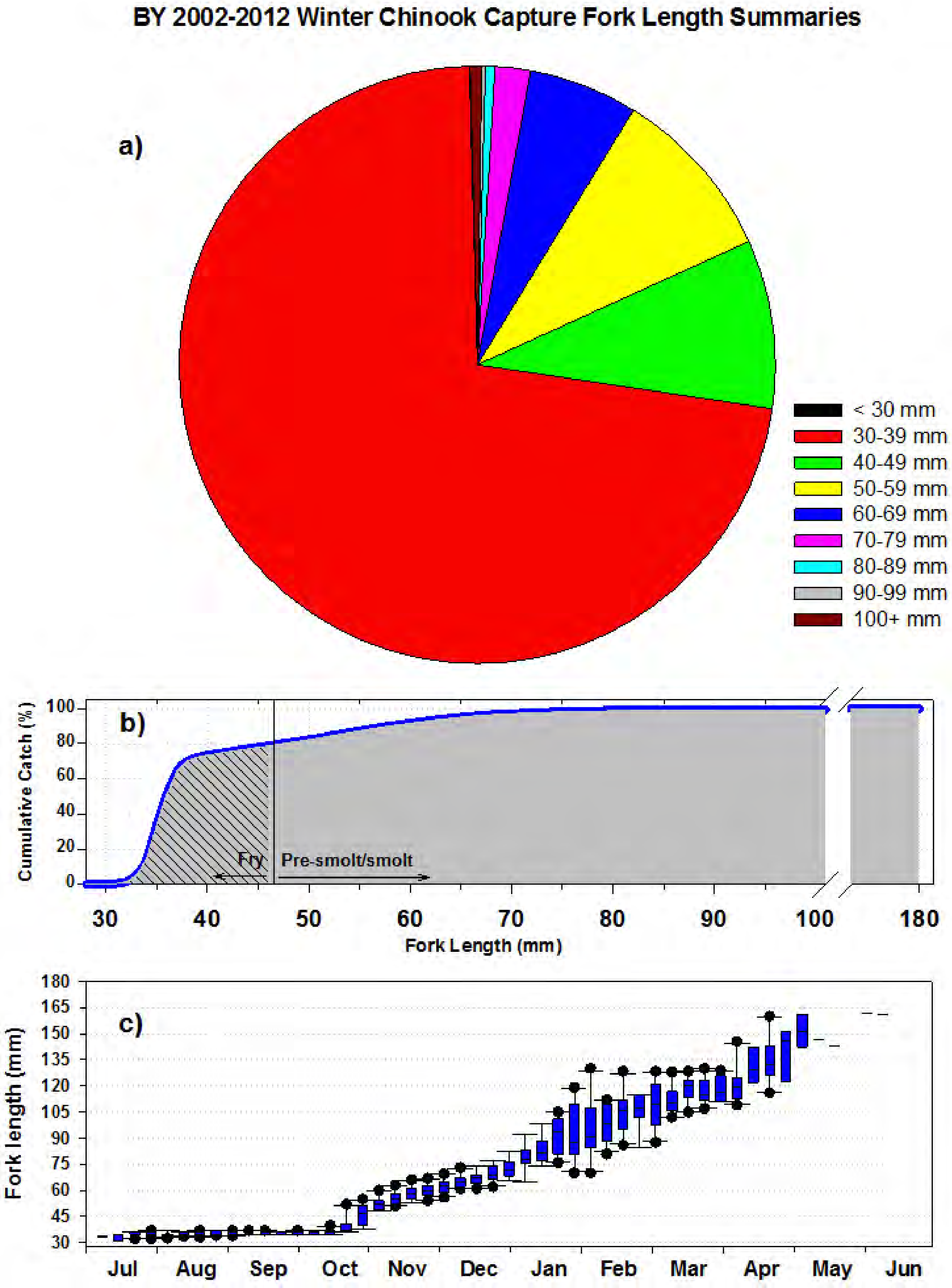


Figure 6. Winter Chinook fork length (a) capture proportions, (b) cumulative capture size curve, and (c) average weekly median boxplots for winter Chinook sampled by rotary traps at RBDD between July 2002 and June 2013.

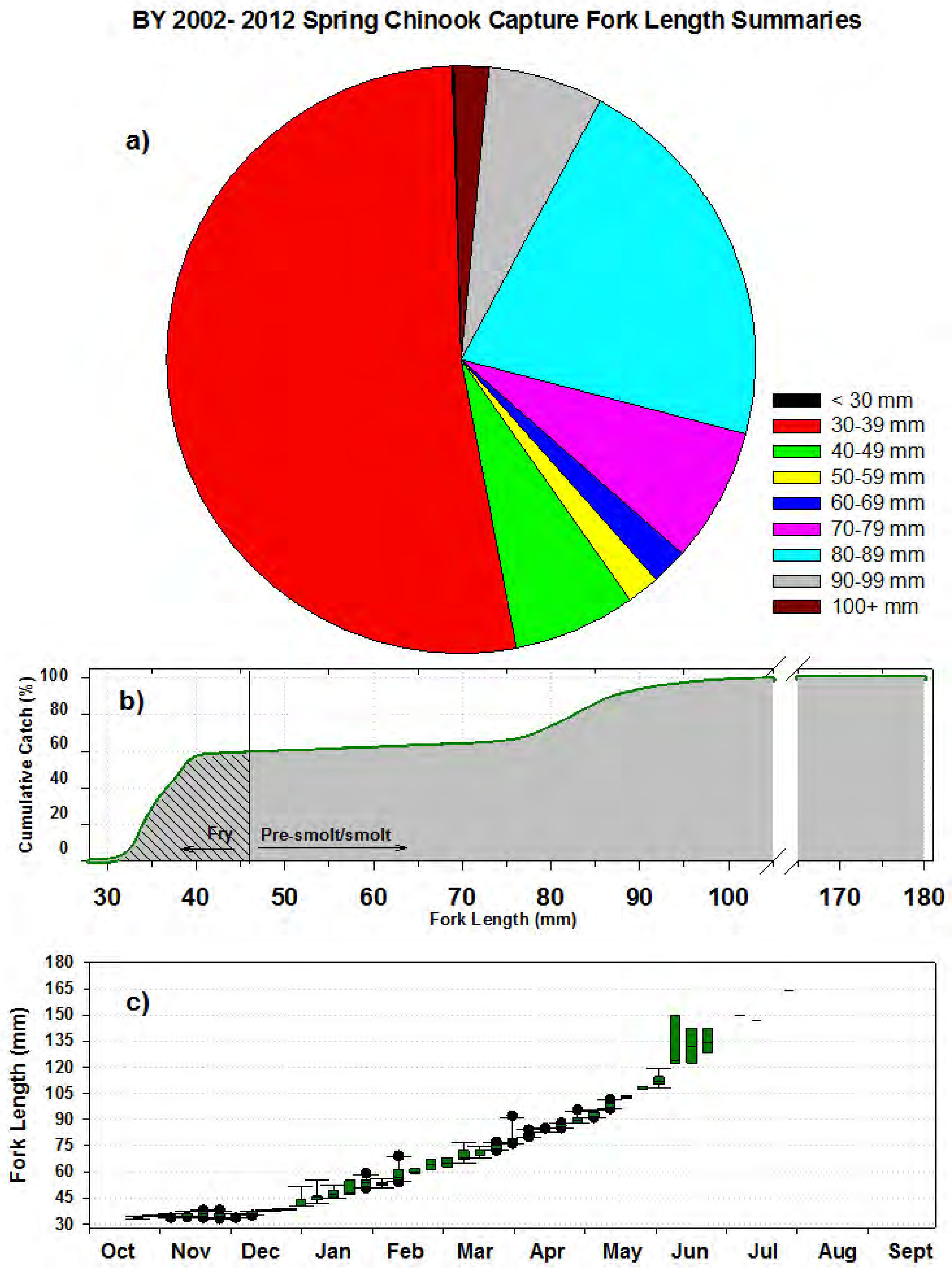


Figure 7. Spring Chinook fork length (a) capture proportions, (b) cumulative capture size curve, and (c) average weekly median boxplots for spring Chinook sampled by rotary traps at RBDD between October 2002 and September 2013.

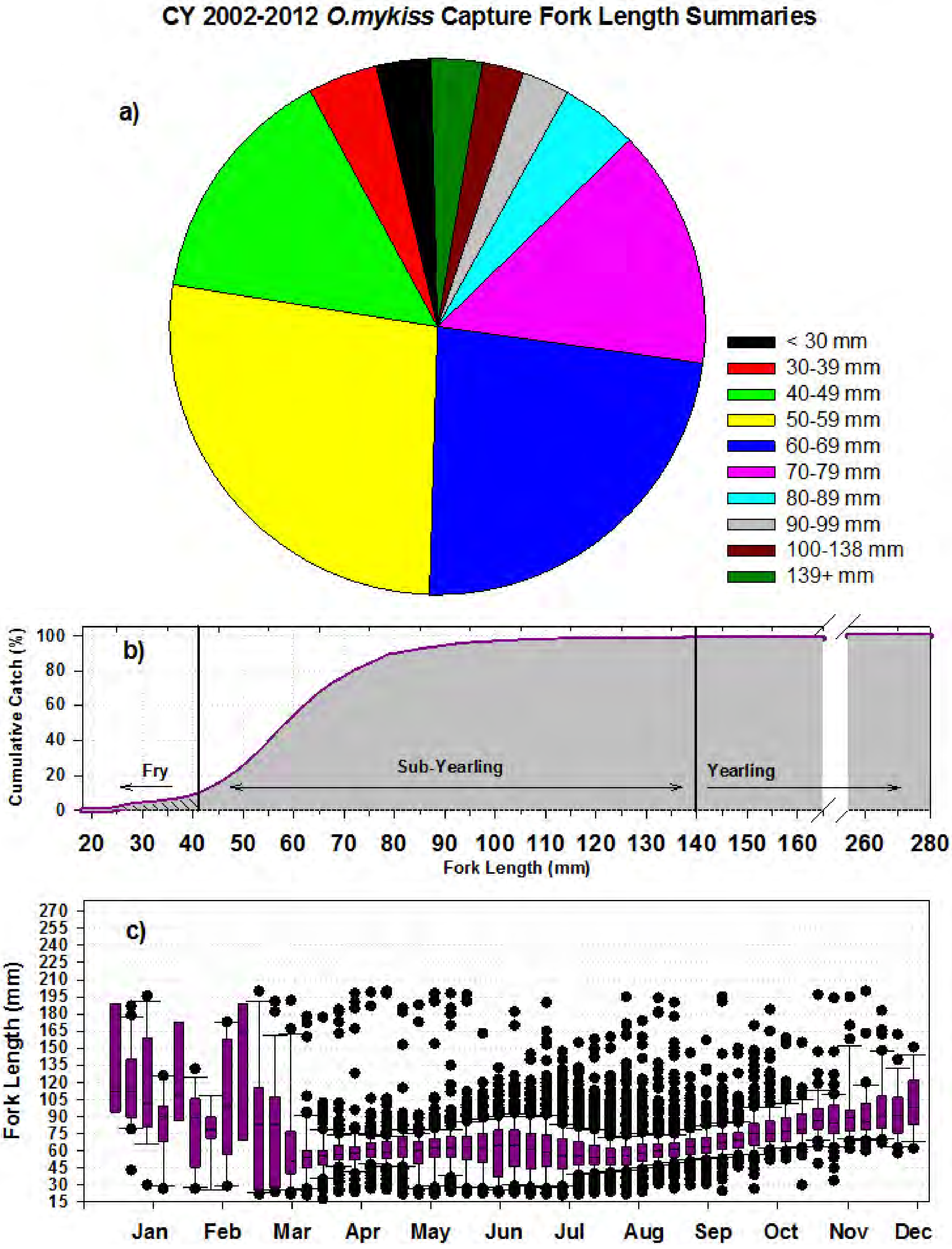


Figure 8. *O. mykiss* fork length (a) capture proportions, (b) cumulative capture size curve, and (c) average weekly median boxplots for *O. mykiss* sampled by rotary traps at RBDD between April 2002 and December 2012.

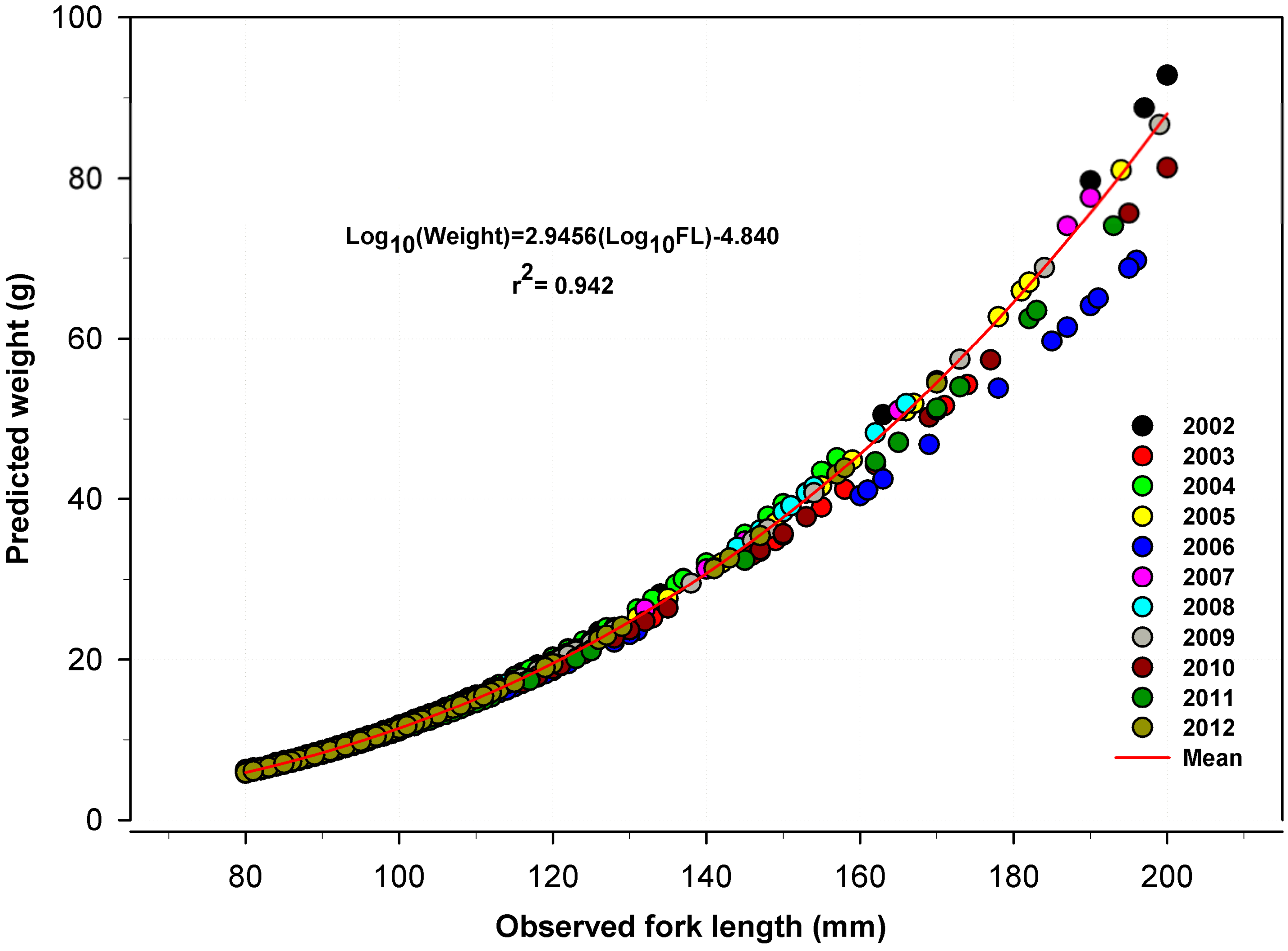


Figure 9. Predicted weight (g) for *O. mykiss* with measured fork lengths (FL) between 80 and 200 mm using annual weight-length regression equation.

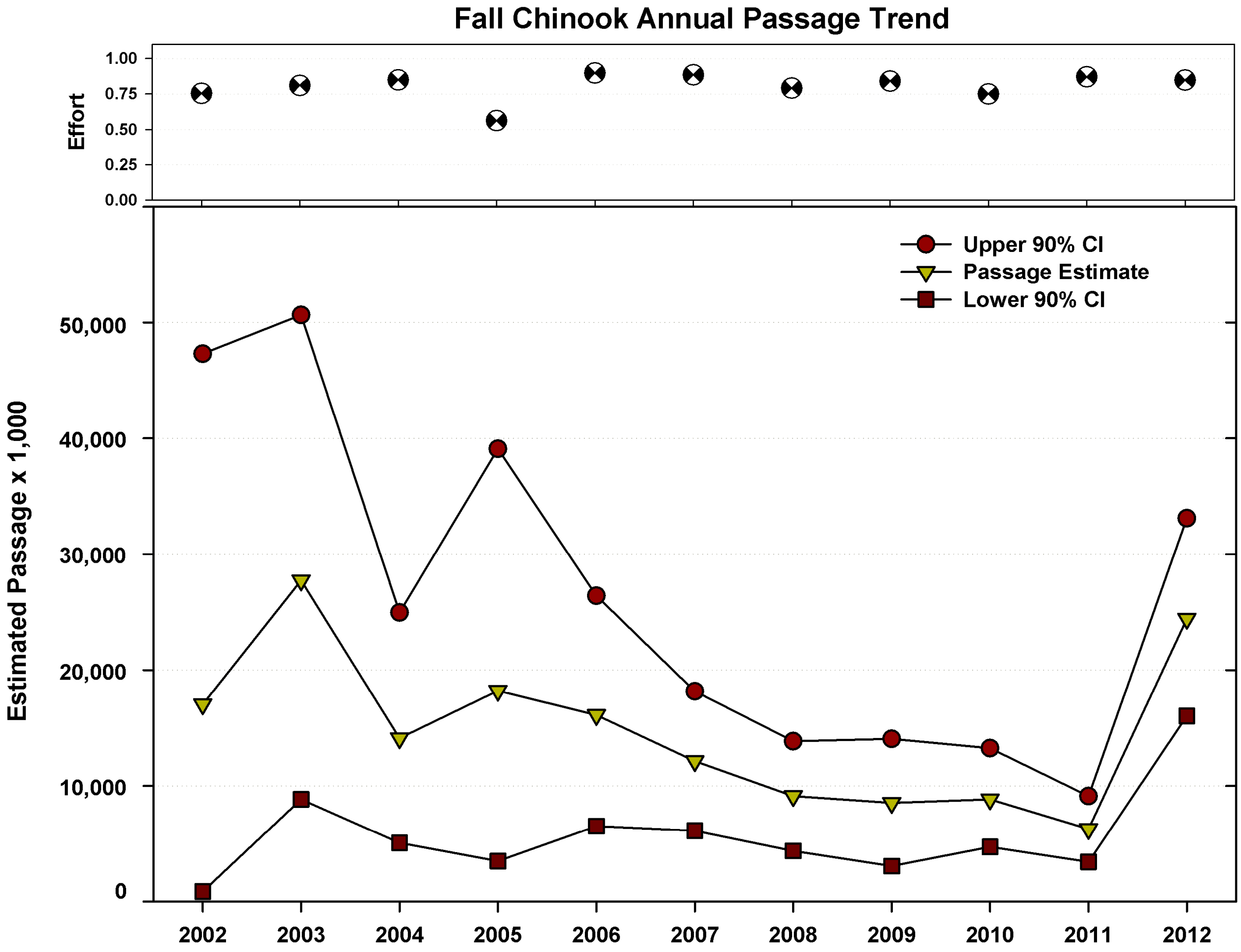


Figure 10. RBDD rotary trap fall Chinook annual sample effort and passage estimates with 90% confidence intervals (CI) for the period December 2002 through September 2013

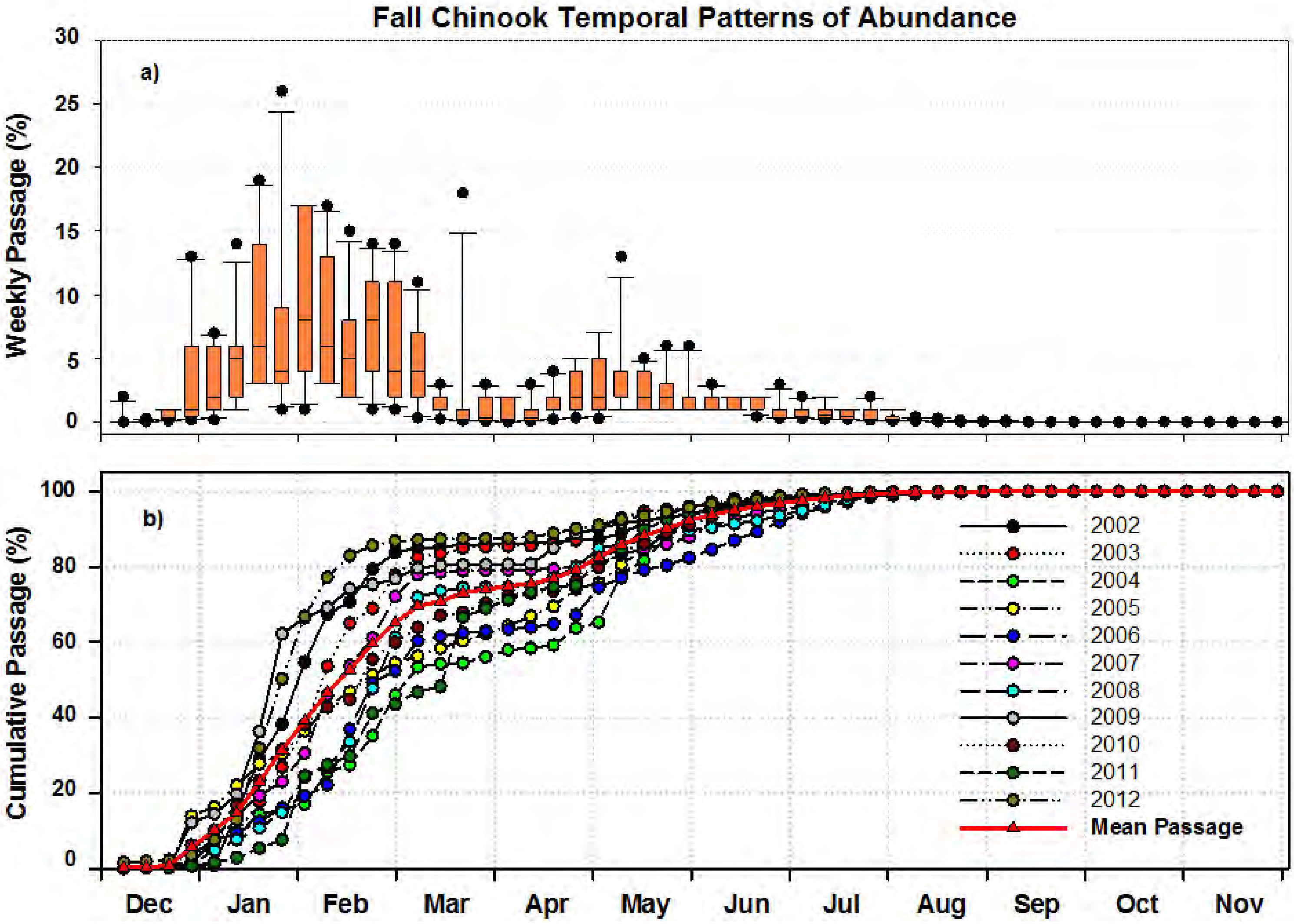


Figure 11. RBDD rotary trap fall Chinook (a) boxplots of weekly passage estimates relative to annual total passage estimates and (b) cumulative weekly passage with 11-year mean passage trend line for the period December 2002 through September 2013.

