Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Chinook salmon outmigration survival in wet and dry years in California's Sacramento River

Journal:	*Canadian Journal of Fisheries and Aquatic Sciences*
Manuscript ID:	cjfas-2014-0528.R1
Manuscript Type:	Article
Date Submitted by the Author:	19-May-2015
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
Keyword:	SALMON < Organisms, FRESHWATER ENVIRONMENT < General, MIGRATION < General, TELEMETRY < General, SURVIVAL < General

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 18^{th} 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 ($\widehat{\phi}$) along with its respective standard error of the beta estimate ($\widehat{SE}logit(\widehat{\phi})$) by using the formula (Eqn 2):

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

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 ($-\log_e(\textit{survival})$) 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.

ACKNOWLEDGEMENTS

Funding for the project was provided by a CALFED Bay Delta program grant, project U-05-SC-047 (A.P.K and R.B.M principle investigators). We are grateful for the help from many technicians and volunteers including (but not limited to): Ian Cole, Alison Collins, Nicholas Delaney, Heidi Fish, Alex Hearn, Andrew Jones, and Ian Ralston. Special thanks to Kevin Niemela, Kurtis Brown, and Scott Hamelburg of U.S. Fish and Wildlife Service (USFWS) and the helpful staff of the Coleman National Fish Hatchery for providing late-fall run Chinook salmon smolts and logistical support for this study. The California Fish Tracking Consortium allowed the realization of this project through the collaboration and data sharing of several academic, federal, and state institutions. Sean Hayes, Ann-Marie Osterback, and anonymous reviewers provided valuable comments that improved the manuscript.

REFERENCES

Ammann, A.J., Michel, C.J., and MacFarlane, R.B. 2013. The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. Environmental Biology of Fishes **96**(2-3): 135-143.

Azat, J. 2015. GrandTab 2015.04.15 California Central Valley Chinook Population Database Report. CA Department of Fish and Wildlife.

Baker, P.F., and Morhardt, J.E. 2001. Survival of Chinook Salmon Smolts in the Sacramento-San Joaquin Delta and Pacific Ocean. *In* Contributions to the Biology of Central Valley Salmonids. *Edited by* L.R. Brown. California Department of Fish and Game, Sacramento, California. pp. 163-182.

Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences **52**(6): 1327-1338.

Brandes, P.L., and McLain, J.S. 2001. Juvenile Chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin Estuary. *In* Contributions to the Biology of Central

Valley Salmonids. *Edited by* L.R. Brown. California Department of Fish and Game, Sacramento, California. pp. 39-138.

Buer, K., Forwalter, D., Kissel, M., and Stohler, B. 1989. The Middle Sacramento River: Human impacts on physical and ecological processes along a meandering river.

Burnham, K.P. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Bethesda, MD. (USA).

California Hatchery Scientific Review Group (CHSRG). 2012. California Hatchery Review Report. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission.

Chapman, D.W., and Knudsen, E. 1980. Channelization and Livestock Impacts on Salmonid Habitat and Biomass in Western Washington. Transactions of the American Fisheries Society **109**(4): 357-363.

Cohen, A.N., and Carlton, J.T. 1998. Accelerating Invasion Rate in a Highly Invaded Estuary. Science **279**(5350): 555-558.

Connor, W.P., Burge, H.L., Yearsley, J.R., and Bjornn, T.C. 2003. Influence of Flow and Temperature on Survival of Wild Subyearling Fall Chinook Salmon in the Snake River. North American Journal of Fisheries Management **23**(2): 362-375.

Cormack, R.M. 1964. Estimates of Survival from the Sighting of Marked Animals. Biometrika **51**(3/4): 429-438.

Ferrari, M.C.O., Ranaker, L., Weinersmith, K.L., Young, M.J., Sih, A., and Conrad, J.L. 2014. Effects of turbidity and an invasive waterweed on predation by introduced largemouth bass. Environmental Biology of Fishes **97**(1): 79-90.

Fisher, F.W. 1994. Past and Present Status of Central Valley Chinook Salmon. Conservation Biology **8**(3): 870-873.

Garland, R.D., Tiffan, K.F., Rondorf, D.W., and Clark, L.O. 2002. Comparison of Subyearling Fall Chinook Salmon's Use of Riprap Revetments and Unaltered Habitats in Lake Wallula of the Columbia River. North American Journal of Fisheries Management **22**(4): 1283-1289.

