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RIVER AND ESTUARINE SURVIVAL AND MIGRATION OF YEARLING SACRAMENTO RIVER CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS AND THE INFLUENCE OF ENVIRONMENT

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

LIST OF TABLES

Chapter 1

Chapter 2

ABSTRACT

RIVER AND ESTUARINE SURVIVAL AND MIGRATION OF YEARLING SACRAMENTO RIVER CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS AND THE INFLUENCE OF ENVIRONMENT

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Identifying where sources of enhanced mortality of outmigrating Chinook salmon (smolts) occur, and the movement patterns associated with this life stage, are critical steps in the preservation and conservation of imperiled salmonids in California's Sacramento River system. To that end, 200-300 late-fall run Chinook salmon yearling smolts were acoustically tagged per year and tracked during their outmigration in California's Sacramento River during 2007-2009. Total outmigration survival to the ocean environment varied from 3.1% (± 1.5 S.E.) to 5.5% (±1.2 S.E.), depending on the release year, with an all year total outmigration survival of 3.9% (± 0.6 S.E.), substantially lower than published survival of other West Coast yearling Chinook salmon smolt emigrations. The migration rates of the smolts that successfully reached the ocean varied significantly based on release location, from an average of 14.32 $\text{km}\cdot\text{day}^{-1}$ (± 1.32 S.E.) to 23.53 $\text{km}\cdot\text{day}^{-1}$ (± 3.64 S.E.). The high spatial resolution of survival estimates of Chinook salmon (*Oncorhynchus tshawytscha*) revealed that smolts exhibited relatively low survival (92-97% $\text{survival}\cdot 10\text{km}^{-1}$) in the upper reaches of the Sacramento River, as well as in the

Sacramento River Delta and San Francisco Estuary (67-94% survival·10km^{-1}). No significant inter-annual variation in survival, total river migration rates, or smaller scale movement rates were found, potentially due to similar hydrographic conditions among the three years. Survival did fluctuate significantly depending on month of release and river reach. Several natural and anthropogenic factors that are known to affect smolt survival rates were assessed; variables associated with river channelization, turbidity and sinuosity were all found to have positive relationships with survival within the river, suggesting increases in these variables may increase survival (likely by means of reducing predation). Smolts exhibited strong nocturnal movements while in the less turbid and channelized upper regions of the river which dissipated to temporally uniform movements in the more turbid and channelized lower regions of the river, suggesting that eased predatory action may have caused smolts to discontinue the nocturnal strategy. Survival data suggests a refocusing of fisheries and resource managers' efforts, specifically with regards to hatchery release strategies and the current concentration of mitigation efforts in the delta.

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INTRODUCTION

In California's Central Valley (comprised of the Sacramento and San Joaquin Rivers, as well as their tributaries), freshwater salmon ecology has become inextricably associated with human interests. In a watershed where 47% of historical salmon spawning, migration and rearing habitats are inaccessible due to dams (Yoshiyama et al. 2001), an estimated 40% of the historical, pre-colonization river discharge is lost to water exports (Nichols et al. 1986). Finally, where approximately 90% of historical Central Valley wetlands, which are important for salmonid rearing, have disappeared to allow for agriculture and flood control (Frayer et al. 1989), one must think of this watershed as, at best, an altered ecosystem. As a result of these modifications and others, the four distinct Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) populations are either endangered, threatened, or a "species of concern" according to the U.S. Endangered Species Act (ESA). Moreover, the commercial importance of water resources and a $255 million salmon fishing industry (Office of the Governor of California 2008) makes habitat and population recovery to pre-colonization levels impossible. It is therefore imperative that we understand the influence of the environment on Chinook salmon survival and behavior, both to assess the impact of current habitat modifications, but also to provide recommendations into how to improve management of this watershed with respects to one of its most valuable resources.

The outmigration of juvenile Chinook salmon (smolts) is among the most vulnerable life stages during which habitat modification can have strong influences.

During this relatively short life stage, a smolt will sometimes travel hundreds of kilometers and transit several different habitats with varying degrees of anthropogenic modification. Human activities can directly influence smolt survival, but also indirectly through the intermediary of changed environmental conditions. Thus, the focus of my first chapter is on survival patterns of a population of outmigrating Central Valley Chinook salmon smolts, on the environmental factors that correlate with them, and finally, an assessment of the influence of watershed modification.

Salmonids employ numerous life-history strategies to maximize fitness and survival. Specifically, movement patterns during migration contribute to survivability, and different migration strategies can vary in their effectiveness (Stearns 1976). For example, Chinook salmon have two distinct early life history strategies to maximize survival and growth: “ocean-type” juveniles that leave the river and travel to the ocean weeks after hatching and “stream-type” juveniles that feed in the river for up to one year and outmigrate to the ocean at a much larger size (Gilbert 1912). Depending on the river and ocean conditions for each year, one of these life history strategies may result in better survival than the other. In this investigation, I have therefore quantified movement during the outmigration of “stream-type” juveniles, highlighted potential movement strategies and associations with the environment, and discussed the sources of mortality that may have shaped them in the second chapter of this thesis.

The fisheries and resource management applications of the information collected in this study are invaluable in many regards. This study has provided high spatial and temporal resolution survival estimates, illuminating regions of particularly high and low survival. These estimates, coupled with environmental data, will allow resource managers to concentrate mitigation efforts on specific mortality hot-spots while benefiting from evidence for potential causality for both low and high survival. This study also provides managers with a detailed description of the outmigration of the smolts in question, and the correlations with environmental variables, allowing them to better predict the consequences of anthropogenic activities that occur along the migratory corridor, or predict migration dynamics of future cohorts facing environmental changes. Finally, and perhaps most importantly, this study has discerned survival and movement dynamics that may be shared by the ESA. listed Chinook salmon runs in the Central Valley, adding to a knowledge base that will be fundamental to conservation actions.