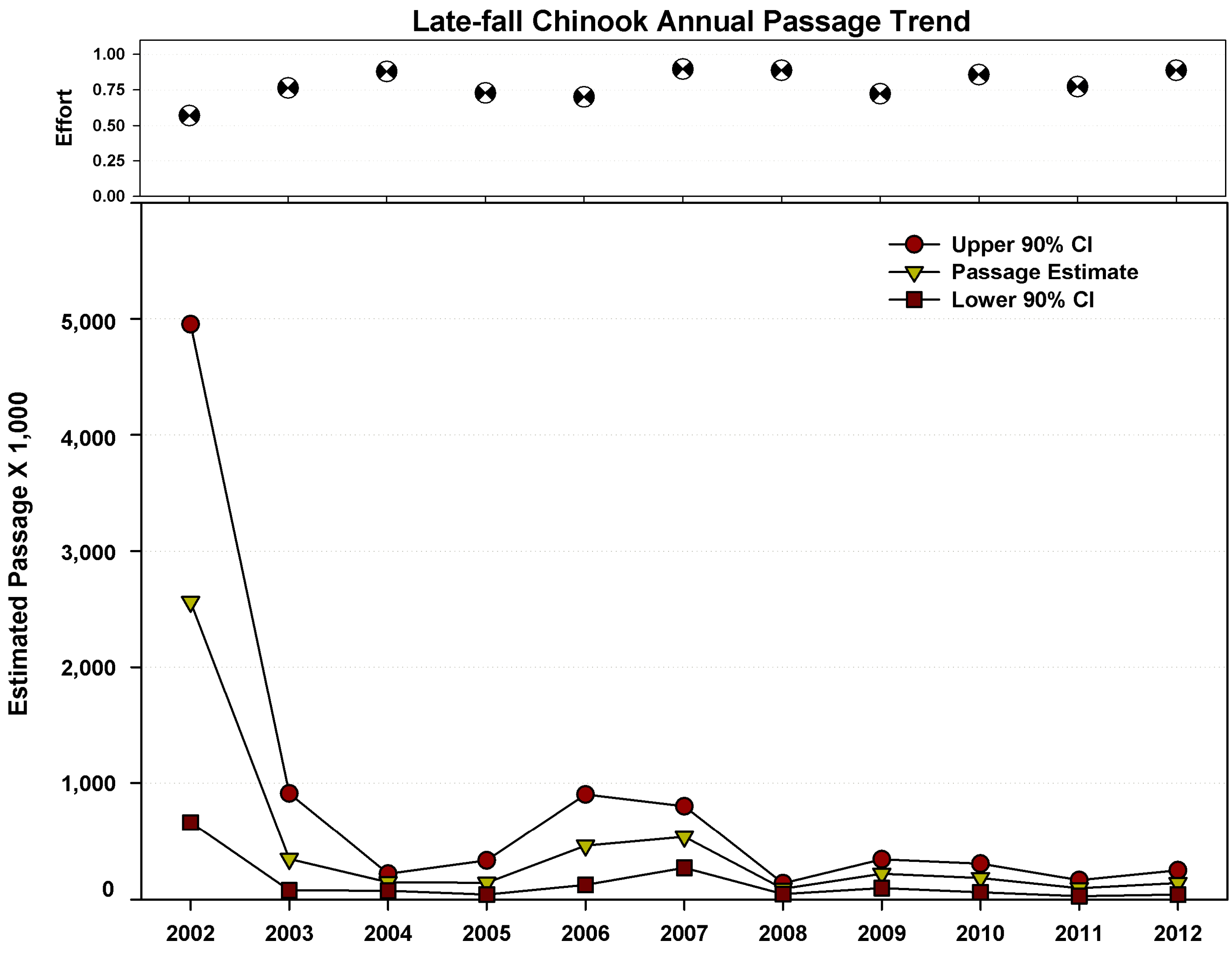


Figure 12. RBDD rotary trap late-fall Chinook annual sample effort and passage estimates with 90% confidence intervals (CI) for the period April 2002 through March 2013.

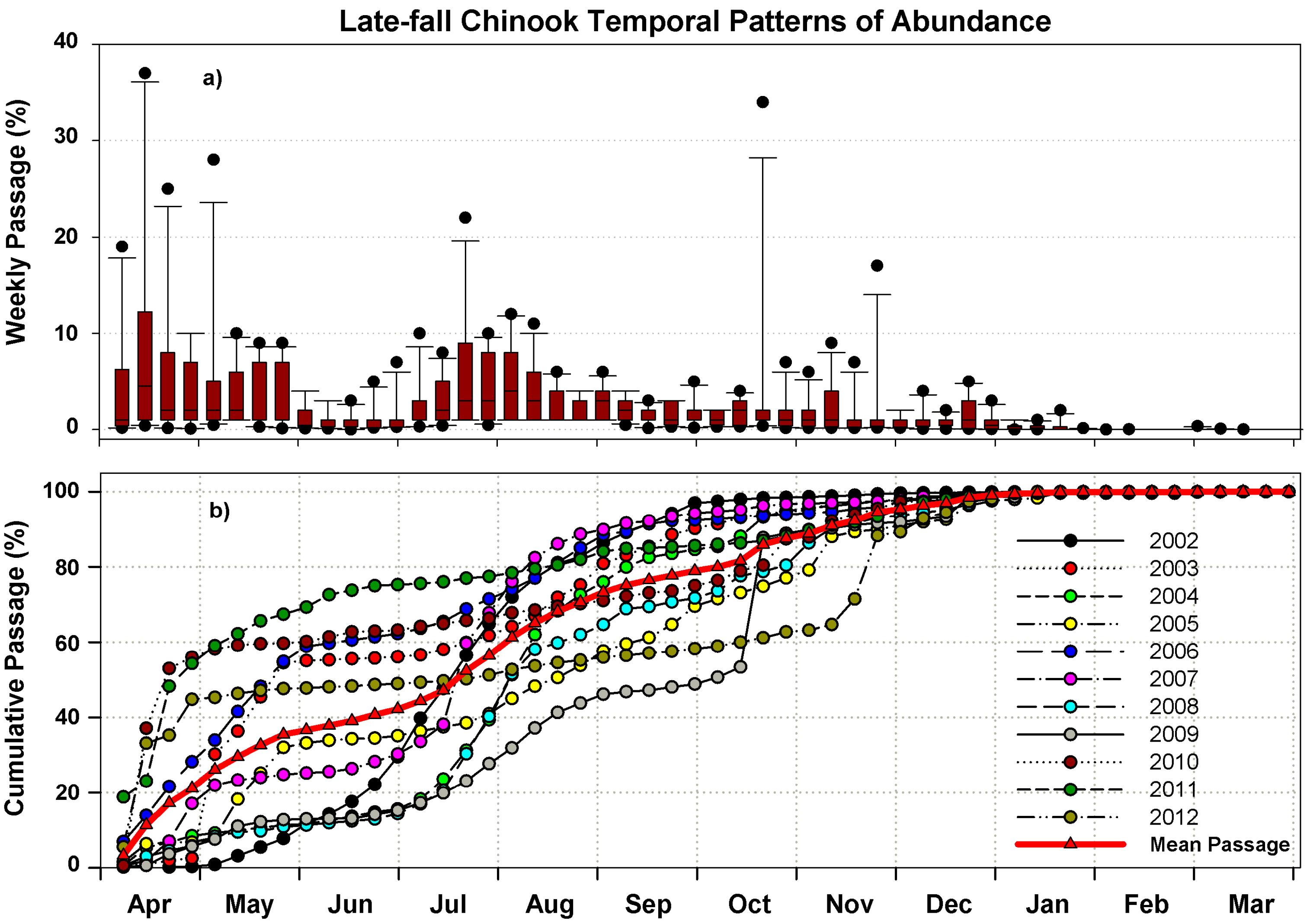


Figure 13. RBDD rotary trap late-fall Chinook (a) boxplots of weekly passage estimates relative to annual total passage estimates and (b) cumulative weekly passage with 11-year mean passage trend line for the period April 2002 through March 2013.

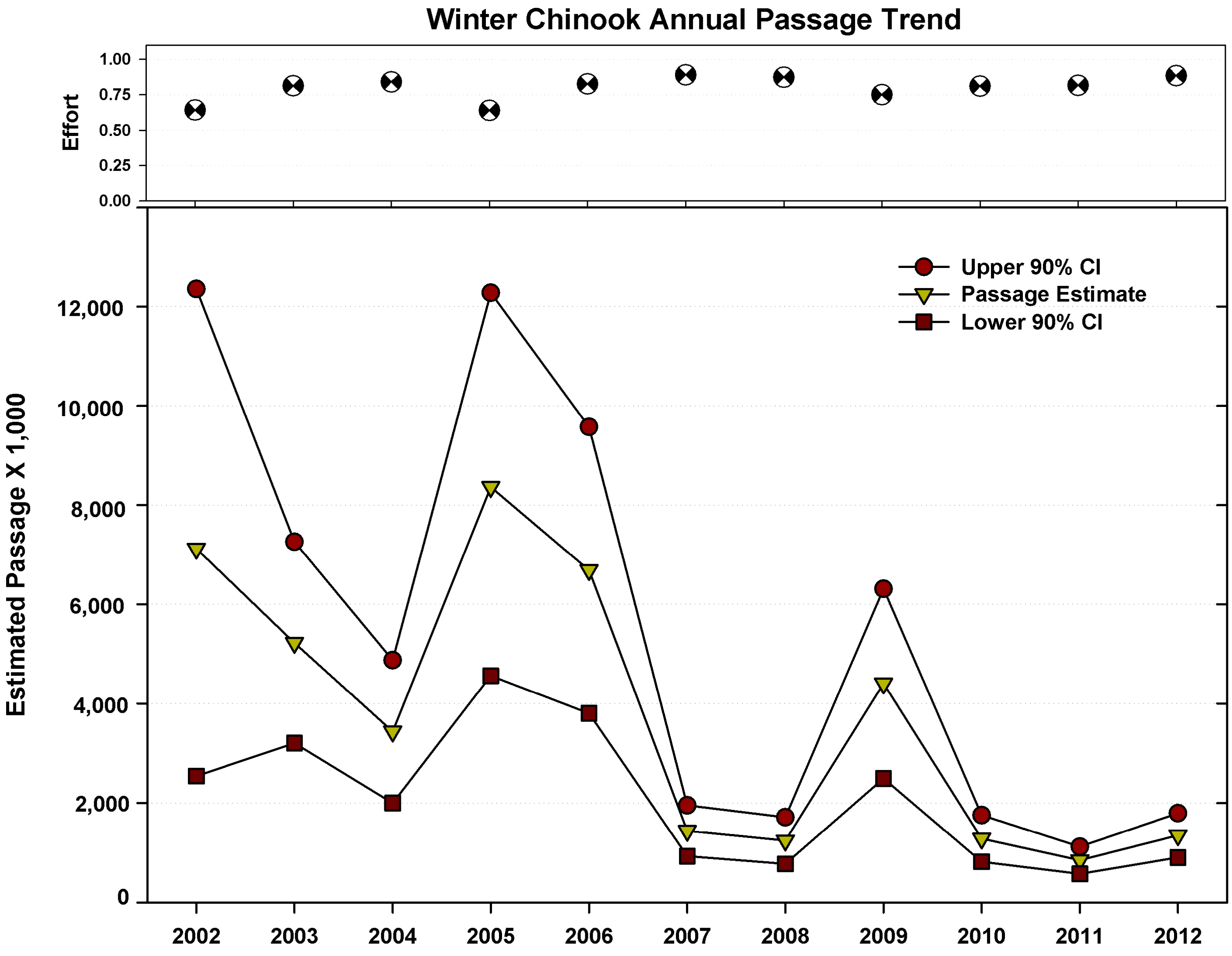


Figure 14. RBDD rotary trap winter Chinook annual sample effort and passage estimates with 90% confidence intervals (CI) for the period July 2002 through June 2013.

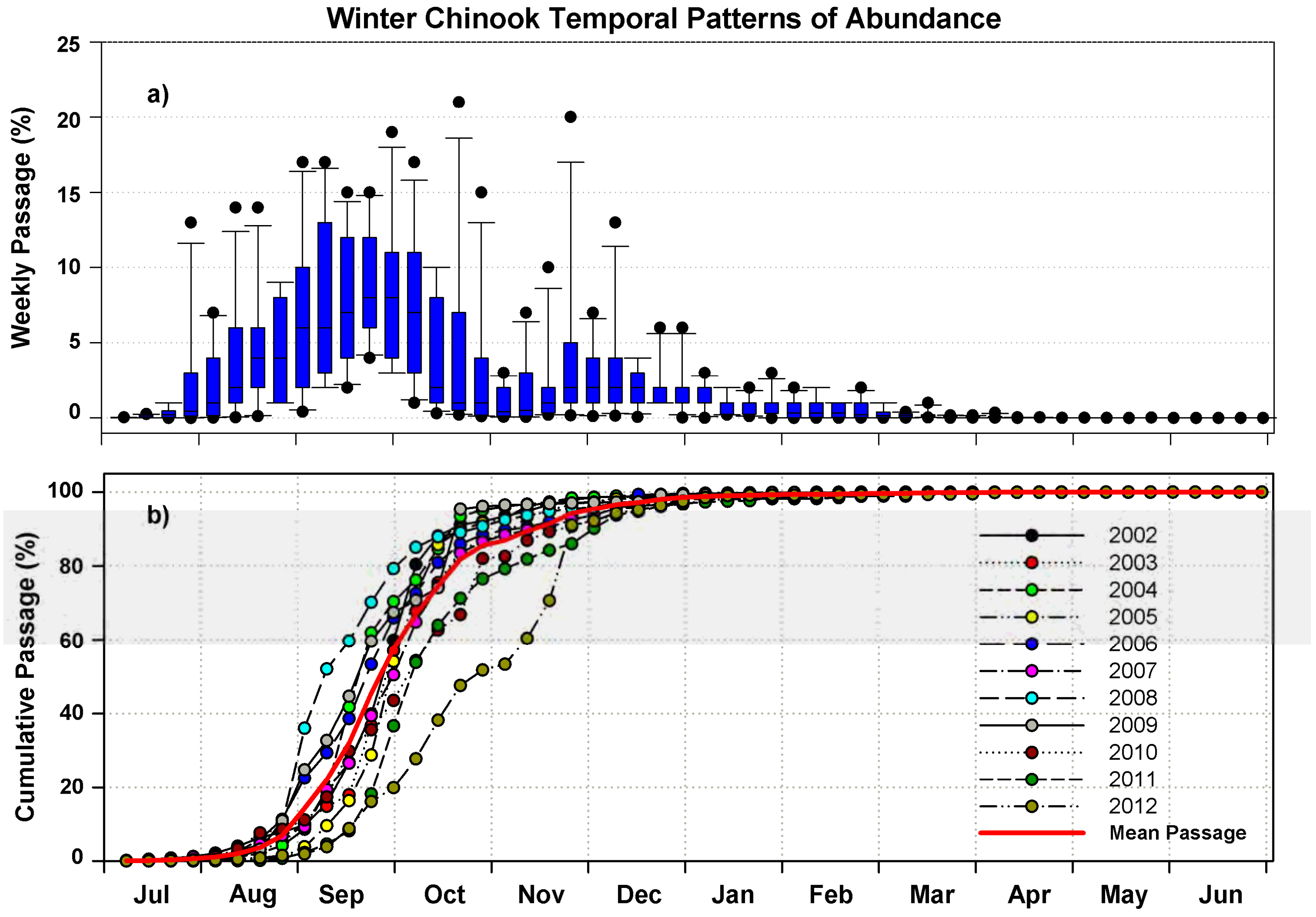


Figure 15. RBDD rotary trap winter Chinook (a) boxplots of weekly passage estimates relative to annual total passage estimates and (b) cumulative weekly passage with 11-year mean passage trend line for the period July 2002 through June 2013.

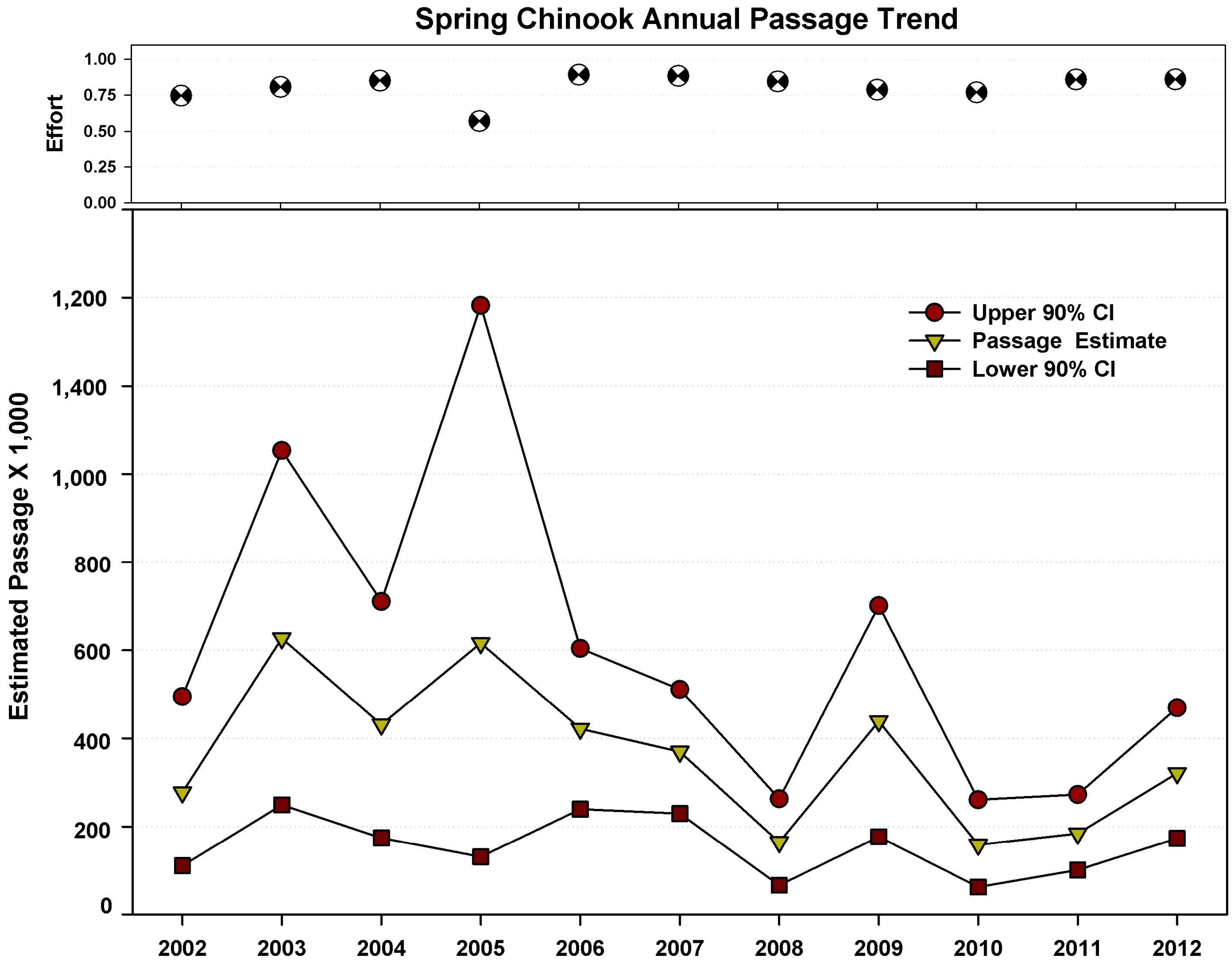
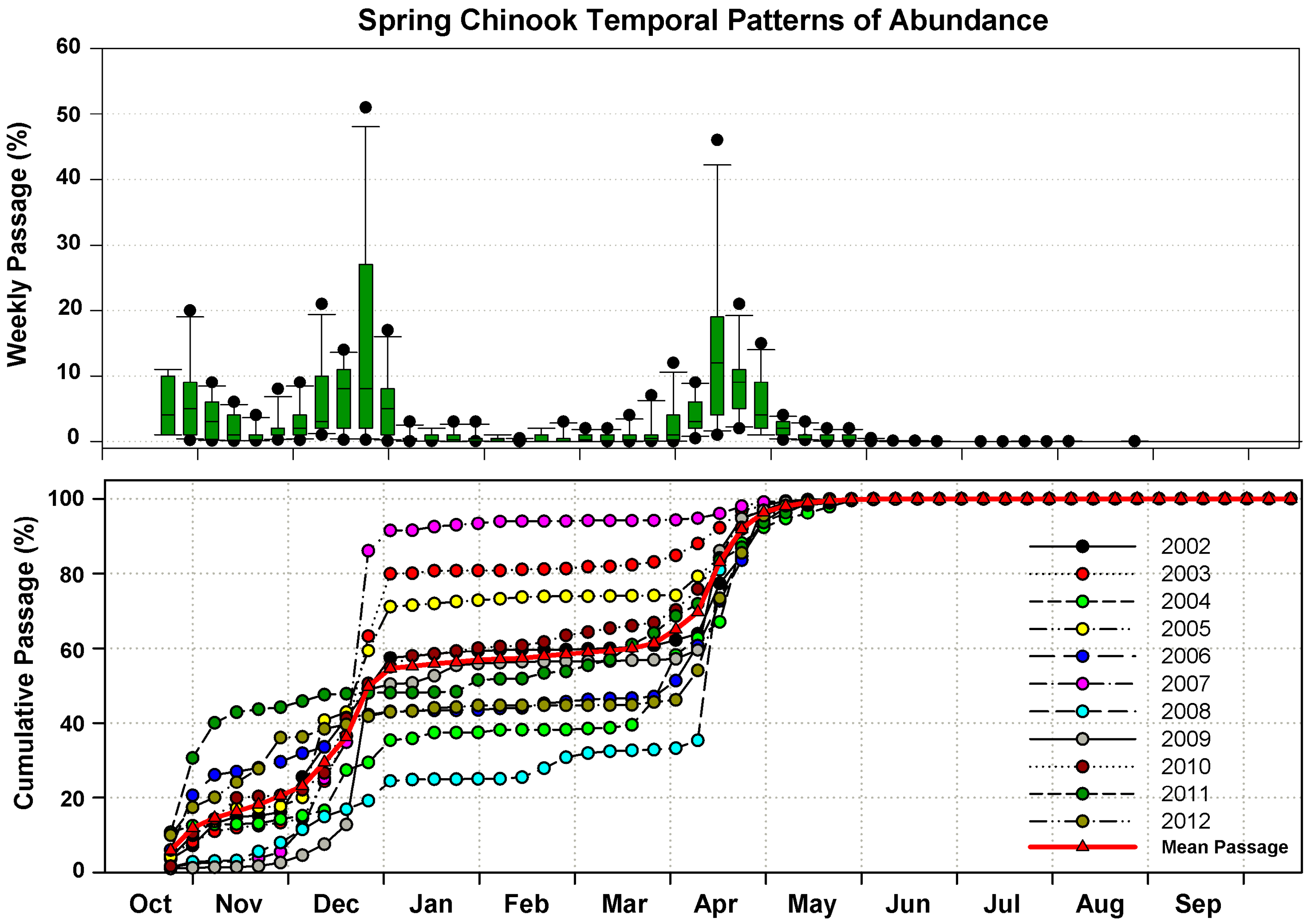


Figure 16. RBDD rotary trap spring Chinook annual sample effort and passage estimates with 90% confidence intervals (CI) for the period October 2002 through September 2013.