Giorgi, A.E., Hillman, T., Stevenson, J.S., Hays, S.G., and Peven, C.M. 1997. Factors that influence the downstream migration rates of juvenile salmon and steelhead through the hydroelectric system in the mid-Columbia River basin. North American Journal of Fisheries Management **17**(2): 268-282.

Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society **127**(2): 275-285.

Harnish, R.A., Johnson, G.E., McMichael, G.A., Hughes, M.S., and Ebberts, B.D. 2012. Effect of Migration Pathway on Travel Time and Survival of Acoustic-Tagged Juvenile Salmonids in the Columbia River Estuary. Transactions of the American Fisheries Society **141**(2): 507-519.

Healey, M.C. 1991. Pacific Salmon Life Histories *Edited by* C.G.a.L. Margolis. University of British Columbia Press, Vancouver. pp. 312-230.

Hogasen, H.R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences **127**: i-viii, 1-128.

Jolly, G.M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. Biometrika **52**(1/2): 225-247.

Kjelson, M., Raquel, P.F., and Fisher, F.W. 1981. Influences of freshwater inflow on chinook salmon (*Oncorhynchus tshawystcha*) in the Sacramento-San Joaquin Estuary, U.S. Fish and Wildlife Service, pp. 88-108.

Laake, J., and Rexstad, E. 2008. RMark—an alternative approach to building linear models in MARK. *In* Program MARK: A Gentle Introduction. *Edited by* E. Cooch and G.C. White.

Larry, R.B., and Marissa, L.B. 2009. Effects of hydrologic infrastructure on flow regimes of California's Central Valley rivers: Implications for fish populations. River Research and Applications **26**(6): 751-765.

Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. Ecological Monographs **62**(1): 67-118.

MacFarlane, R.B., and Norton, E.C. 2002. Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin **100**(2): 244-257.

Magnusson, A., and Hilborn, R. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the US Pacific Coast. Estuaries **26**(4B): 1094-1103.

McMichael, G.A., Eppard, M.B., Carlson, T.J., Carter, J.A., Ebberts, B.D., Brown, R.S., Weiland, M., Ploskey, G.R., Harnish, R.A., and Deng, Z.D. 2010. The Juvenile Salmon Acoustic Telemetry System: A New Tool. Fisheries **35**(1): 9-22.

Melnychuk, M.C., Korman, J., Hausch, S., Welch, D.W., McCubbing, D.J.F., and Walters, C.J. 2014. Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. Canadian Journal of Fisheries and Aquatic Sciences **71**(6): 831-846.

Michel, C.J. 2010. River and estuarine survival and migration of yearling Sacramento River Chinook Salmon (*Oncorhynchus tshawytscha*) smolts and the influence of environment, Ecology and Evolutionary Biology, University of California - Santa Cruz, Santa Cruz, CA.

Michel, C.J., Ammann, A.J., Chapman, E.D., Sandstrom, P.T., Fish, H.E., Thomas, M.J., Singer, G.P., Lindley, S.T., Klimley, A.P., and MacFarlane, R.B. 2013. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*). Environmental Biology of Fishes **96**(2-3): 257-271.

Moyle, P.B. 2002. Inland Fishes of California. University of California Press, Berkeley, California.

Moyle, P.B., Yoshiyama, R.M., Wikramanayake, E.D., and Williams, J.E. 1995. Fish Species of Special Concern. California Department of Fish and Game, Sacramento, CA.

Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E., and Skalski, J.R. 2001. Survival Estimates for Migrant Yearling Chinook Salmon and Steelhead Tagged with Passive Integrated Transponders in the Lower Snake and Lower Columbia Rivers, 1993-1998. North American Journal of Fisheries Management **21**(2): 269-282.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. Fisheries **16**(2): 4-21.

Nichols, F.H., Cloern, J.E., Luoma, S.N., and Peterson, D.H. 1986. The Modification of an Estuary. Science **231**(4738): 567-573.

O'Farrell, M.R., Mohr, M.S., Palmer-Zwahlen, M.L., and Grover, A.M. 2013. The Sacramento Index (SI). NOAA Technical Memorandum. U.S. Department of Commerce.

Palmer-Zwahlen, M., and Kormos, B. 2013. Recovery of Coded-Wire Tags from Chinook Salmon in California's Central Valley Escapement and Ocean Harvest in 2011.

Perry, R.W., Skalski, J.R., Brandes, P.L., Sandstrom, P.T., Klimley, A.P., Ammann, A., and MacFarlane, B. 2010. Estimating Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento-San Joaquin River Delta. North American Journal of Fisheries Management **30**(1): 142-156.

Powell, L.A. 2007. Approximating variance of demographic parameters using the Delta Method: A reference for avian biologists. The Condor **109**(4): 949-954.

Rechisky, E.L., Welch, D.W., Porter, A.D., Furey, N.B., and Hinch, S.G. 2014. Telemetry-based estimates of early marine survival and residence time of juvenile Sockeye salmon in the Strait of Georgia and Discovery Passage, 2013. State of the Physical, Biological and Selected Fishery Resources of Pacific Canadian Marine Ecosystems in 2013, Canadian Technical Report of Fisheries and Aquatic Sciences, Fisheries & Oceans Canada: 123-127.

Rechisky, E.L., Welch, D.W., Porter, A.D., Jacobs-Scott, M.C., and Winchell, P.M. 2013. Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. Proceedings of the National Academy of Sciences **110**(17): 6883-6888.

Rechisky, E.L., Welch, D.W., Porter, A.D., Jacobs, M.C., and Ladouceur, A. 2009. Experimental measurement of hydrosystem-induced delayed mortality in juvenile Snake River spring Chinook salmon (*Oncorhynchus tshawytscha*) using a large-scale acoustic array. Canadian Journal of Fisheries and Aquatic Sciences **66**(7): 1019-1024.

Sandstrom, P.T., Smith, D.L., and Mulvey, B. 2013. Two-dimensional (2-D) Acoustic Fish Tracking at River Mile 85, Sacramento River, California. U.S. Army Corps of Engineers, Engineer Research and Development Center.

Schmetterling, D.A., Clancy, C.G., and Brandt, T.M. 2001. Effects of Riprap Bank Reinforcement on Stream Salmonids in the Western United States. Fisheries **26**(7): 6-13.

Seber, G.A. 1982. The estimation of animal abundance and related parameters. Chapman, London and Macmillan.

Seber, G.A.F. 1965. A Note on the Multiple-Recapture Census. Biometrika **52**(1/2): 249-259.

Skalski, J.R., Smith, S.G., Iwamoto, R.N., Williams, J.G., and Hoffmann, A. 1998. Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences **55**(6): 1484-1493.

Smith, S.G., Muir, W.D., Hockersmith, E.E., Zabel, R.W., Graves, R.J., Ross, C.V., Connor, W.P., and Arnsberg, B.D. 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall chinook salmon. North American Journal of Fisheries Management **23**(3): 939-961.

Snider, B., and Titus, R.G. 1998. Evaluation of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, November 1995-July 1996. Stream Evaluation Program Technical Report. California Department of Fish and Game.

Snider, B., and Titus, R.G. 2000a. Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1996-September 1997. Stream Evaluation Program Technical Report. California Department of Fish and Game.

Snider, B., and Titus, R.G. 2000b. Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1997-September 1998. Stream Evaluation Program Technical Report. California Department of Fish and Game.

Snider, B., and Titus, R.G. 2000c. Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1998-September 1999. Stream Evaluation Program Technical Report. California Department of Fish and Game.

Vincik, R.F., Titus, R.G., and Snider, B. 2006. Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, September 1999-September 2000. Lower Sacramento River Juvenile Salmonid Emigration Program Technical Report. California Department of Fish and Game.

Welch, D.W., Melnychuk, M.C., Rechisky, E.R., Porter, A.D., Jacobs, M.C., Ladouceur, A., McKinley, R.S., and Jackson, G.D. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Canadian Journal of Fisheries and Aquatic Sciences **66**(5): 736-750.

Welch, D.W., Rechisky, E.L., Melnychuk, M.C., Porter, A.D., Walters, C.J., Clements, S., Clemens, B.J., McKinley, R.S., and Schreck, C. 2008. Survival of Migrating Salmon Smolts in Large Rivers With and Without Dams. PLoS. Biol. **6**(10): 2101-2108.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**(1 supp 1): 120 - 139.