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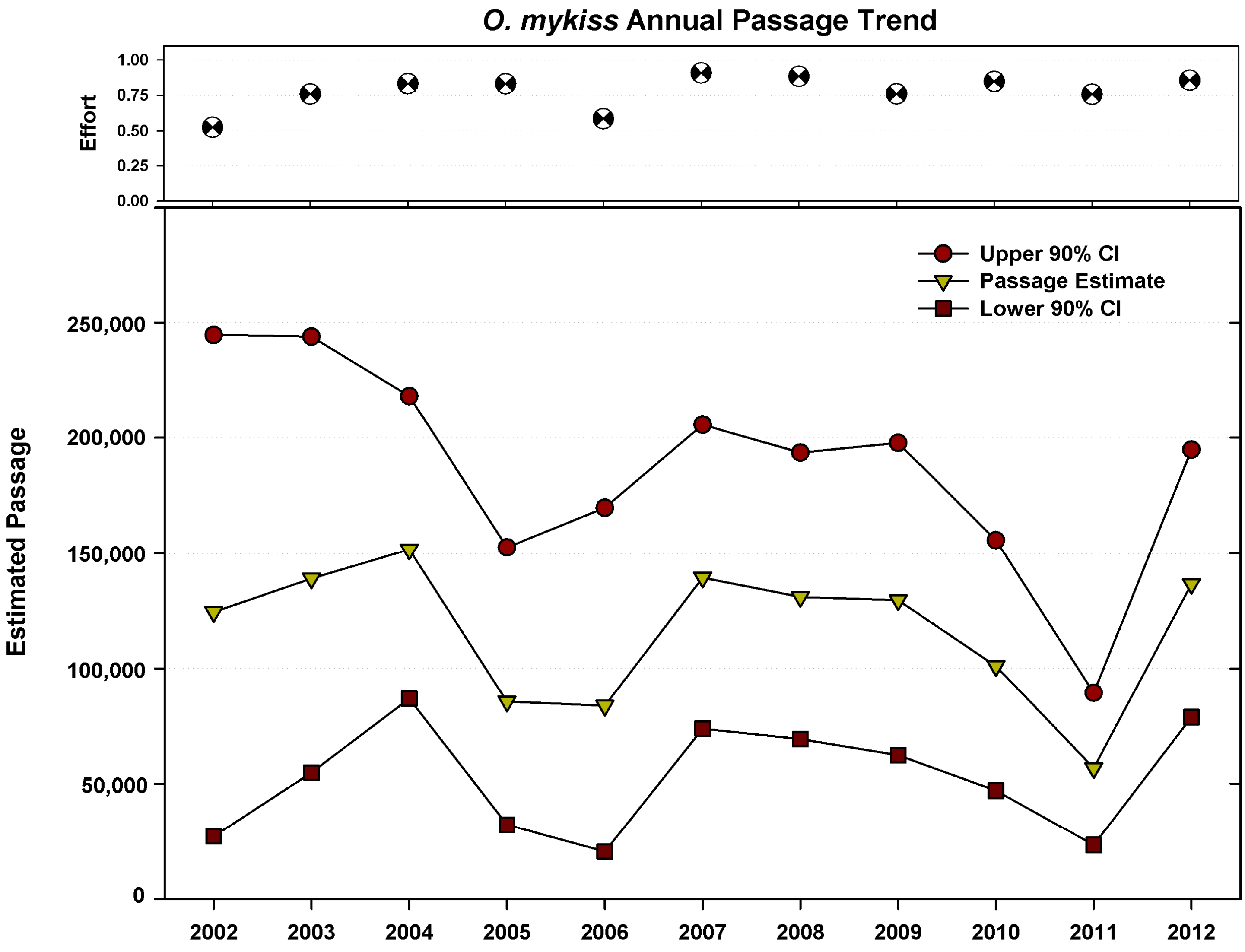

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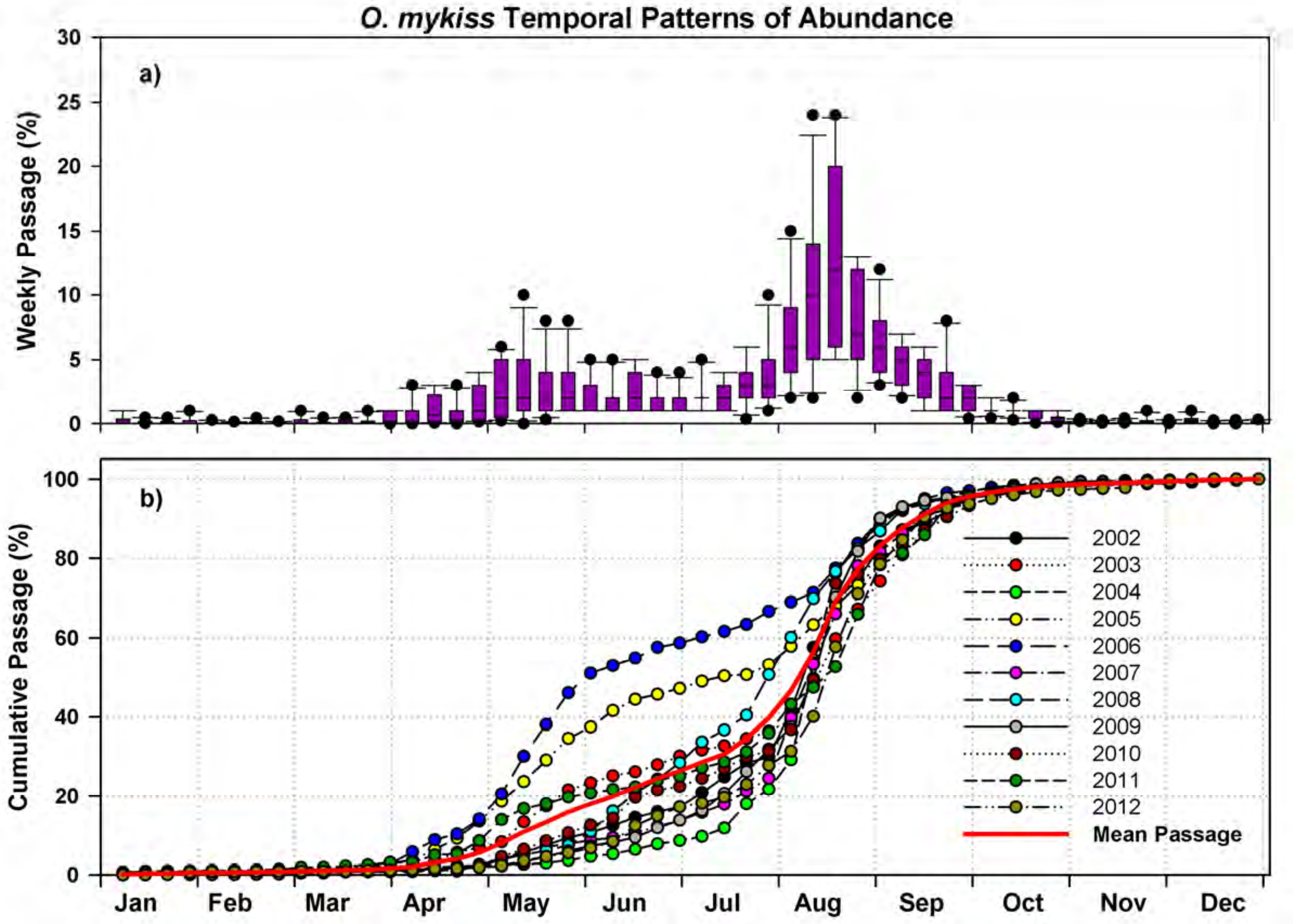

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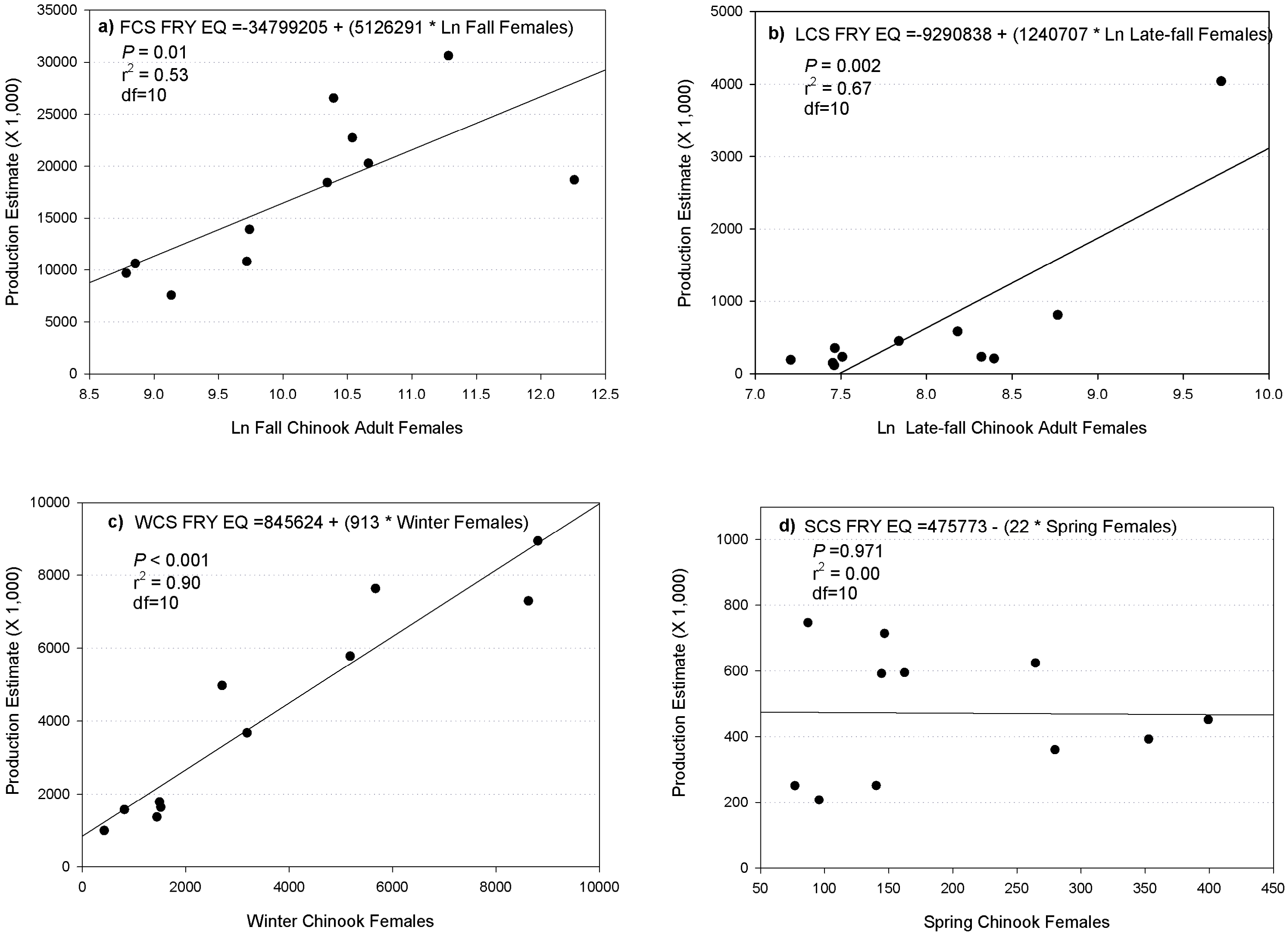

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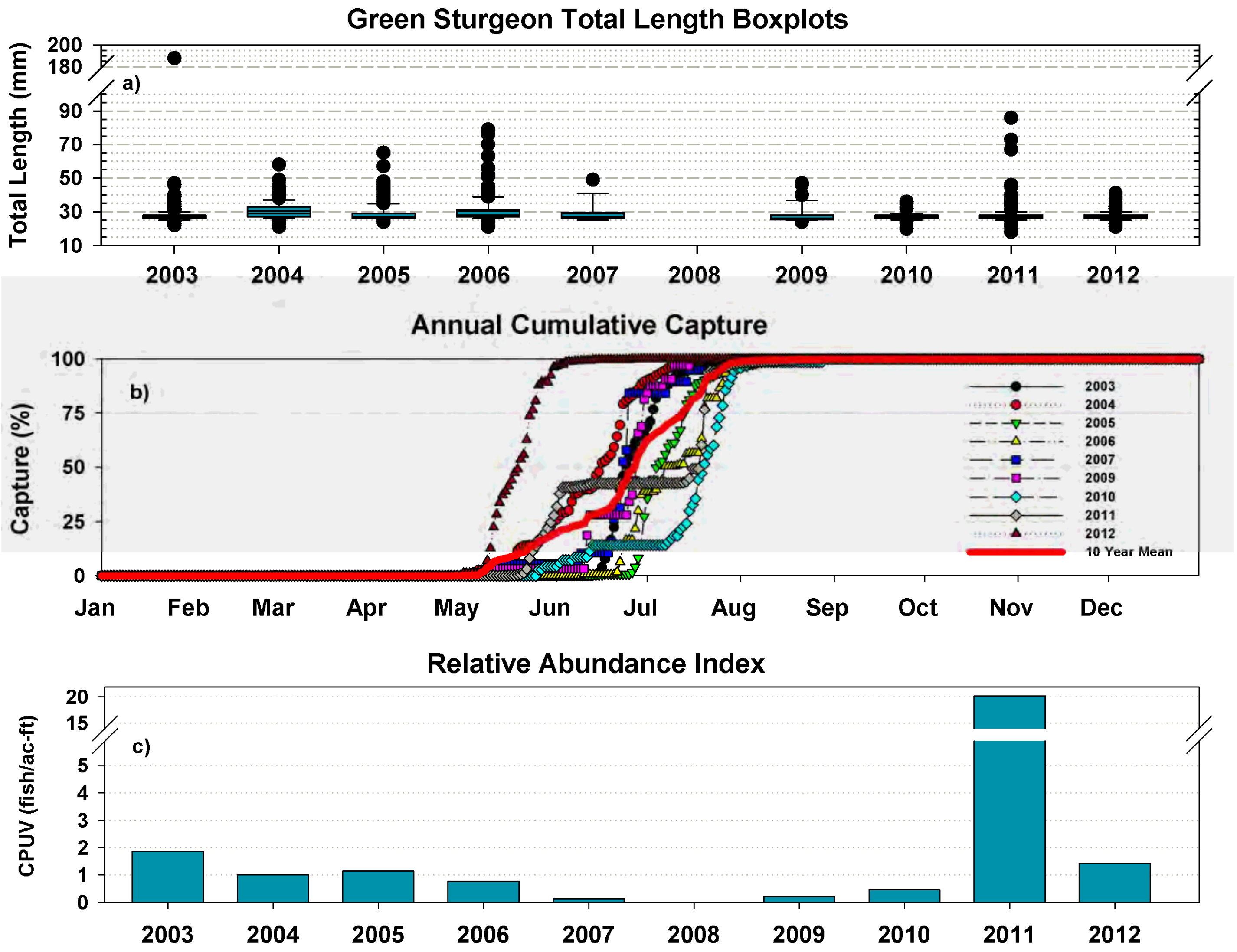

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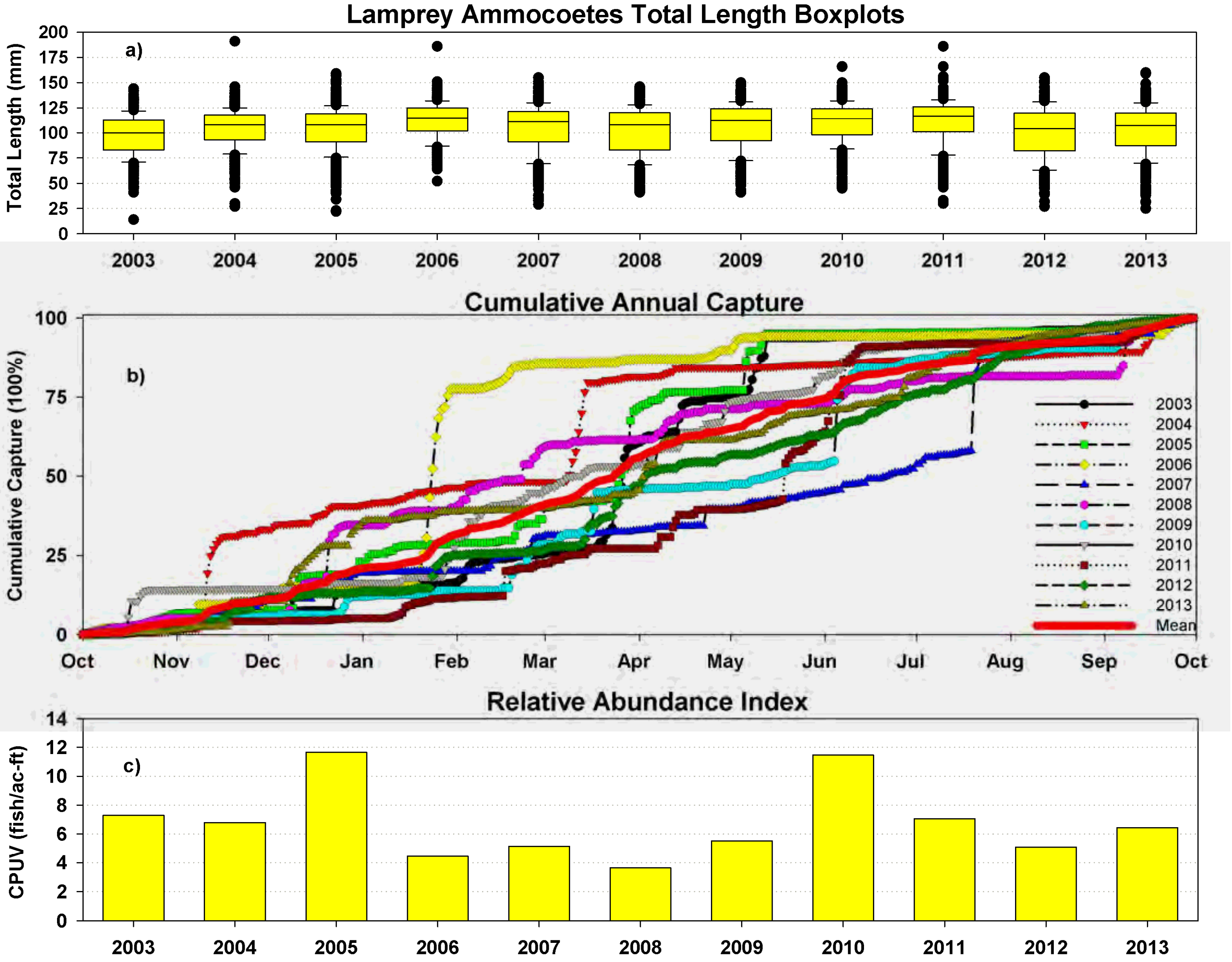