Williams, J.G. 2006. Central Valley Salmon: A Perspective on Chinook and Steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science **4**(3).

Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., and Moyle, P.B. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. *In* Contributions to the Biology of Central Valley Salmonids. *Edited by* R.L. Brown. California Department of Fish and Game, Sacramento, California. pp. 71-176.

Young, P.S., Cech, J.J., Jr., and Thompson, L.C. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. Reviews in Fish Biology and Fisheries **21**(4): 713-731.

Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America. Fisheries Management and Ecology **21**(2): 155-168.

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

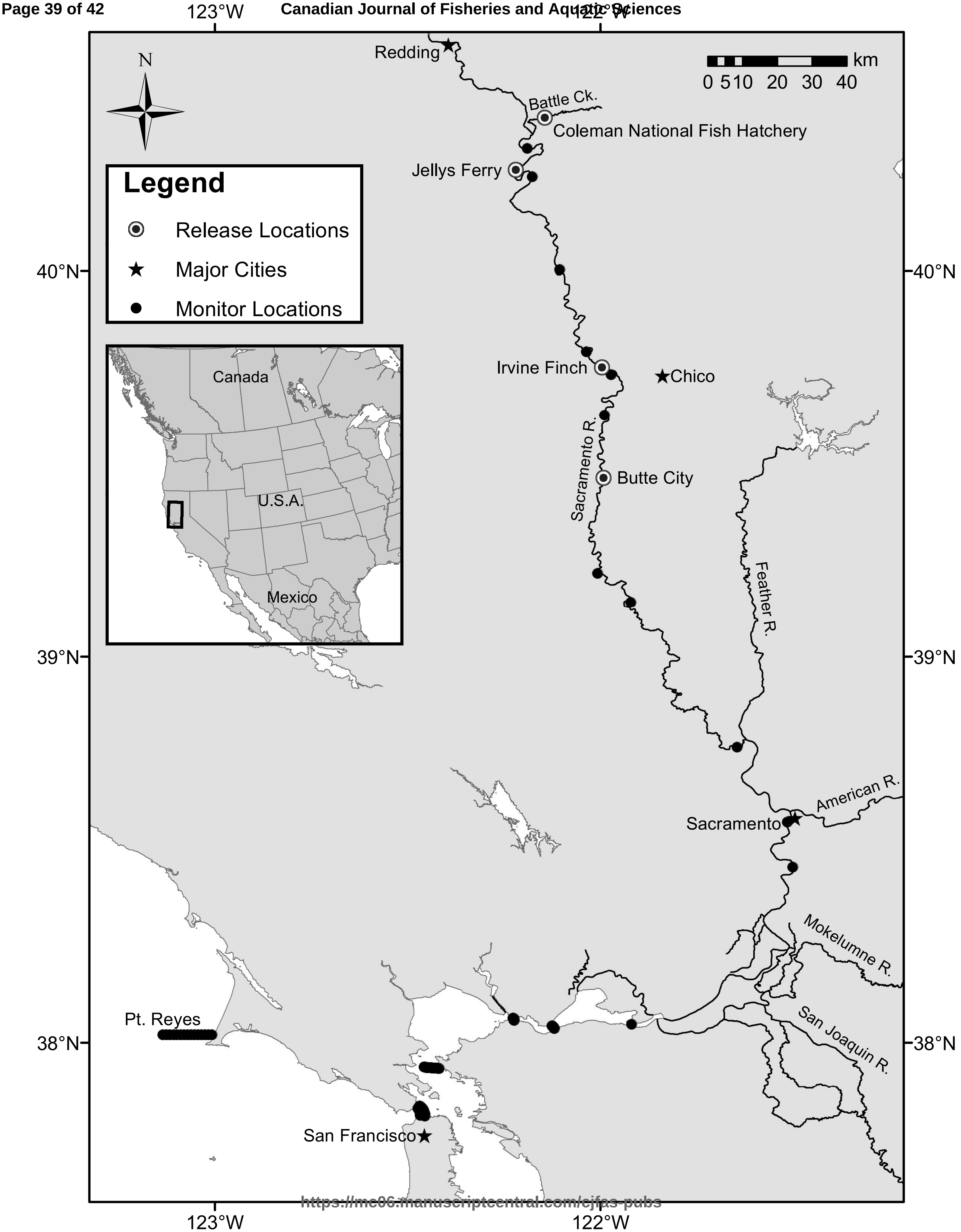
Figure Captions

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.