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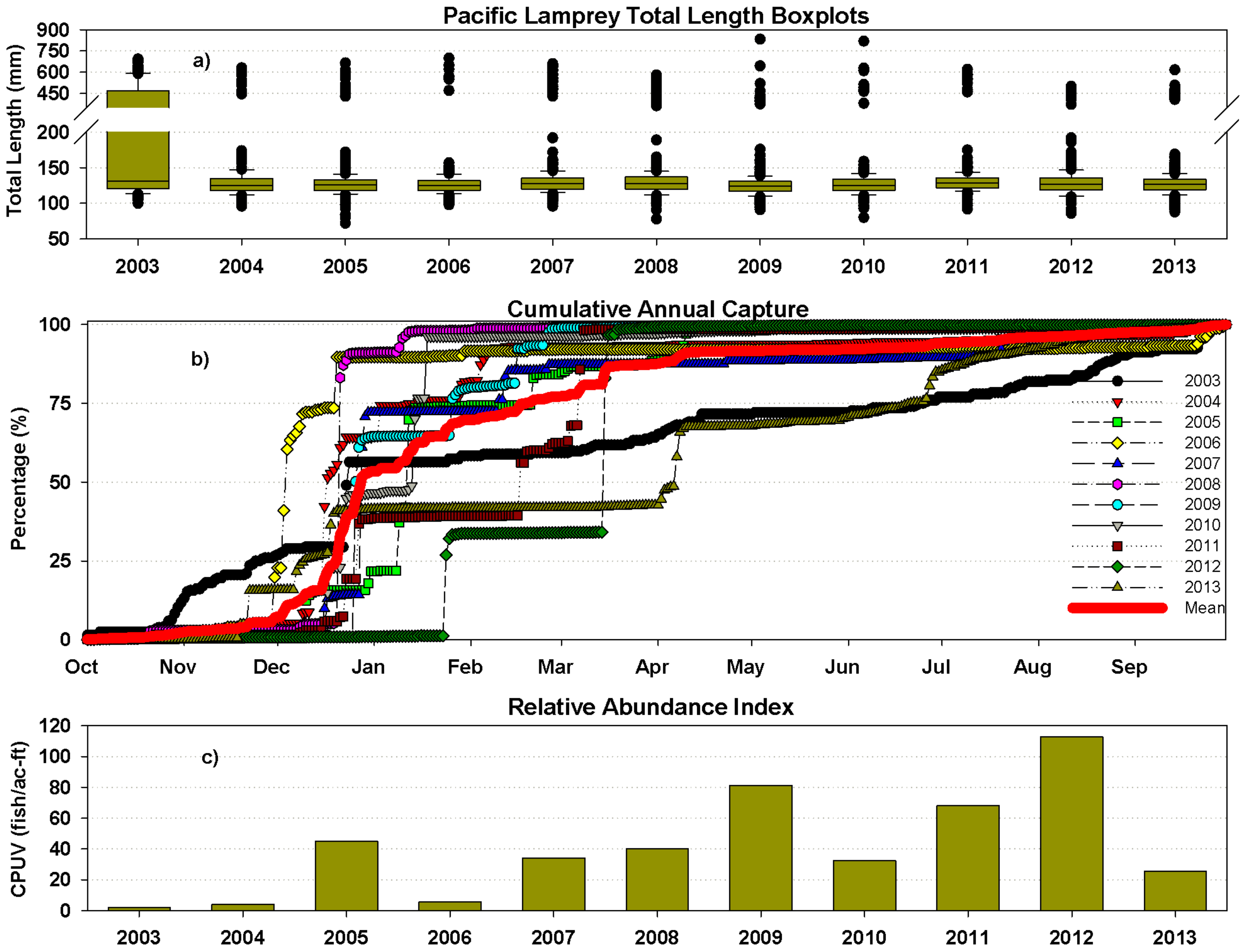

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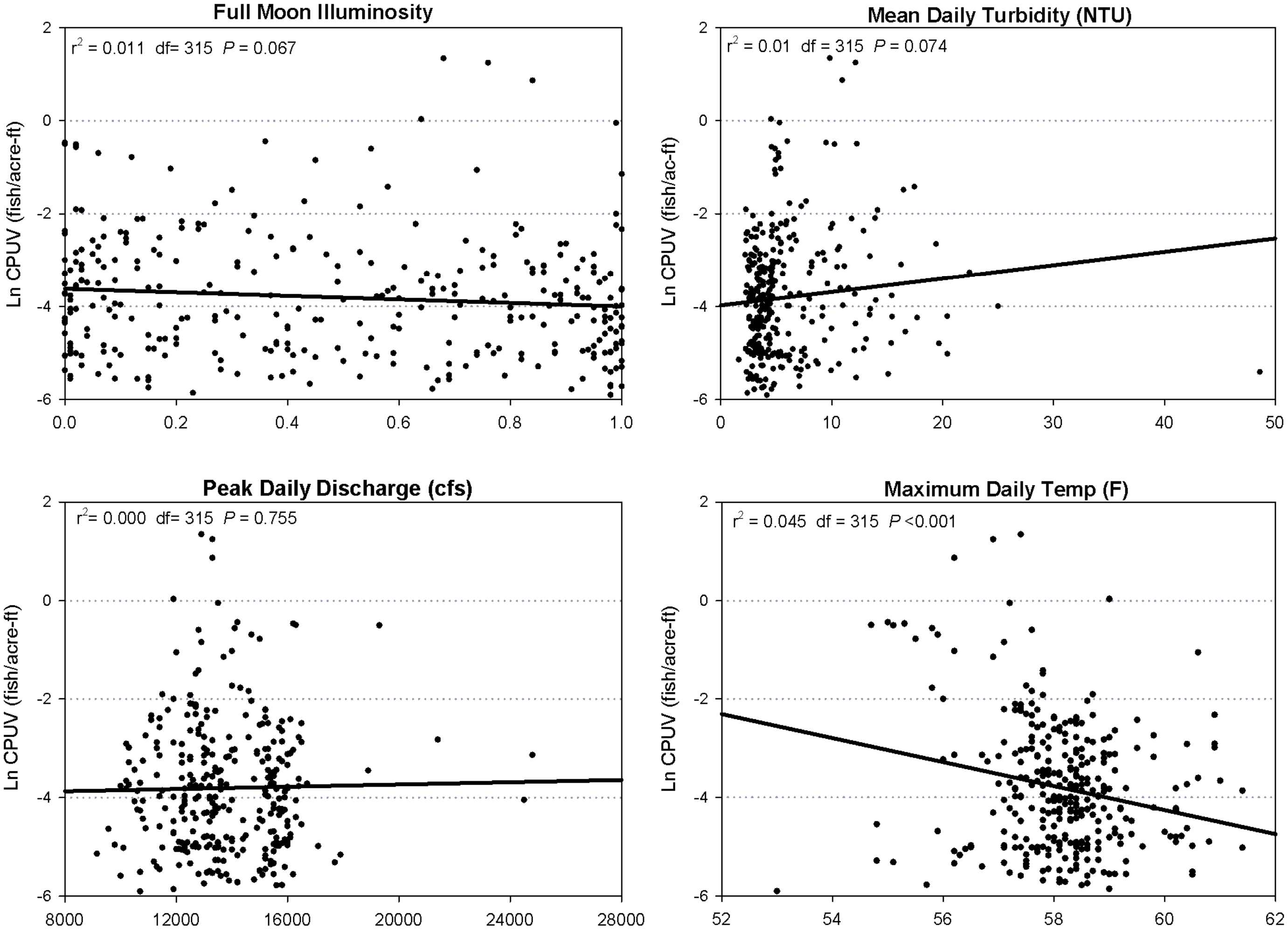
Green Sturgeon Relative Abundance Environmental Covariate Analyses



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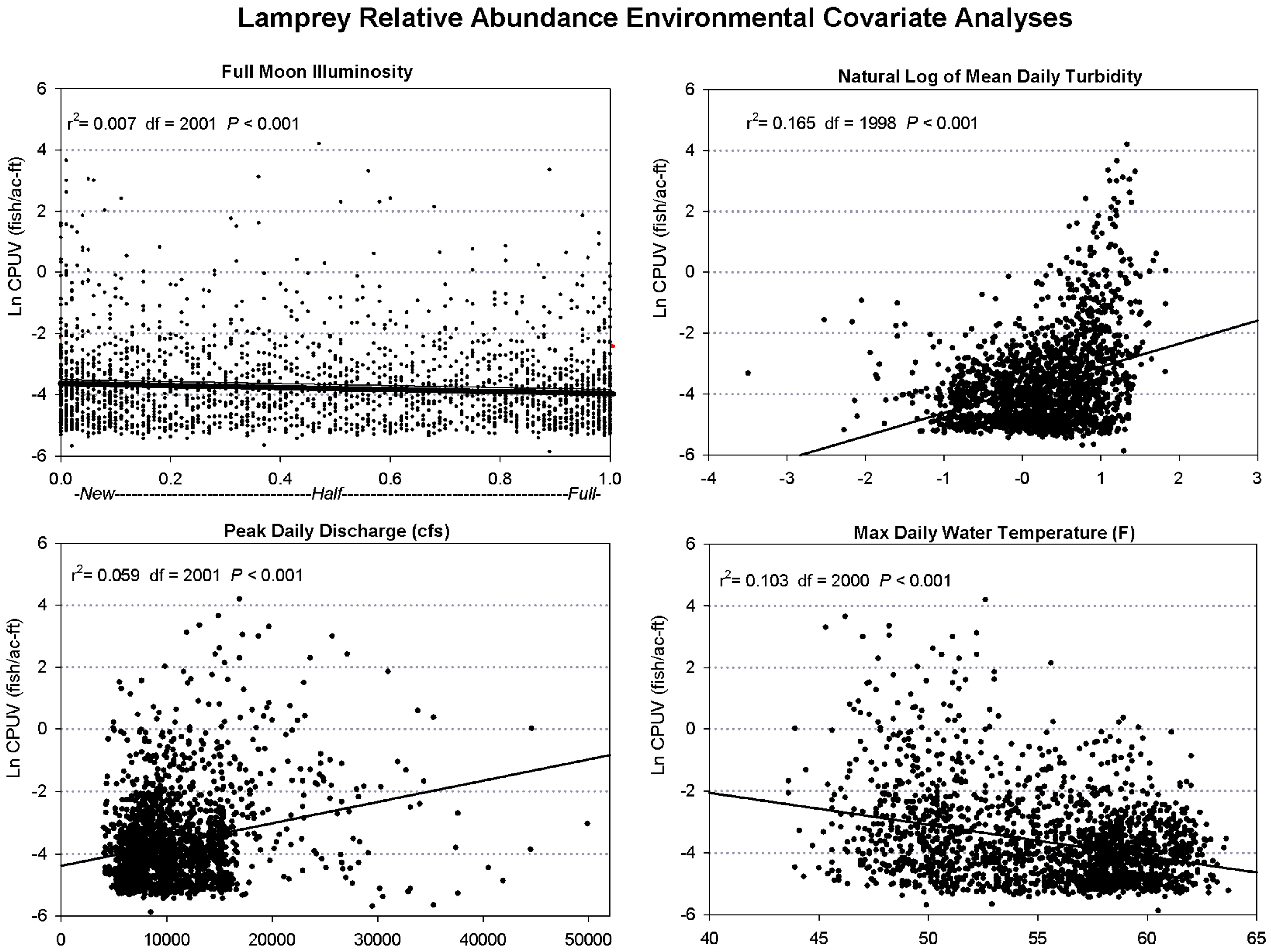

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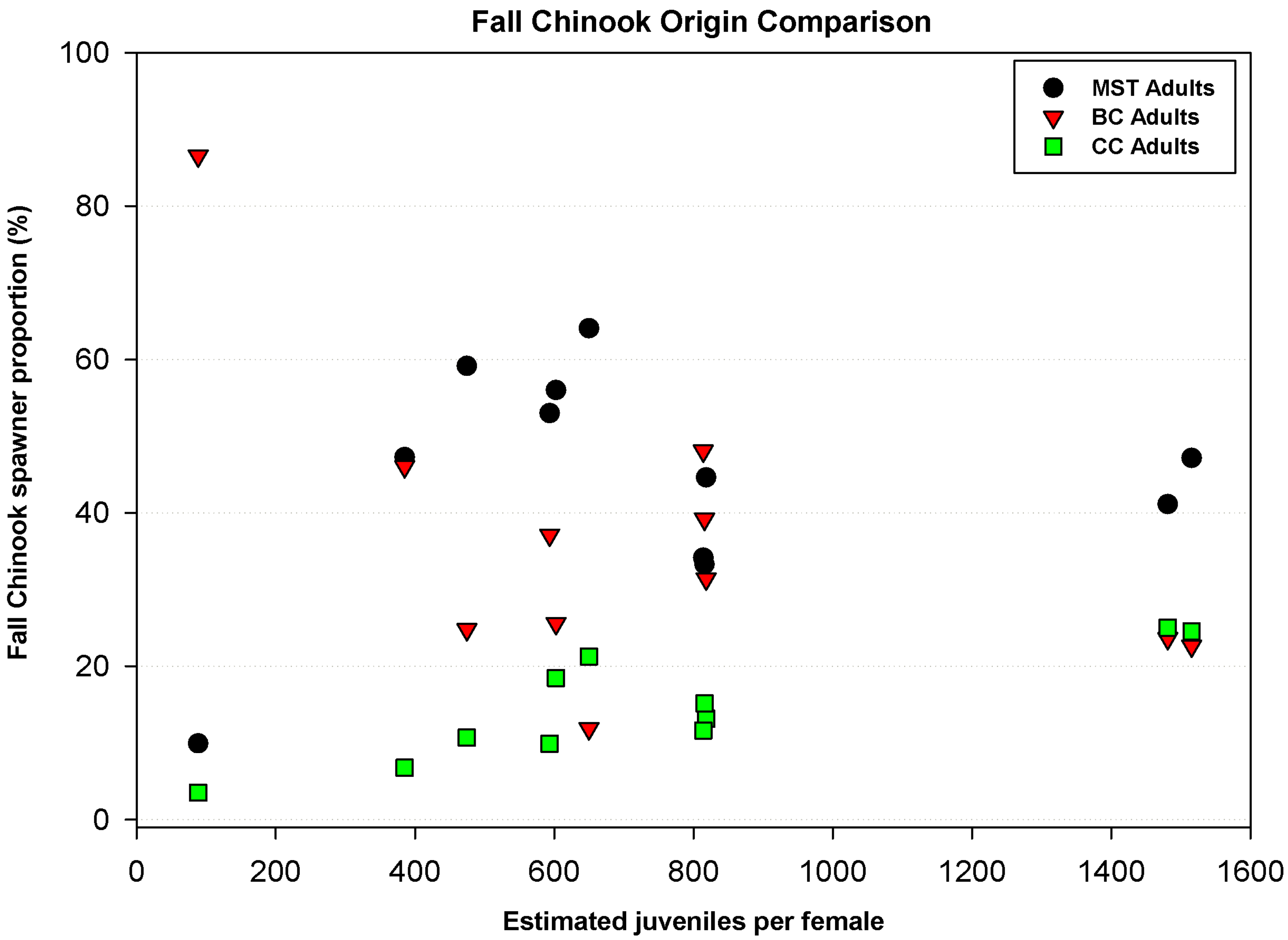

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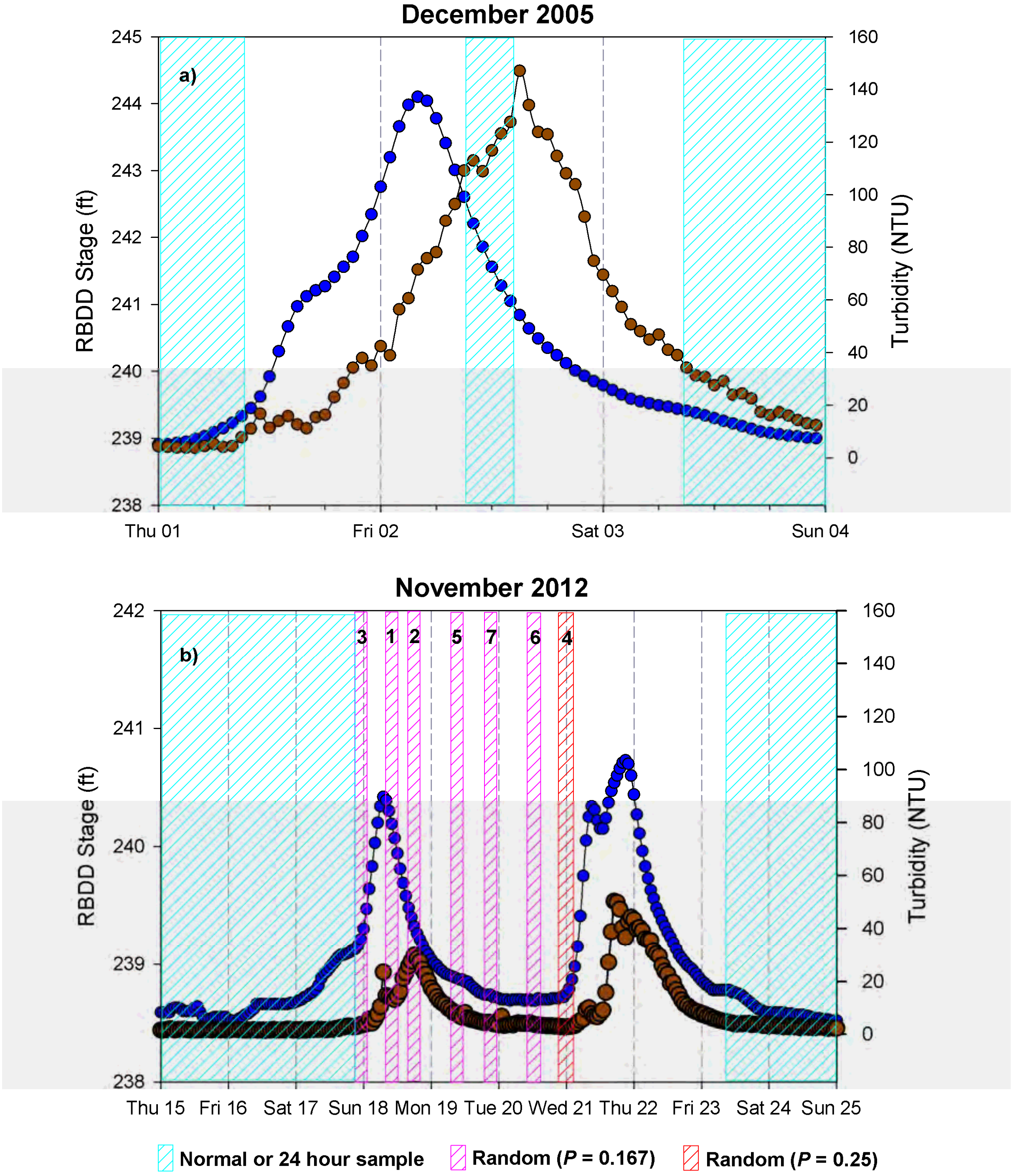

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Fall Chinook

Table A1. Summary of RBDD rotary trap annual effort, fall Chinook fry (<46 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period December 2002 through September 2013.

Brood Year	Effort	Estimated Fry Passage	Low 90% CI	Up 90% CI
2002	0.76	14,687,984	348,386	42,027,818
2003	0.81	23,612,094	6,953,966	44,283,689
2004	0.85	7,946,496	3,449,094	12,447,378
2005	0.56	11,740,225	2,452,034	24,687,255
2006	0.90	10,152,406	3,458,524	17,567,355
2007	0.88	9,594,099	4,834,813	14,353,810
2008	0.79	6,684,332	3,335,617	10,033,164
2009	0.84	6,900,302	2,190,210	11,662,489
2010	0.75	6,302,961	3,432,017	9,502,694
2011	0.87	4,437,956	2,380,436	6,498,878
2012	0.85	21,375,192	14,332,396	28,700,826

Table A2. Summary of RBDD rotary trap annual effort, fall Chinook pre-smolt/smolt (>45 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period December 2002 through September 2013.

Brood Year	Effort	Estimated Smolt Passage	Low 90% CI	Up 90% CI
2002	0.76	2,350,433	505,837	5,318,021
2003	0.81	4,124,773	1,879,521	6,393,281
2004	0.85	6,161,742	1,626,946	12,527,167
2005	0.56	6,470,030	1,041,939	14,426,210
2006	0.90	5,955,245	3,056,683	8,855,302
2007	0.88	2,537,504	1,291,848	3,821,912
2008	0.79	2,431,215	1,034,851	3,827,754
2009	0.84	1,632,074	868,002	2,396,298
2010	0.75	2,539,519	1,288,830	3,850,851
2011	0.87	1,833,305	1,029,403	2,637,509
2012	0.85	3,054,227	1,692,494	4,416,322

Late-Fall Chinook

Table A3. Summary of RBDD rotary trap annual effort, late-fall Chinook fry (<46 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period April 2002 through March 2013.

Brood Year	Effort	Estimated Fry Passage	Low 90% CI	Up 90% CI
2002	0.57	442,393	84,832	901,368
2003	0.76	196,271	4,562	683,458
2004	0.88	24,382	8,802	40,591
2005	0.73	50,274	5,723	175,598
2006	0.70	284,999	41,006	634,496
2007	0.90	144,688	54,397	235,201
2008	0.89	10,489	4,347	17,813
2009	0.72	29,568	13,126	46,360
2010	0.86	113,667	26,705	200,935
2011	0.77	69,686	18,487	120,996
2012	0.89	67,479	9,925	136,431

Table A4. Summary of RBDD rotary trap annual effort, late-fall Chinook pre-smolt/smolt (>45 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period April 2002 through March 2013.

Brood Year	Effort	Estimated Smolt Passage	Low 90% CI	Up 90% CI
2002	0.57	2,117,122	569,453	4,093,545
2003	0.76	149,976	72,089	230,841
2004	0.88	122,779	64,498	181,783
2005	0.73	93,407	35,067	160,738
2006	0.70	175,269	82,005	273,572
2007	0.90	390,932	213,642	568,595
2008	0.89	81,506	41,983	121,166
2009	0.72	190,256	83,201	297,652
2010	0.86	69,771	33,929	106,575
2011	0.77	27,354	9,535	45,914
2012	0.89	73,055	32,567	113,633

Winter Chinook

Table A5. Summary of RBDD rotary trap annual effort, winter Chinook fry (<46 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period July 2002 through June 2013.

Brood Year	Effort	Estimated Fry Passage	Low 90% CI	Up 90% CI
2002	0.64	6,381,286	2,156,758	11,217,962
2003	0.81	4,420,296	2,743,637	6,096,955
2004	0.84	3,087,102	1,812,619	4,361,584
2005	0.64	7,533,380	4,225,130	10,841,630
2006	0.83	5,813,140	3,307,323	8,318,957
2007	0.89	1,158,791	744,804	1,572,817
2008	0.87	1,063,919	662,381	1,465,748
2009	0.75	3,587,134	2,076,422	5,098,125
2010	0.81	875,049	603,549	1,146,644
2011	0.82	638,056	441,983	834,289
2012	0.89	722,048	545,751	898,345

Table A6. Summary of RBDD rotary trap annual effort, winter Chinook pre-smolt/smolt (>45 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period July 2002 through June 2013.