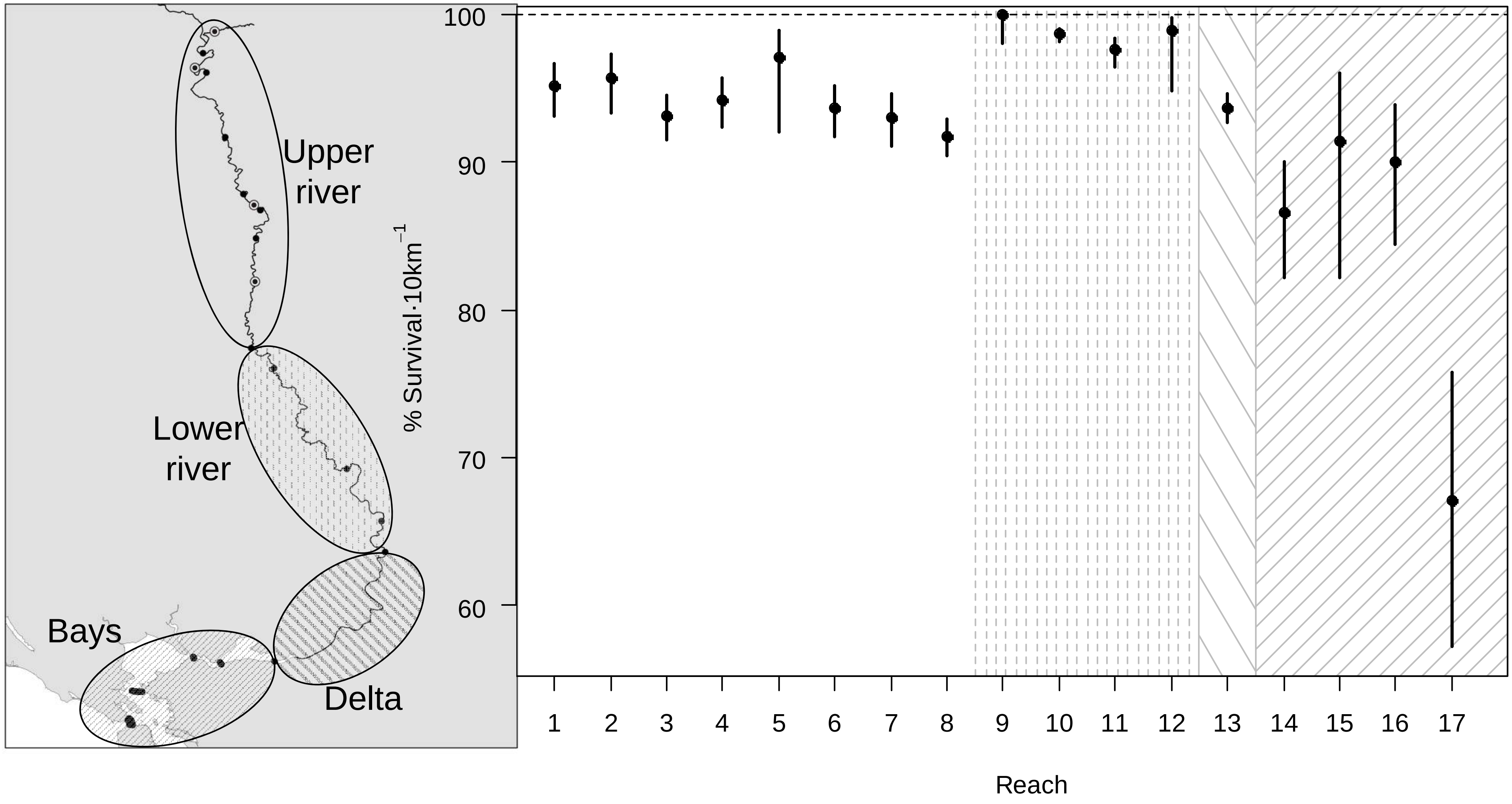
Fig. 2. Percent survival per 10 km per reach for the 2007-2010 study years combined. Figure and map are delimited based on the regions (from upstream to downstream): upper Sacramento River, lower Sacramento River, Sacramento – San Joaquin River Delta, and Suisun/San Pablo/San Francisco Bays. The Sacramento 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.