Brood Year	Effort	Estimated Smolt Passage	Low 90% CI	Up 90% CI
2002	0.64	737,755	373,538	1,149,079
2003	0.81	800,719	453,256	1,169,559
2004	0.84	347,581	179,502	519,265
2005	0.64	829,302	324,860	1,442,763
2006	0.83	873,940	487,244	1,264,701
2007	0.89	281,773	180,254	387,123
2008	0.87	181,071	110,592	252,089
2009	0.75	815,188	410,512	1,222,586
2010	0.81	410,341	210,252	613,810
2011	0.82	210,920	130,861	291,312
2012	0.89	627,771	354,764	900,897

Spring Chinook

Table A7. Summary of RBDD rotary trap annual effort, spring Chinook fry (<46 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period October 2002 through September 2013.

Brood Year	Effort	Estimated Fry Passage	Low 90% CI	Up 90% CI
2002	0.75	159,084	67,900	255,023
2003	0.81	502,386	189,371	857,899
2004	0.85	155,053	59,655	250,451
2005	0.57	427,719	111,396	925,898
2006	0.89	174,186	114,642	233,907
2007	0.89	336,714	212,765	460,712
2008	0.85	40,213	26,016	54,448
2009	0.79	219,627	91,683	347,845
2010	0.77	89,213	39,829	138,597
2011	0.86	88,355	63,469	113,274
2012	0.86	134,028	82,843	185,271

Table A8. Summary of RBDD rotary trap annual effort, spring Chinook pre-smolt/smolt (>45 mm FL) passage estimates and lower and upper 90% confidence intervals (CI), by brood year for the period October 2002 through September 2013.

Brood Year	Effort	Estimated Smolt Passage	Low 90% CI	Up 90% CI
2002	0.75	118,393	43,022	239,870
2003	0.81	124,529	59,434	197,777
2004	0.85	275,898	113,564	460,990
2005	0.57	187,828	19,676	460,441
2006	0.89	247,250	123,621	371,968
2007	0.89	32,787	15,894	51,271
2008	0.85	124,460	40,130	208,954
2009	0.79	218,778	83,930	354,607
2010	0.77	69,753	21,938	123,577
2011	0.86	95,935	37,782	159,702
2012	0.86	186,869	89,566	284,936

Table A9. River Lamprey, *Lampetra ayresi*, annual capture, catch per unit volume (CPUV) and total length summaries for River Lamprey captured by RBDD rotary traps between water year (WY) 2003 and 2013.

WY	Catch	CPUV Fish/ac-ft	Min TL (mm)	Max TL (mm)	Mean (mm)	Median (mm)
2003	0	0.00	-	-	-	-
2004	1	0.01	102	102	102	-
2005	0	0.00	-	-	-	-
2006	0	0.00	-	-	-	-
2007	0	0.00	-	-	-	-
2008	0	0.00	-	-	-	-
2009	0	0.00	-	-	-	-
2010	1	0.01	110	110	110	-
2011	26	0.23	99	151	121	121
2012	4	0.02	128	168	144	140
2013	0	0.00	-	-	-	-
Mean	2.9	0.02	109.8	132.8	119.3	130.5
SD	7.8	0.07	13.0	31.8	18.2	13.4
CV	266.5%	279.2%	11.9%	24.0%	15.3%	10.3%

Table A10. Pacific Brook Lamprey, *Lampetra pacifica,* annual capture, catch per unit volume (CPUV) and total length summaries for Pacific Brook Lamprey captured by RBDD rotary traps between water year (WY) 2003 and 2013.

WY	Catch	CPUV Fish/ac-ft	Min TL (mm)	Max TL (mm)	Mean (mm)	Median (mm)
2003	6	0.06	98	132	116	114.5
2004	1	0.01	159	159	159	-
2005	0	0.00	-	-	-	-
2006	0	0.00	-	-	-	-
2007	0	0.00	-	-	-	-
2008	0	0.00	-	-	-	-
2009	0	0.00	-	-	-	-
2010	1	0.02	120	120	120	120
2011	1	0.01	147	147	147	147
2012	6	0.04	112	156	138	142
2013	21	0.12	110	148	124	122
Mean	3.3	0.02	124.3	143.7	134.0	129.1
SD	6.3	0.04	23.6	14.9	16.9	14.4
CV	192.8%	159.7%	19.0%	10.4%	12.6%	11.2%

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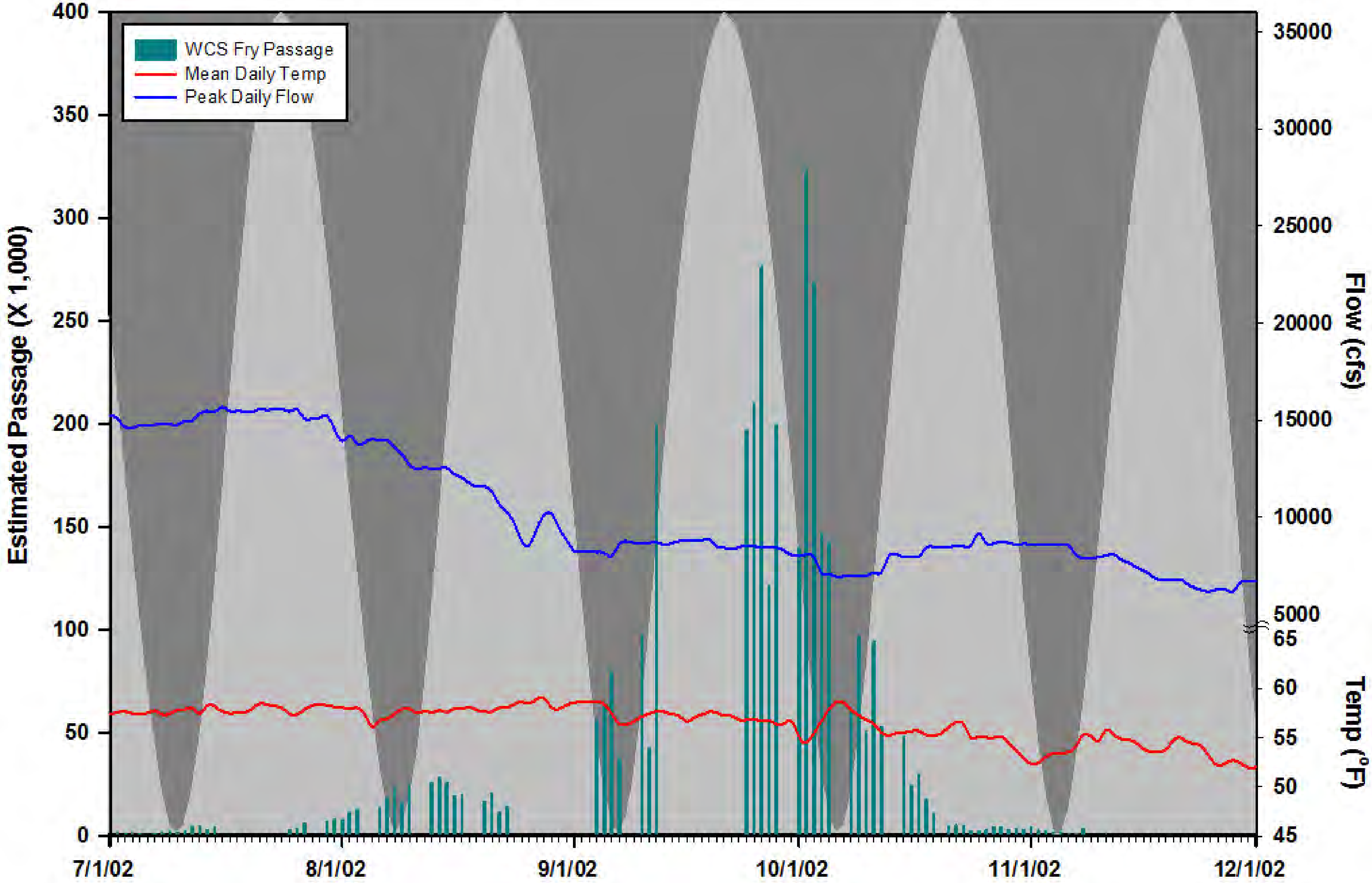

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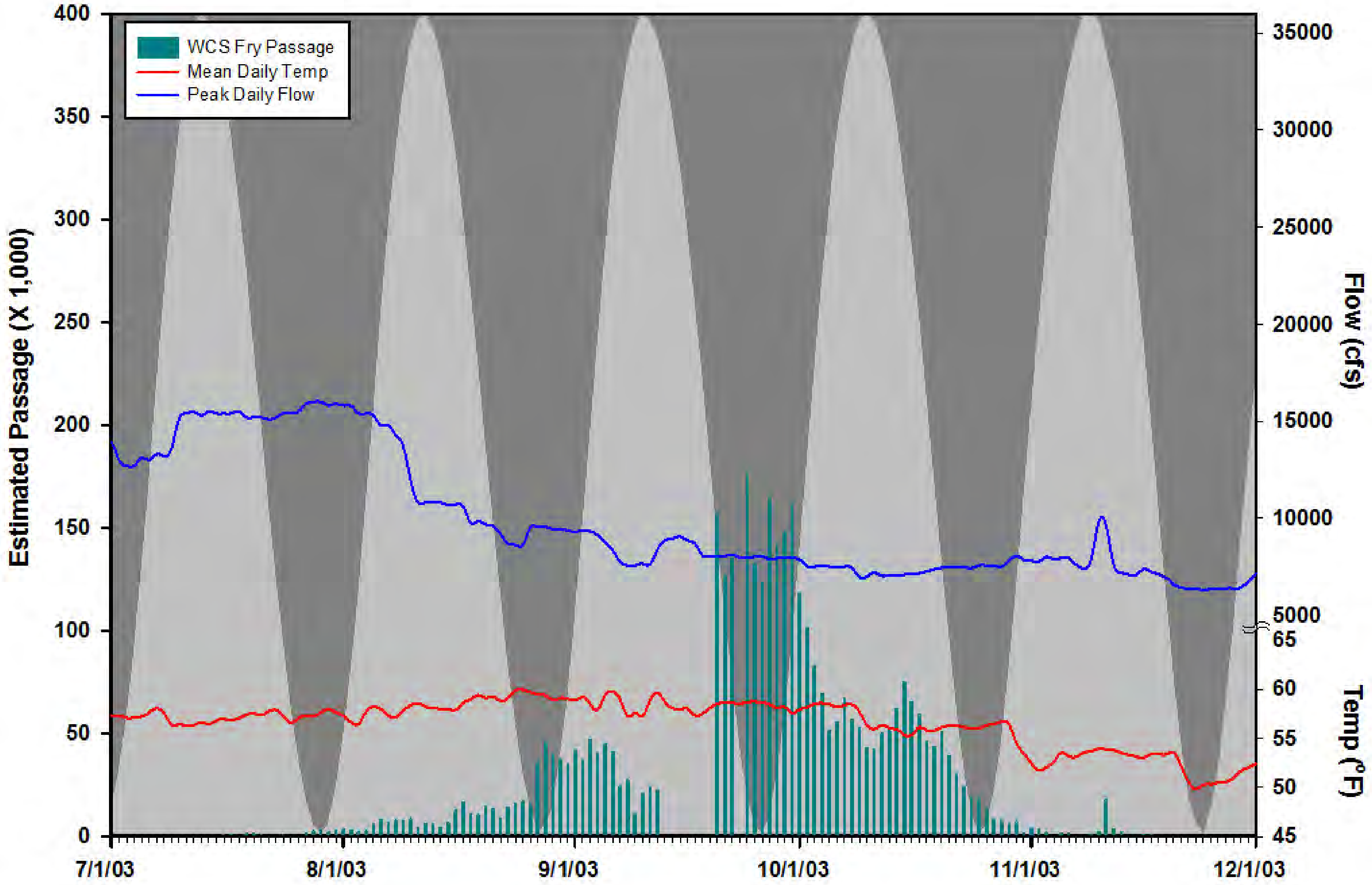


Figure A2. Brood Year 2003 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

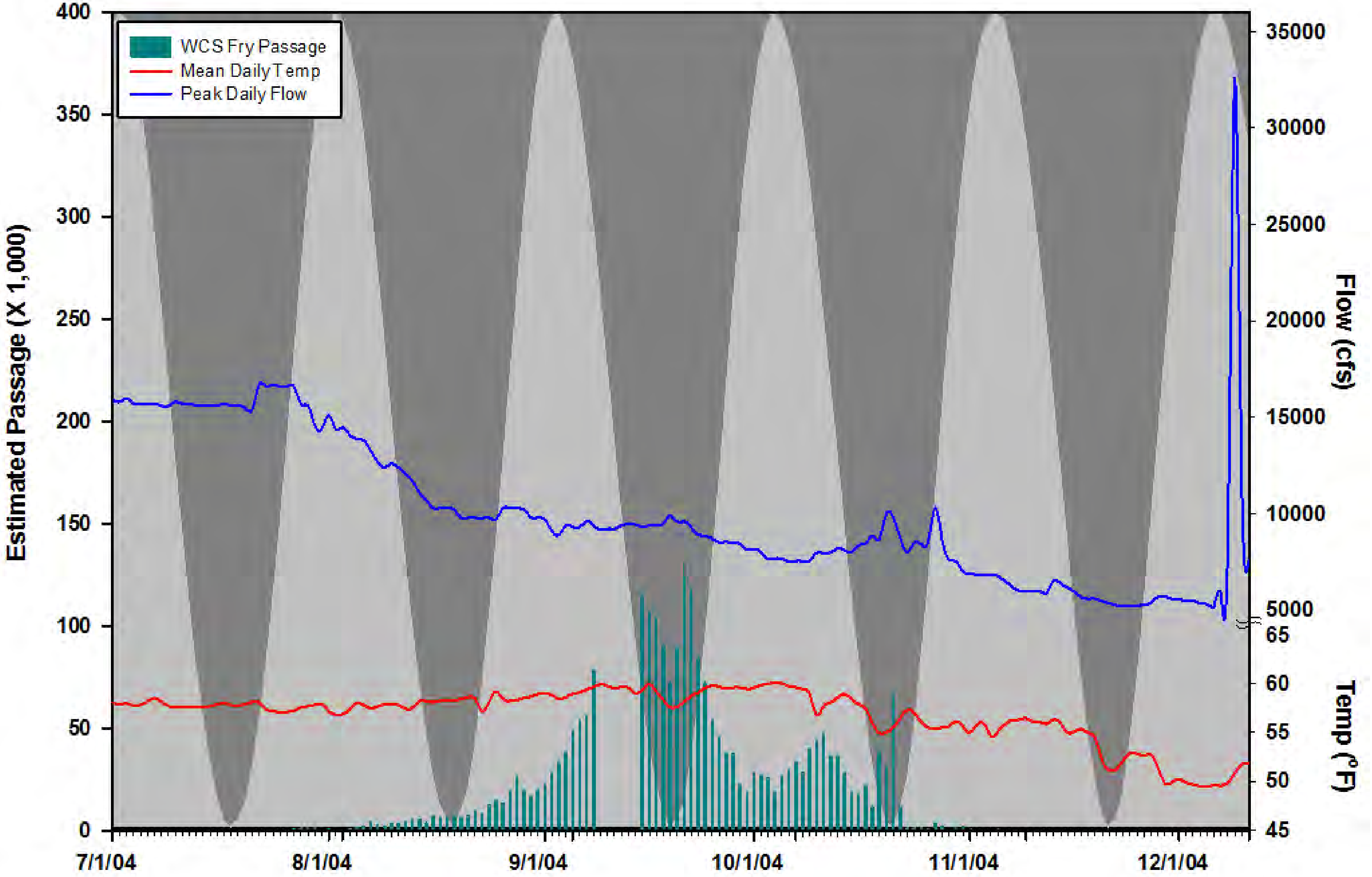
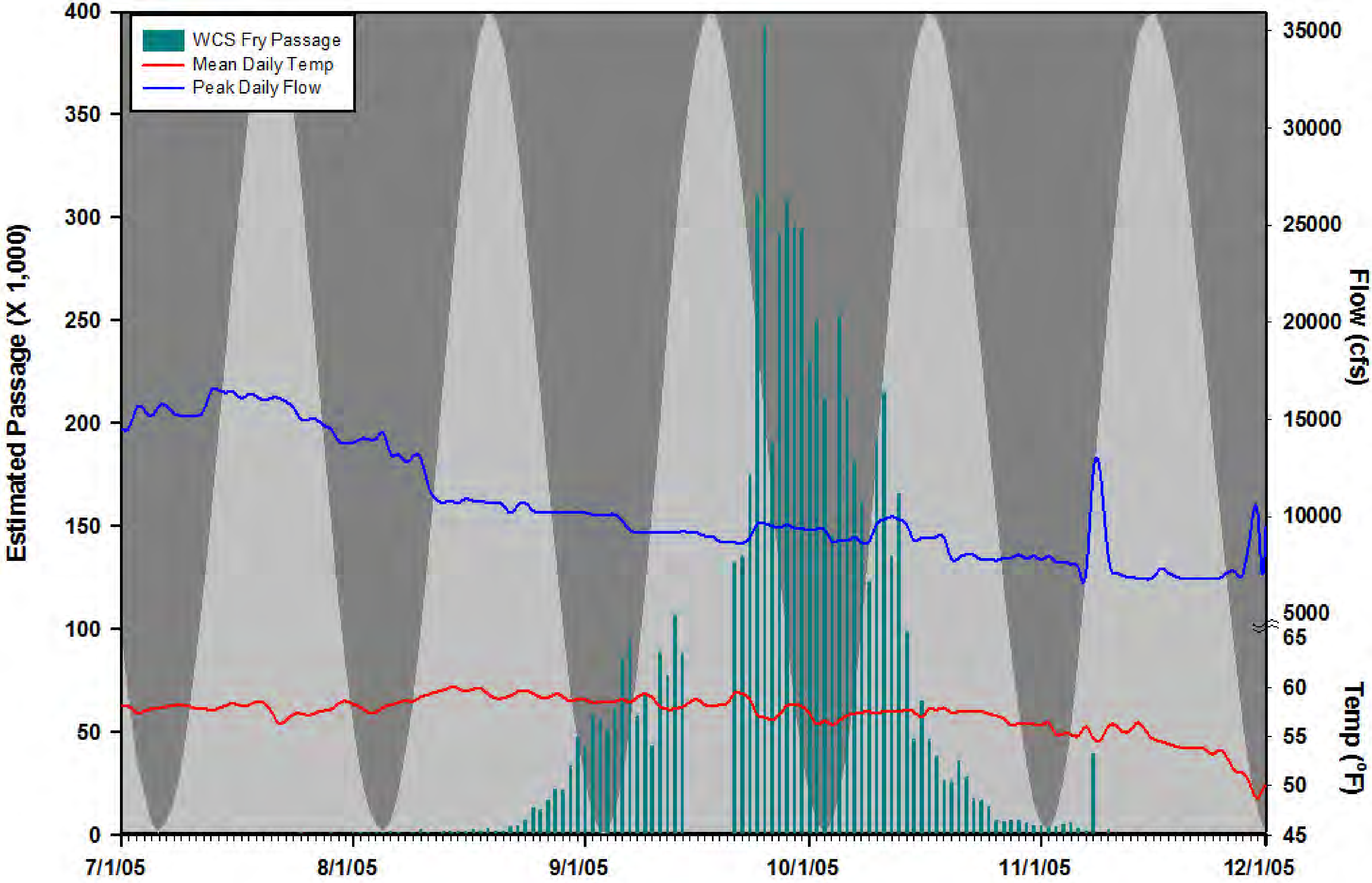


Figure A3. Brood Year 2004 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.



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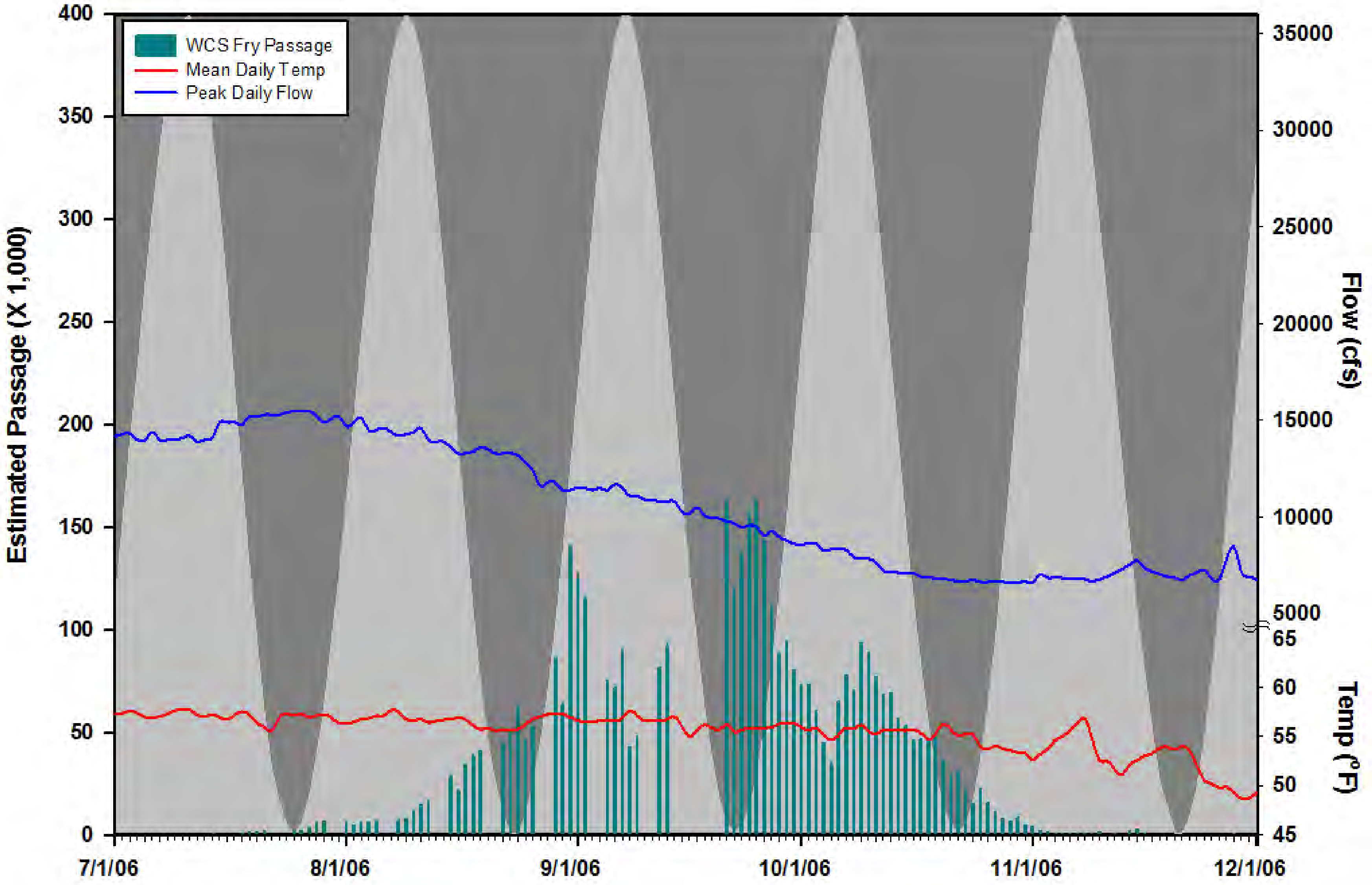

Figure A5. Brood Year 2006 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

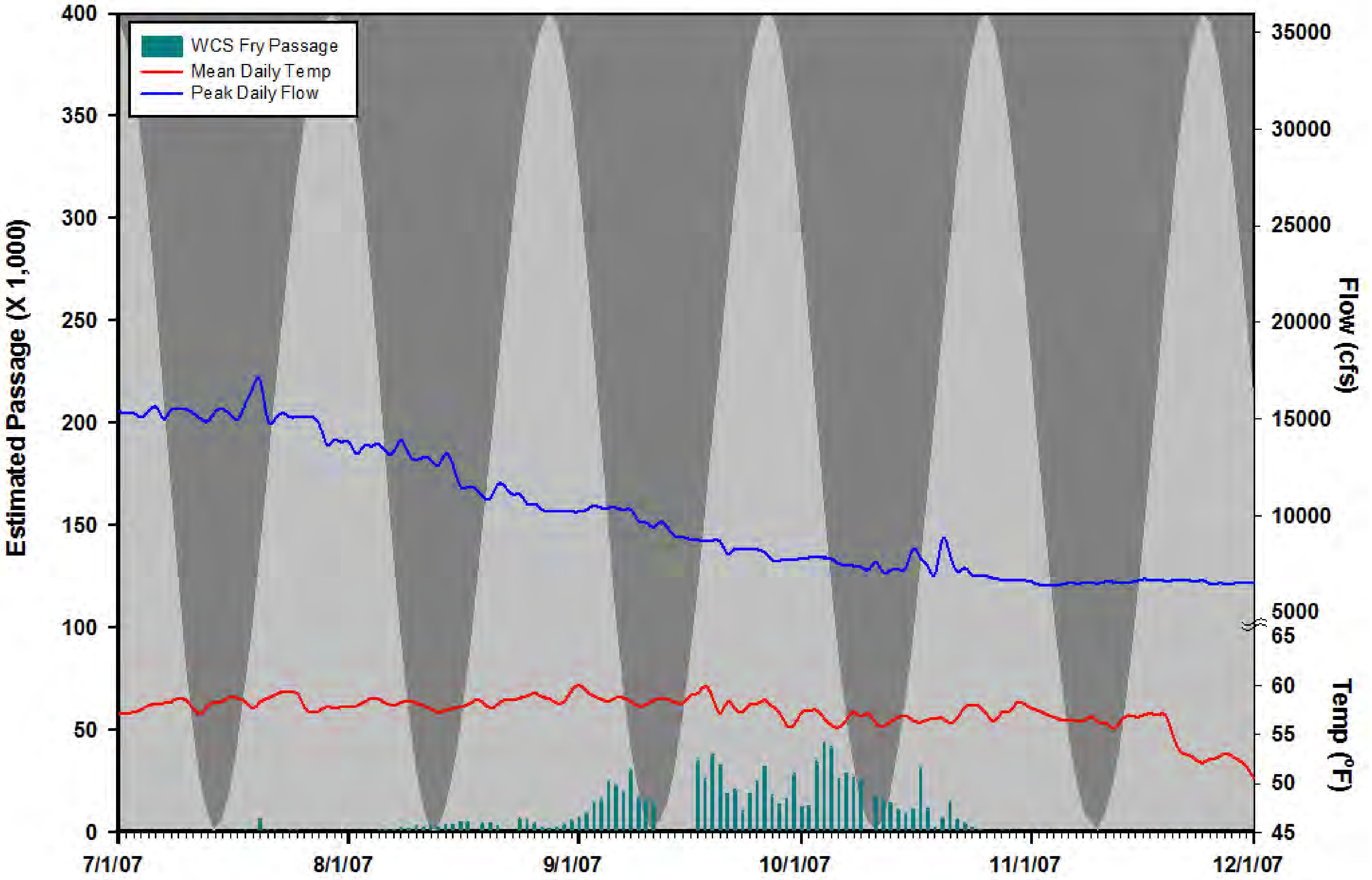

Figure A6. Brood Year 2007 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

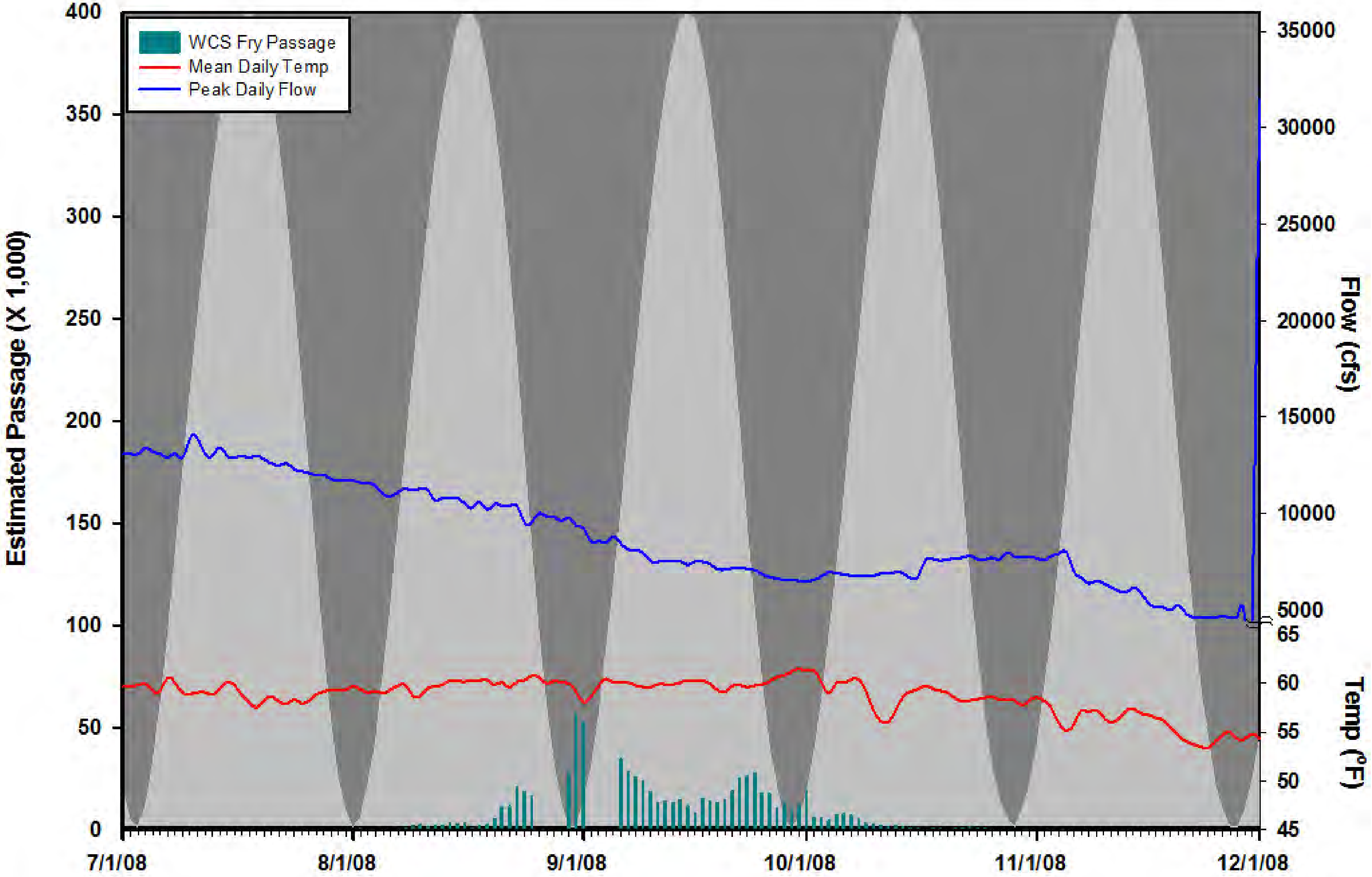

Figure A7. Brood Year 2008 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

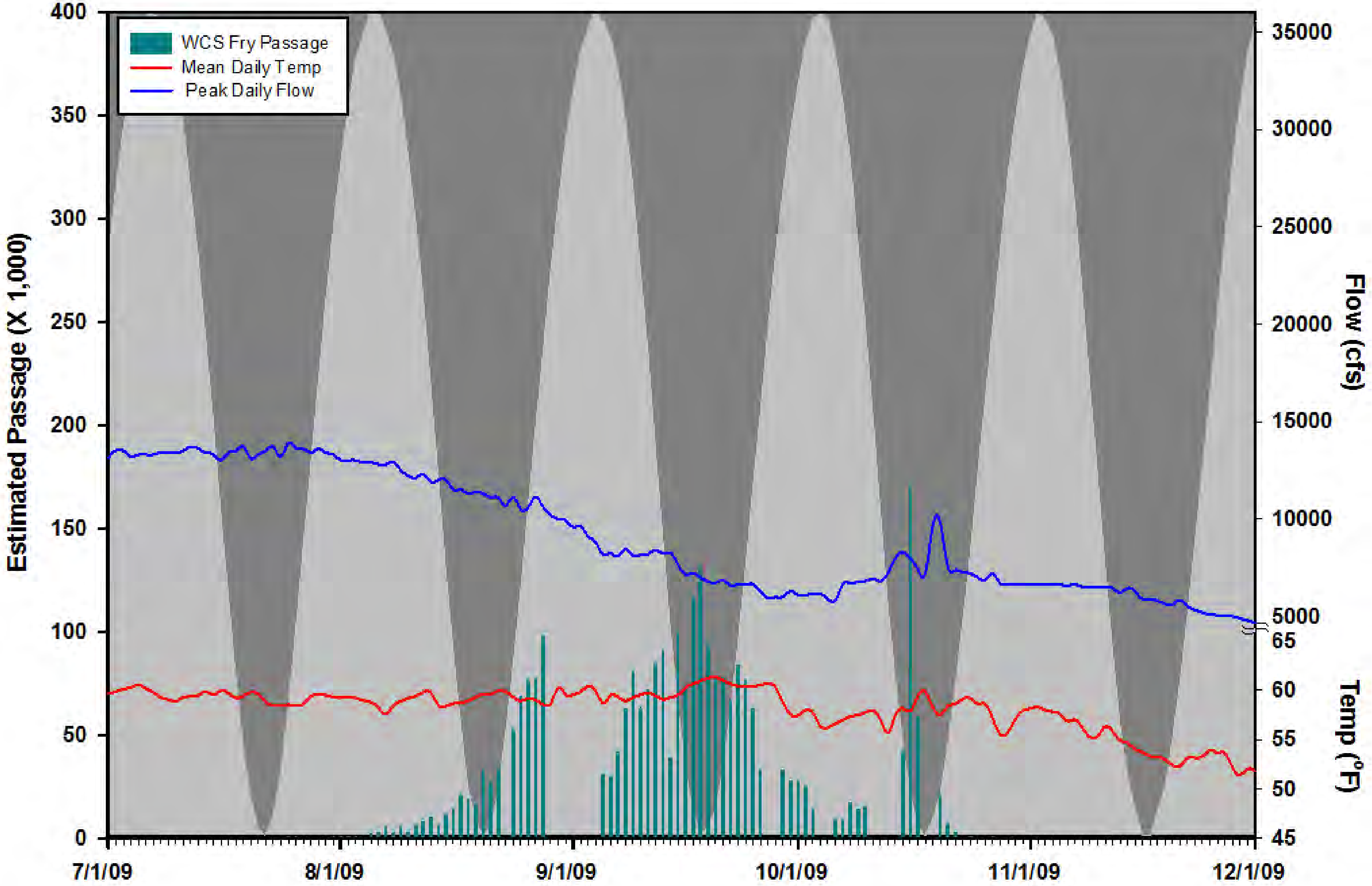

Figure A8. Brood Year 2009 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

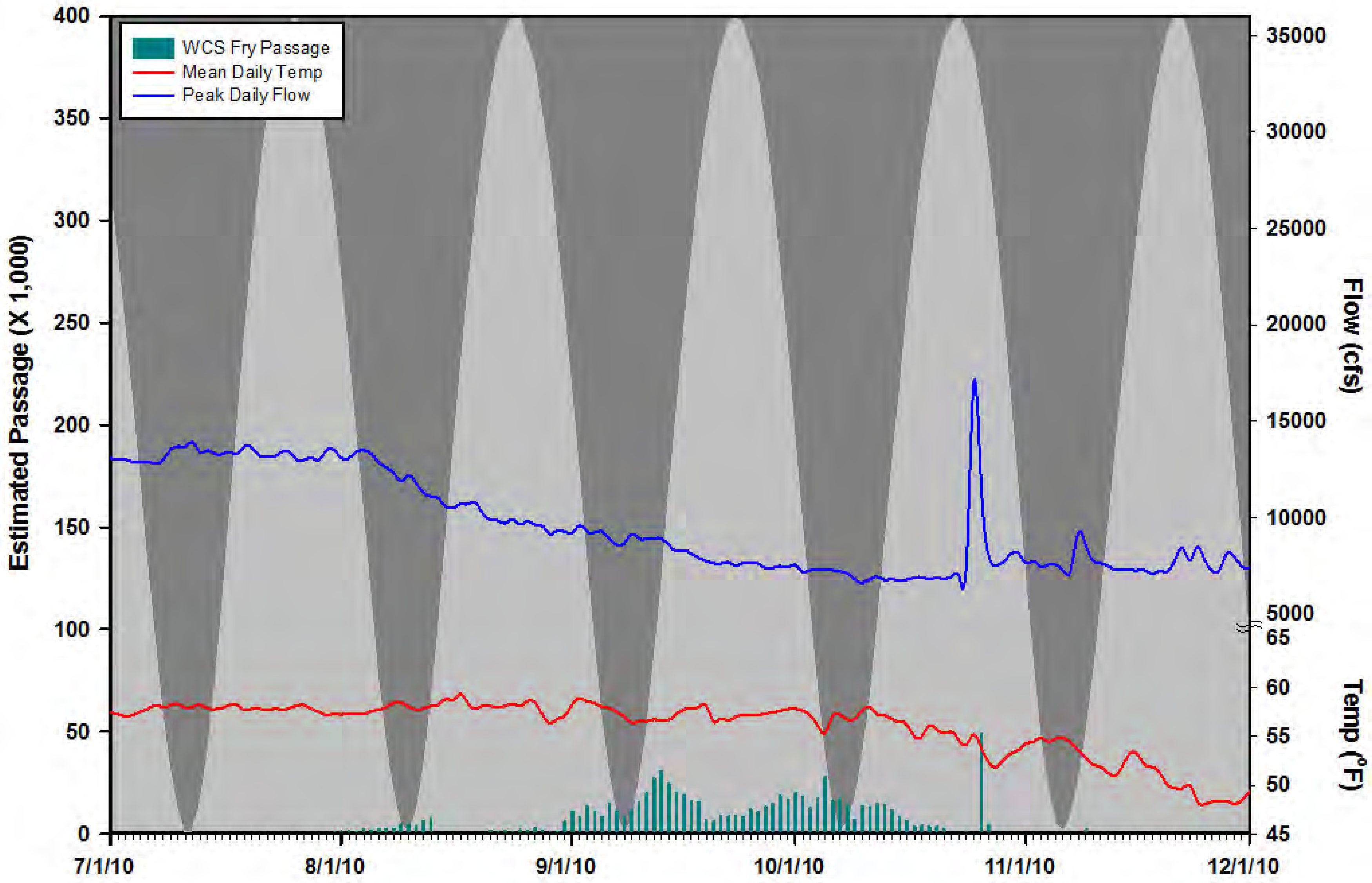

Figure A9. Brood Year 2010 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

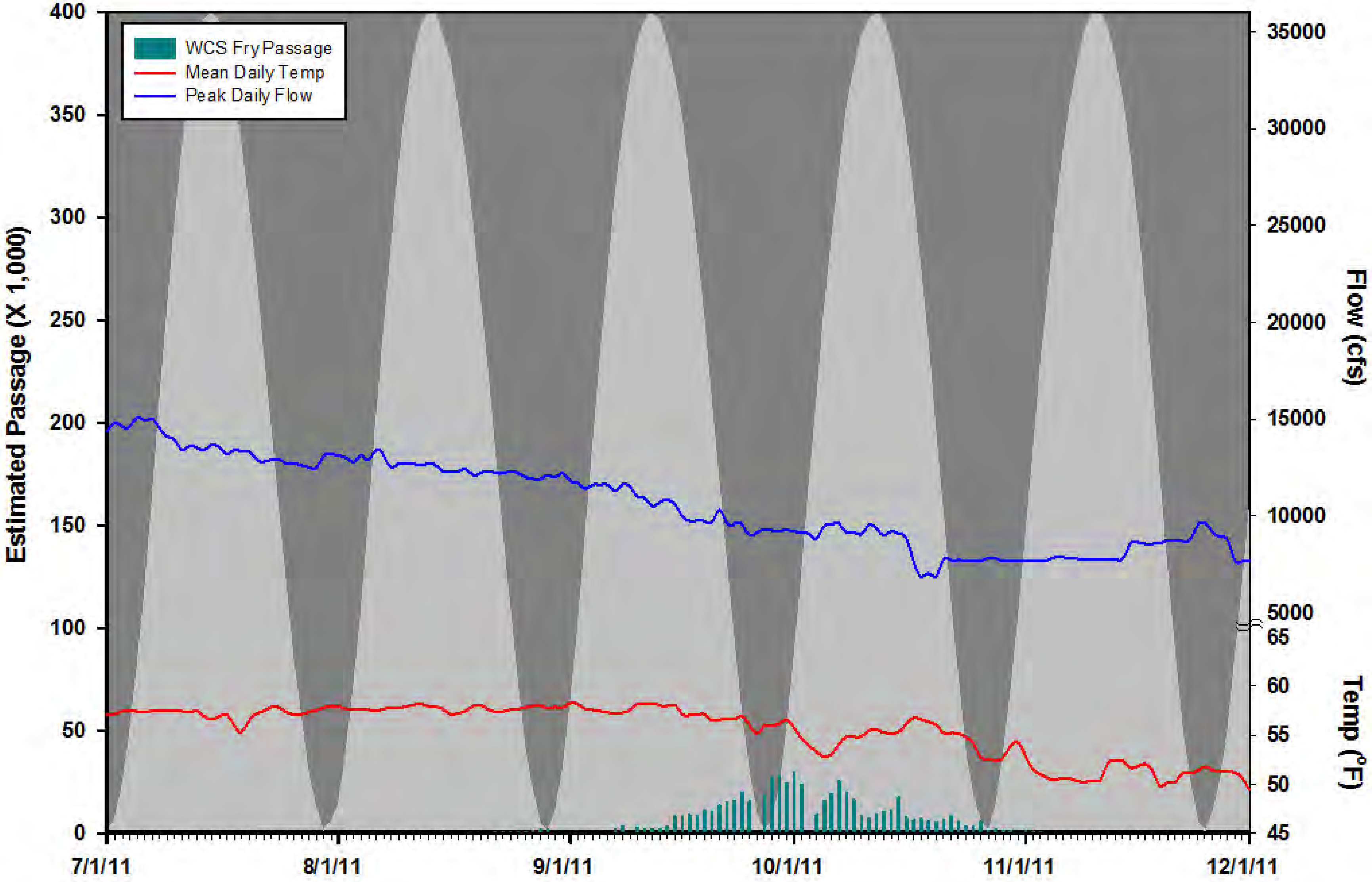

Figure A10. Brood Year 2011 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