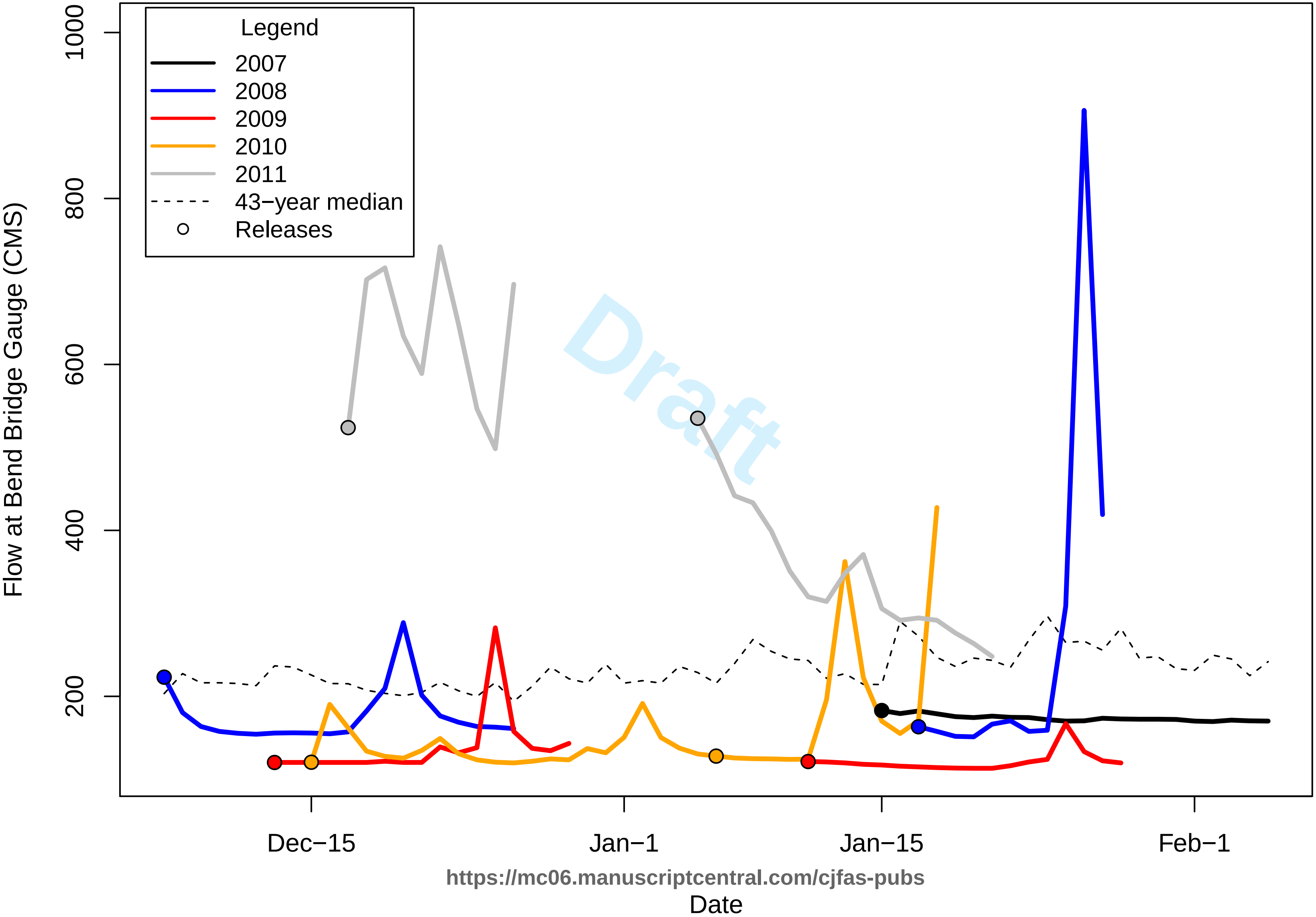
Fig. 4. Percent survival per major region for all five study years. Regions include river, delta, bays, and the percent survival for the entire watershed "All". Error bars represent 95% confidence intervals.