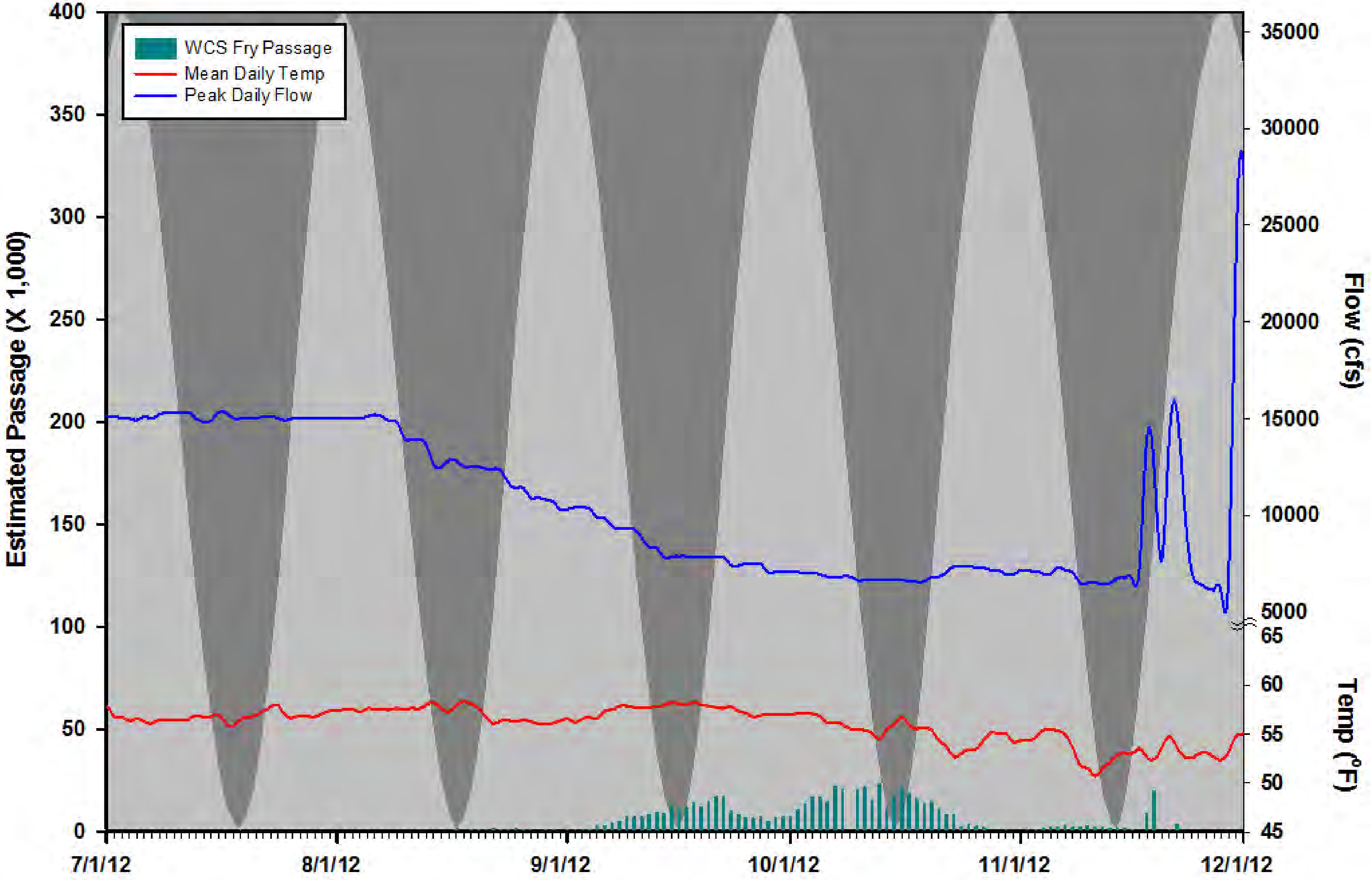

Figure A11. Brood Year 2012 winter Chinook fry passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

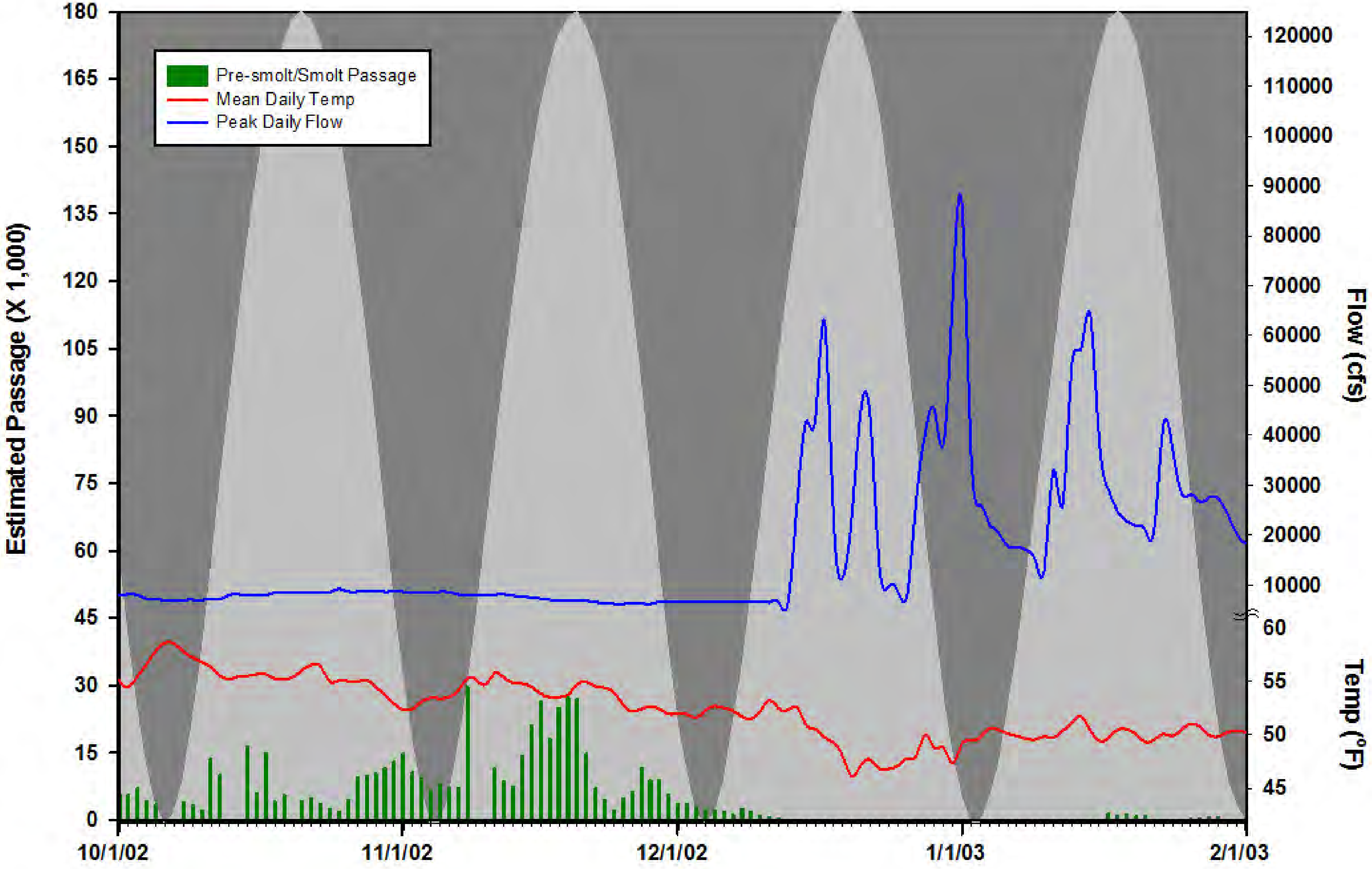

Figure A12. Brood Year 2002 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

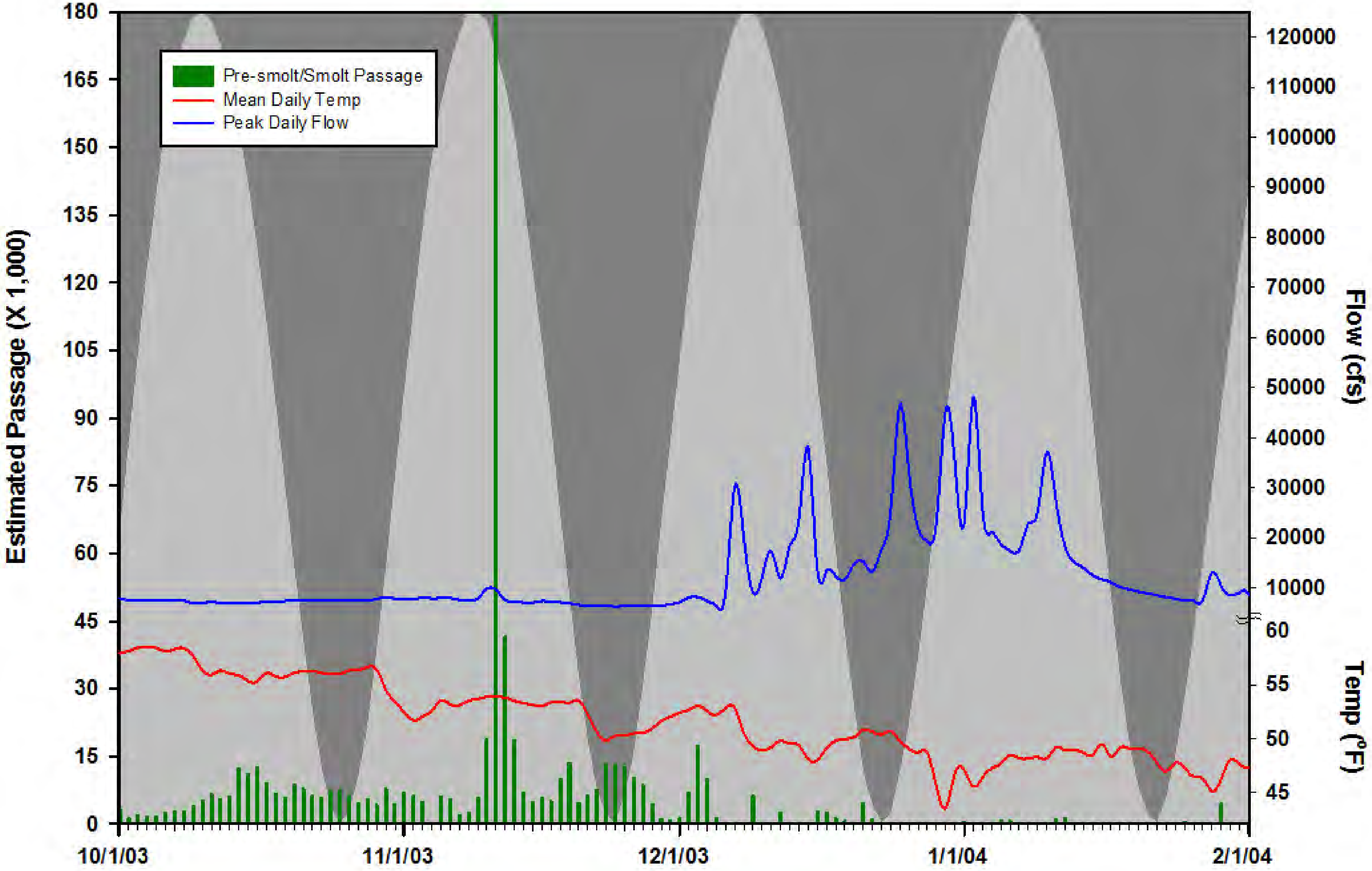

Figure A13. Brood Year 2003 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

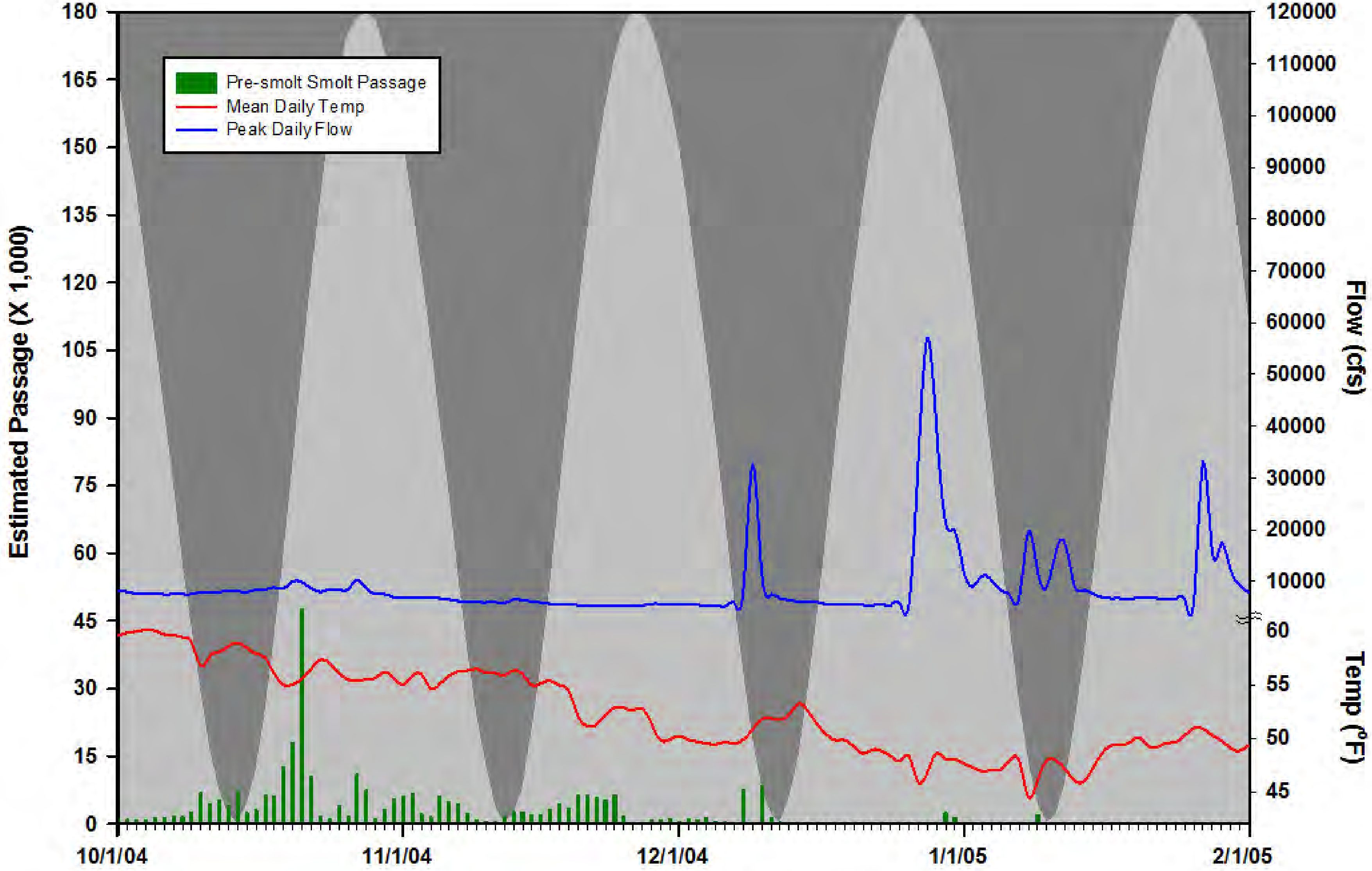

Figure A14. Brood Year 2004 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

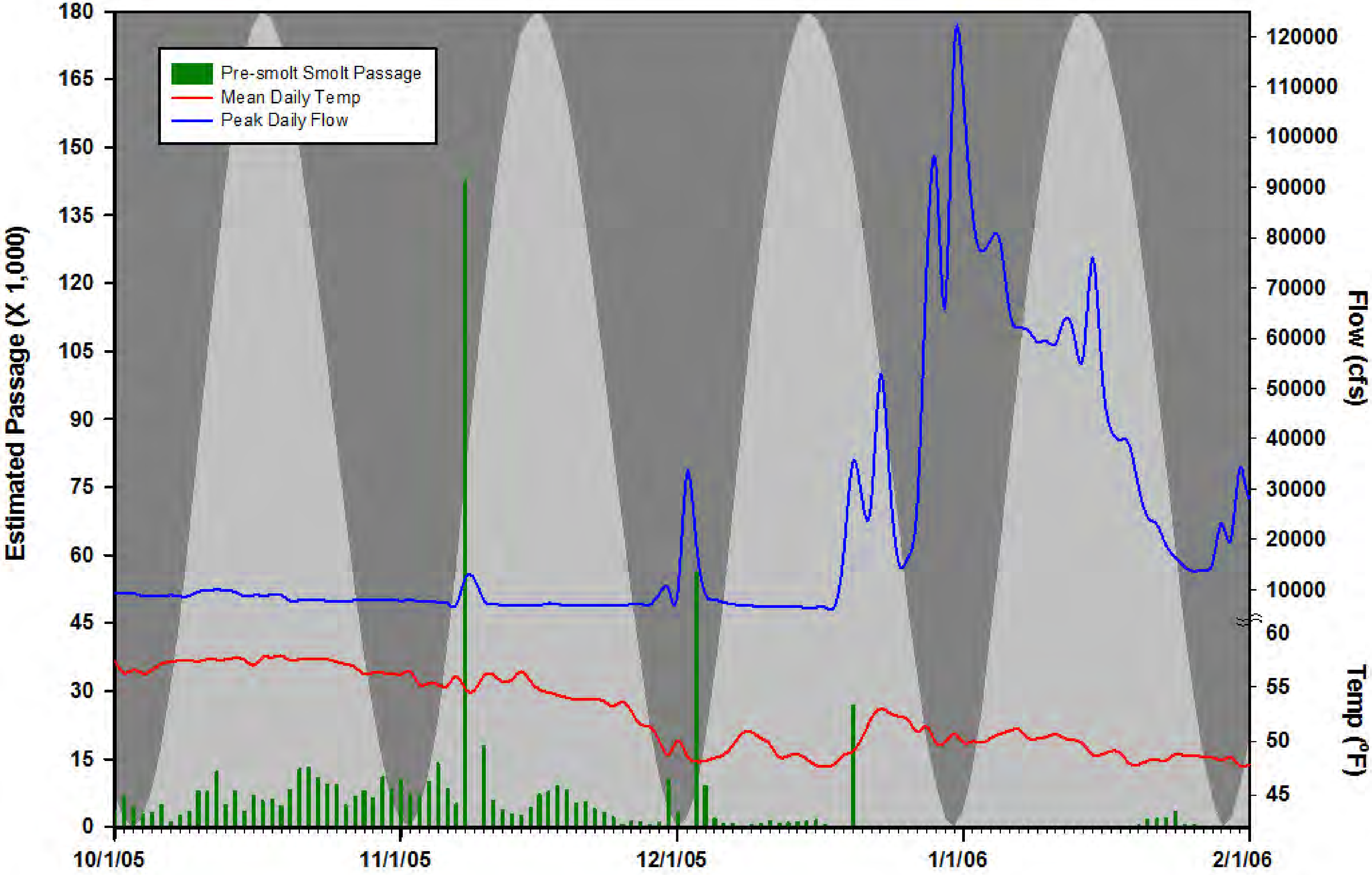

Figure A15. Brood Year 2005 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

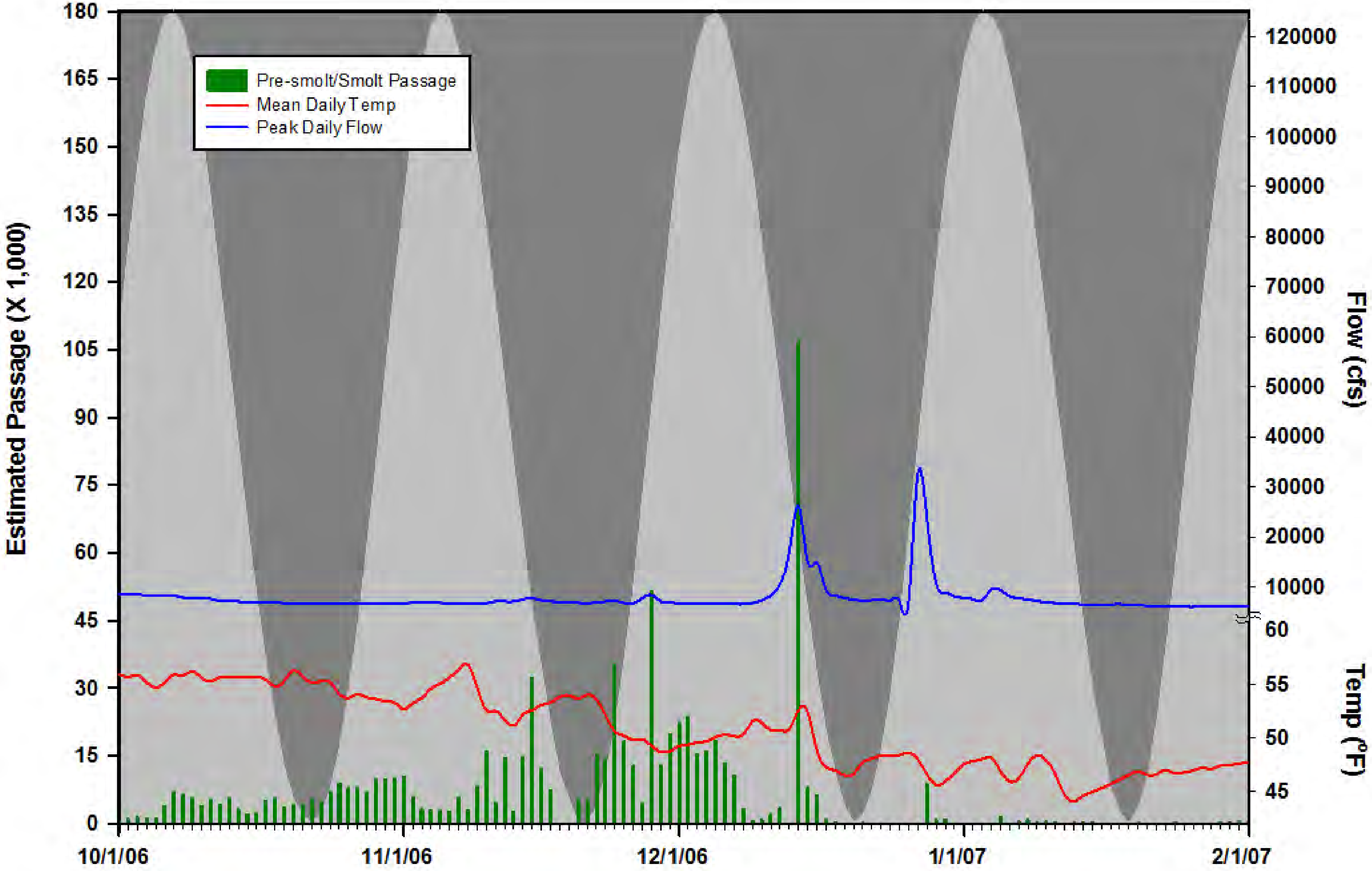

Figure A16. Brood Year 2006 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

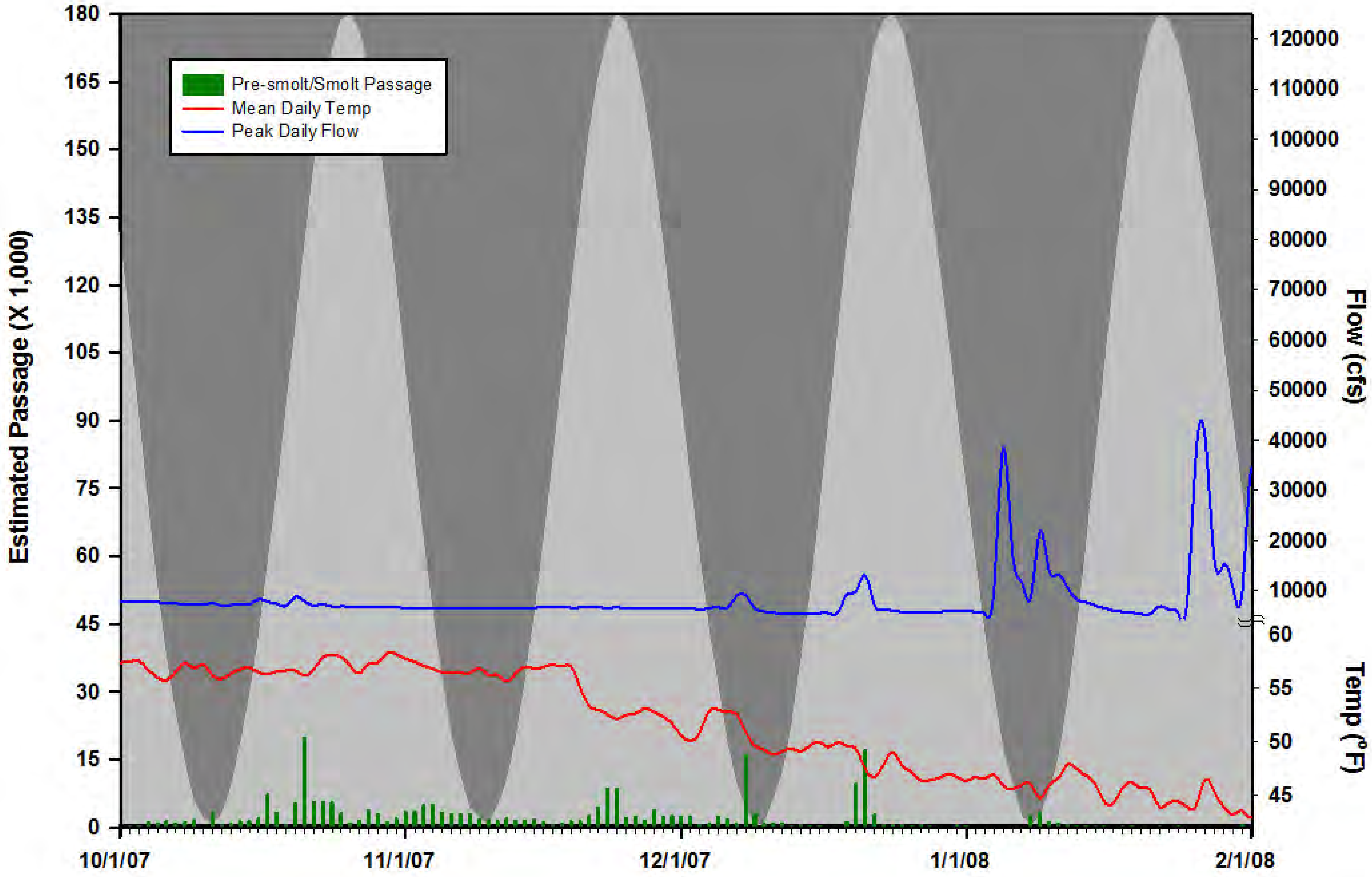

Figure A17. Brood Year 2007 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

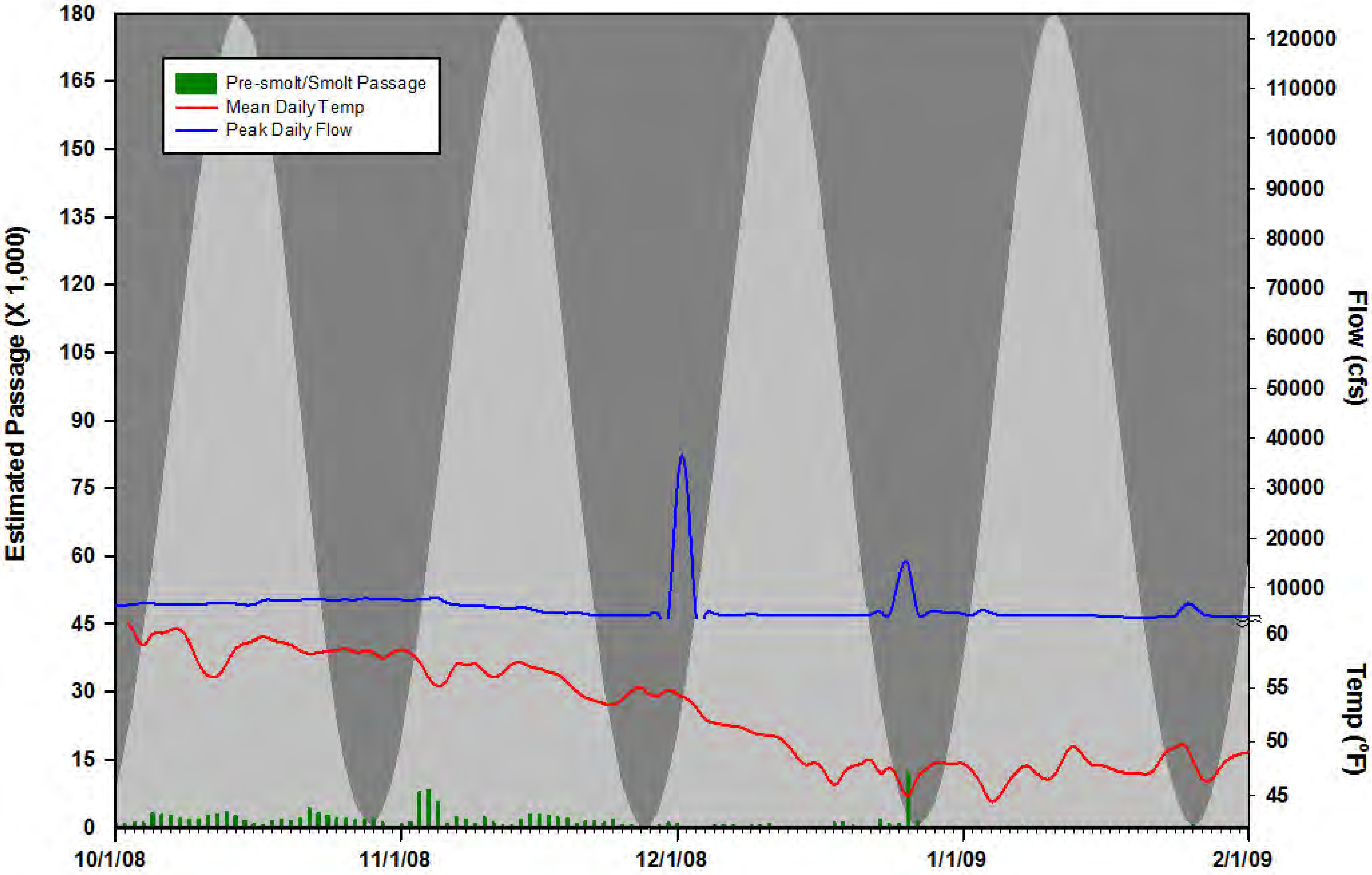

Figure A18. Brood Year 2008 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

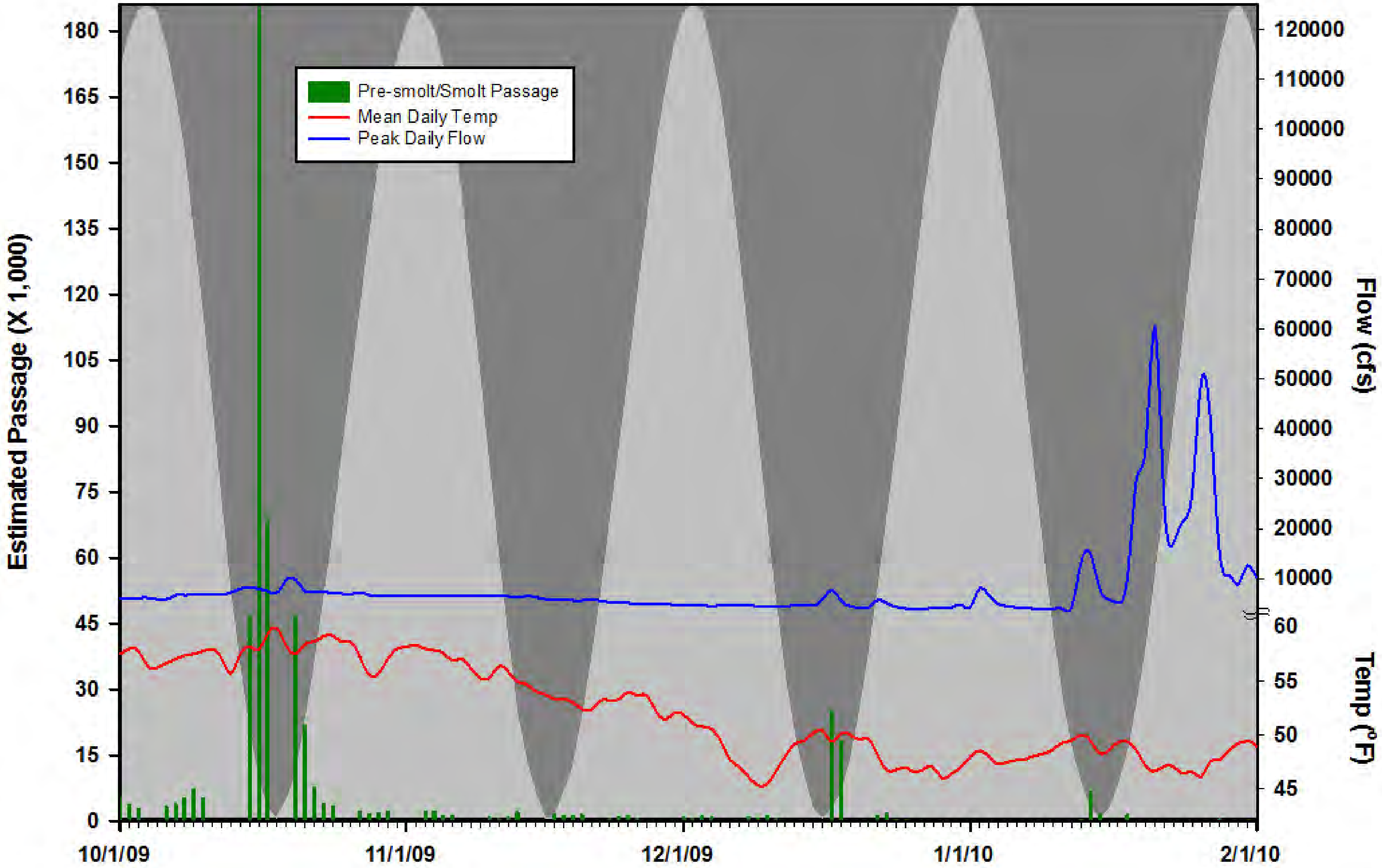

Figure A19. Brood Year 2009 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

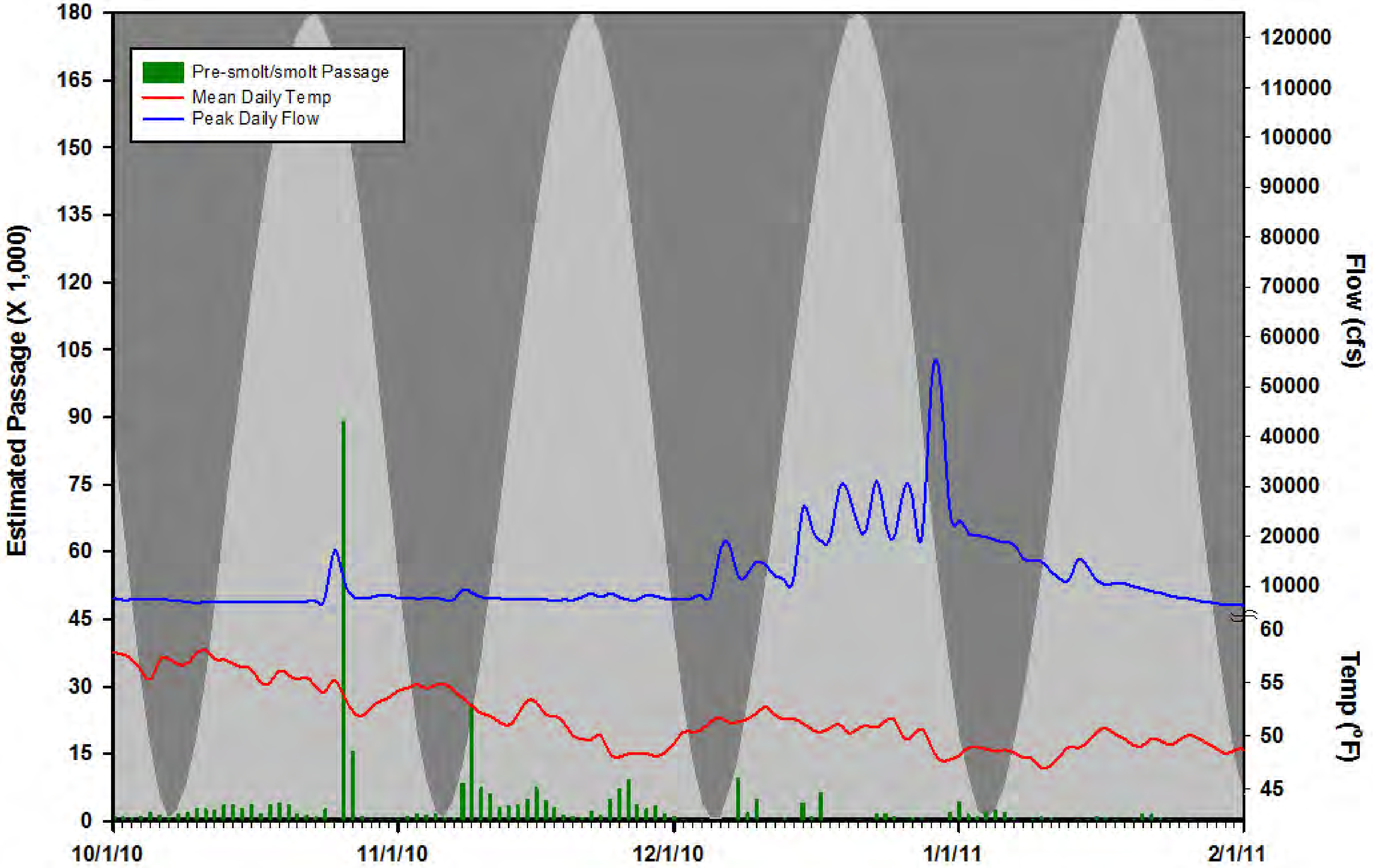

Figure A20. Brood Year 2010 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

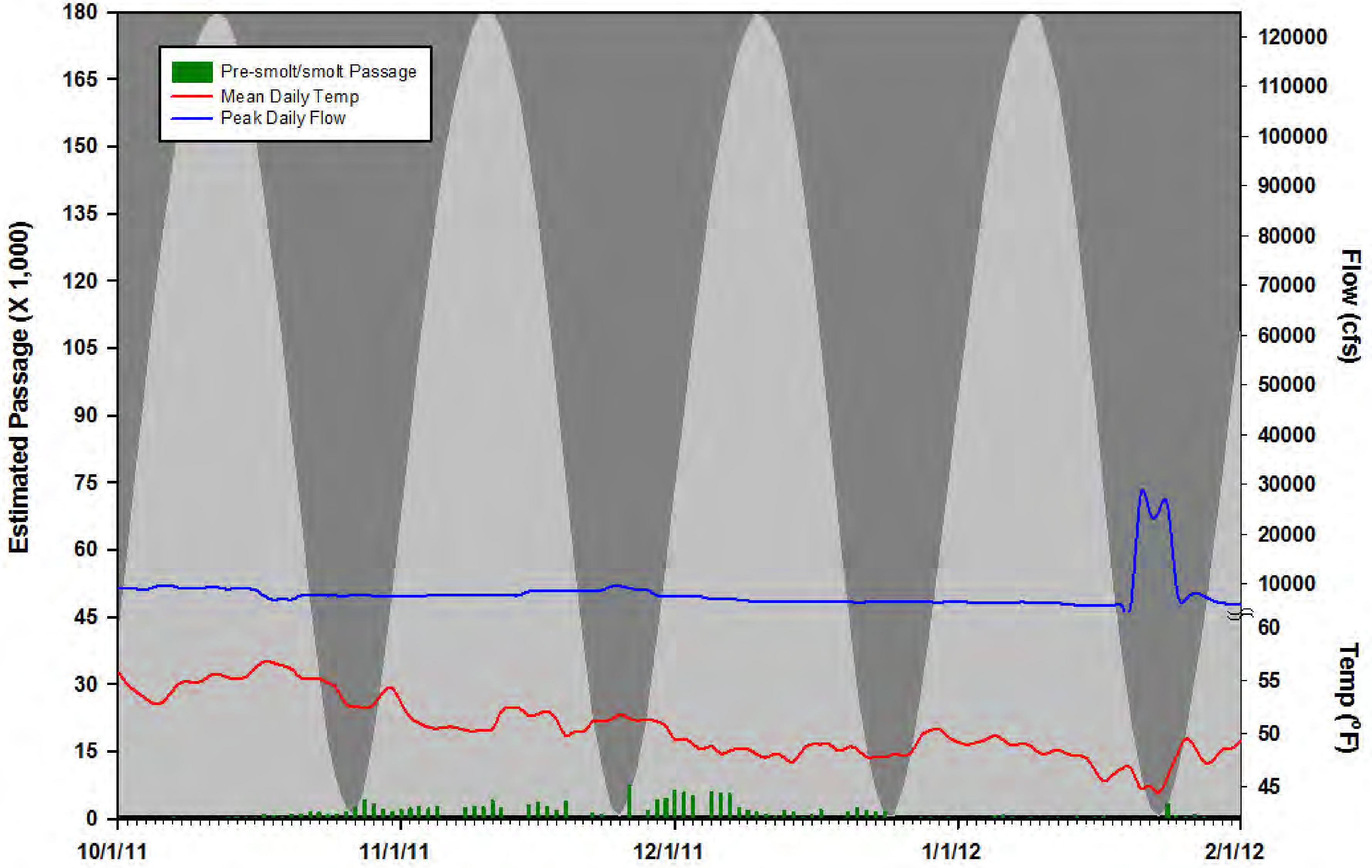

Figure A21. Brood Year 2011 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.

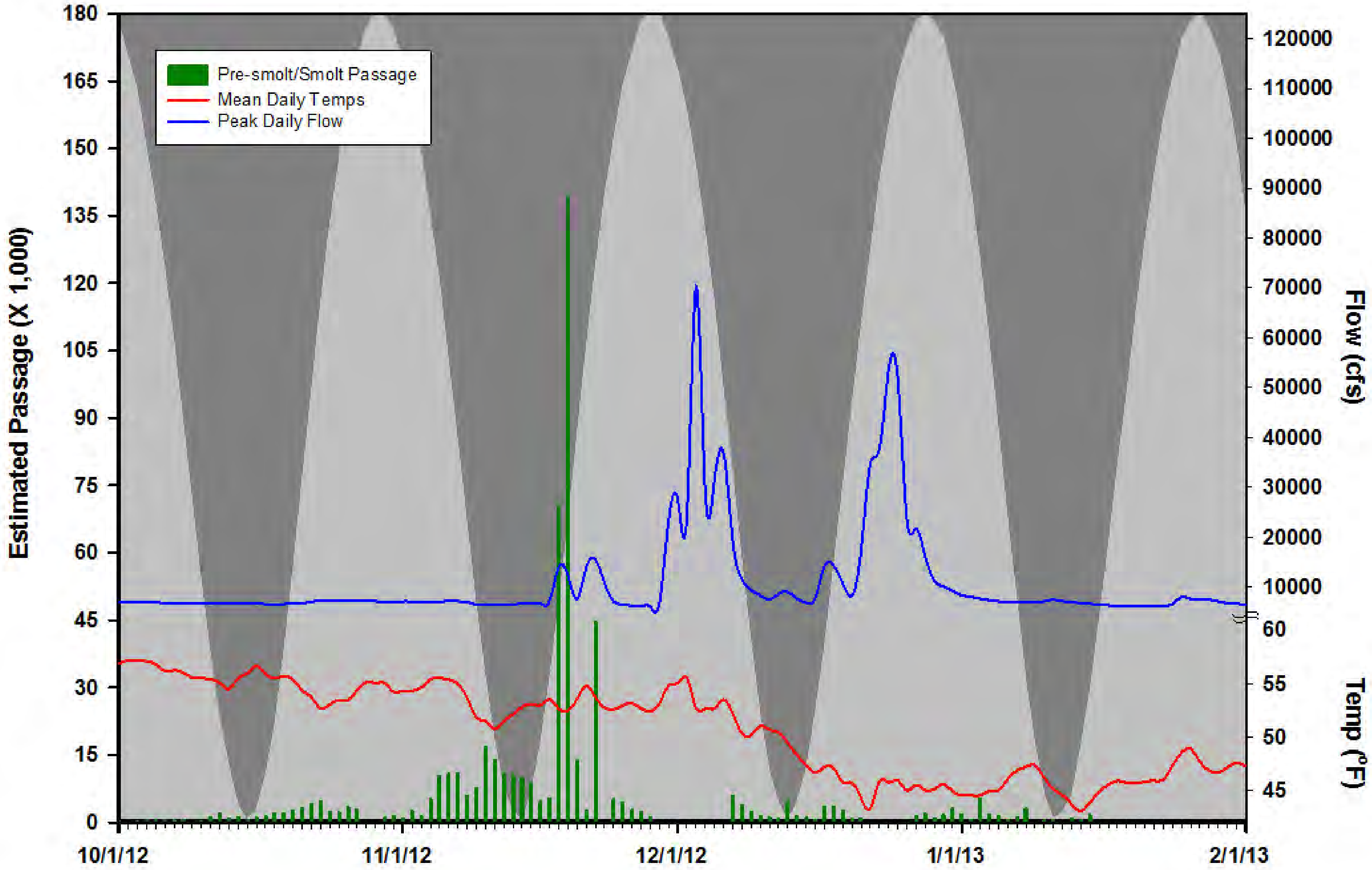

Figure A22. Brood Year 2012 winter Chinook pre-smolt/smolt passage with moon illuminosity indicated by back ground shading (peak of light gray equals full moon), mean daily water temperatures (red), and peak daily flows (blue) at Red Bluff Diversion Dam.