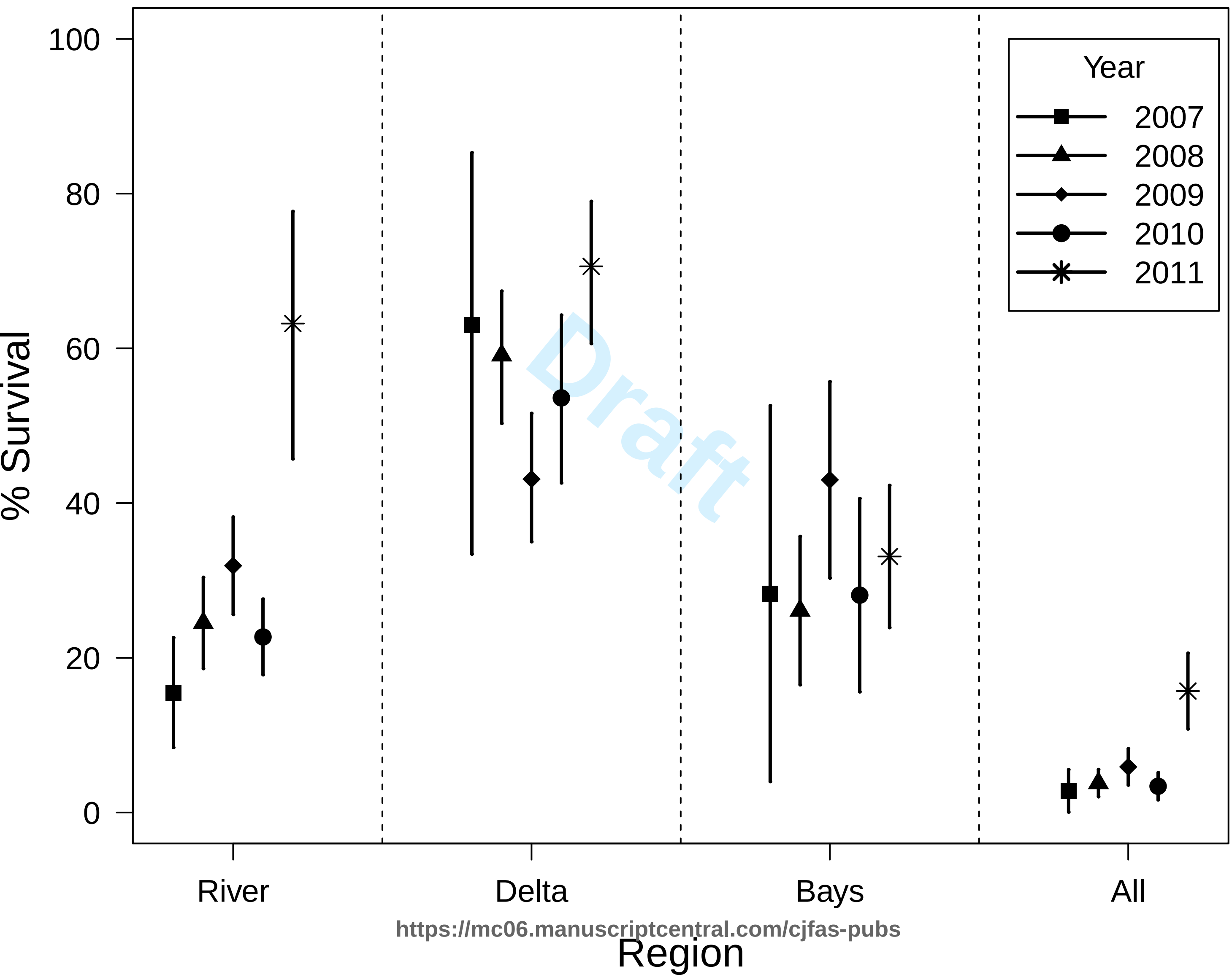


123°W
122°W
N
km
0 5 10 20 30 40
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
Legend
Release Locations
Major Cities
Monitor Locations
40°N
Canada
U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
39°N
American R.
Sacramento
Mokelumne R.
San Joaquin R.
Pt. Reyes
38°N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


Upper river
Lower river
Bays
Delta
% Survival·10km^{-1}
100
90
80
70
60
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Reach

 Canadian Journal of Fisheries and Aquatic Sciences





100
80
60
40
20
0
% Survival
Year
2007
2008
2009
2010
2011
River
Delta
Bays
All
Region