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Chapter 1

River and estuarine survival of yearling Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*) smolts and the influence of environment

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) are a cultural and economic resource to the western United States and Canada, including the state of California. Of the California salmon rivers, the Sacramento River supports the largest, most diverse, and until recently, healthiest salmon stocks. However, since 2007, the largest of the Sacramento River populations, the fall run Chinook salmon, has crashed, and adult returns to the basin have been as low as 25% of the long-term 30-year average (in 2009; Azat 2010). Emergency action has been taken by the Pacific Fisheries Management Council, including a moratorium on commercial and recreational fisheries for coastal and inland waters of the entire state for the 2008-2009 seasons, causing an estimated loss of $255 million and 2,263 jobs (Office of the Governor of California, 2008). This precipitous decline is thought to have been driven by poor ocean conditions (Lindley et al. 2009), but it is clear that it is a combination of many stressors that have brought Sacramento River salmon to such a delicate state (Yoshiyama et al. 1998).

One of the most vulnerable stages in a Chinook salmon's life is the downstream migration of juveniles heading to the ocean from their riverine origins

(Healey 1991). During this life stage, the juvenile salmon undergoes many physiological and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River's Chinook salmon populations, this freshwater journey may be as long as 600 kilometers, transiting many different habitats. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed.

Environmental factors can influence smolt survival directly or indirectly by influencing the distribution and foraging of the smolt predators. For example, Smith et al. (2002) found that survival decreased as river flow decreased for subyearling fall run Chinook salmon in the Snake River; Gregory and Levings found that increased turbidity resulted in increased survival for juvenile Chinook salmon in the Fraser River (1998), and Baker et al. (1995) found that temperature explained a substantial portion of the variation in survival rates for subyearling fall run Chinook salmon in the Sacramento – San Joaquin River Delta, especially as temperatures neared lethally high levels.

Understanding the magnitude and potential variation in smolt mortality is a logistically and quantitatively difficult problem. Cormack (1964), Jolly (1965), and Seber (1965) developed methods for determining temporally explicit survival estimates in rivers via mark-multiple recapture models. Burnham (1987) then developed a spatially explicit approach adapted for estimating survival of migrating fish in rivers, which, for example, was used for survival estimates on a river-reach scale for Columbia River salmon (Muir et al. 2001, Skalski et al. 2001). These quantitative mark-recapture techniques can be expanded to assess what environmental conditions correlate with variations in survival.

In this study, I quantify the spatial and temporal patterns of Chinook salmon survival in the Sacramento River system. I capitalized on one of the largest networks of acoustic monitors in the world developed by the California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu/), and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to utilize these aforementioned techniques on the late-fall run Chinook salmon population in California's Central Valley. Previous investigations of Chinook salmon in the Sacramento River only allowed for low-resolution estimates of survival (Snider 2000 a, b). Additionally, most work had focused on only the Sacramento-San Joaquin River Delta (Baker and Morhardt 2001, Brandes and McLain 2001), a small portion of the smolt migration corridor.

I will address the two following hypotheses:

(1) Total and reach-specific outmigrating late-fall run Chinook salmon smolt survival rates vary spatially and temporally in the Sacramento River, Sacramento-San Joaquin Delta and San Francisco Estuary.

(2) Environmental variables that vary in space and time can explain a substantial portion of variation in reach-specific survival rates.

This represents the first high-resolution analysis of the magnitude and spatial-temporal variation in survival of outmigrating Chinook salmon smolts in the Sacramento River and San Francisco Estuary and the potential natural and anthropogenic drivers of mortality. This represents a leap forward in our understanding of the environmental factors that may influence survival rates of outmigrating Chinook salmon smolts. This knowledge is critical to efforts to mitigate the sources of mortality or predict survival rates of future cohorts facing environmental changes. Finally, assessing what environmental conditions influence variation in late-fall run Chinook salmon survival will help give us insight into factors affecting the survival dynamics of other valued salmon runs in California such as the winter and spring run, listed under the United States Endangered Species Act as endangered and threatened, respectively (Moyle et al. 1995).

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 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 it is estimated that approximately 47% of the historic area that was used for spawning, migration and/or rearing of Chinook salmon is no longer accessible (Yoshiyama et al. 2001). The Sacramento River watershed includes diverse habitats, from a pristine run-riffle river, to a heavily channelized and impacted waterway further south, to an expansive tidally-influenced freshwater delta at its confluence with the San Joaquin River, and finally to the San Francisco Estuary, the largest and most modified estuary on the west coast of the United States (Nichols et al. 1986). 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 unimpounded, it is estimated that current water discharge of the Sacramento and San Joaquin Rivers combined amounts to approximately 40% of the historical, pre-colonization 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, notably reducing the historical winter high flows and flooding (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 anadromy.

Central Valley late-fall run Chinook salmon

The California Central Valley (includes the Sacramento and San Joaquin Rivers, as well as their tributaries) has four distinct Chinook salmon populations (runs) that all migrate at different times of the year. Additionally, these populations demonstrate one of two early life history strategies: "ocean-type" and "stream-type" (Gilbert 1912). Ocean-type Chinook salmon are born in the lower reaches of large rivers and spend very little time (days to weeks) in the river before migrating to the ocean. Stream-type juveniles are born in the headwaters of large rivers and spend up to a year in the river ("yearling"), migrating to the ocean at a relatively large size. Among the different runs and early life history strategies, it becomes clear that different populations have found different migration strategies to maximize survival (Taylor 1990).

The late-fall run is one of the four runs found in the Sacramento River drainage, and is the only to exhibit a predominately stream-type life history (Moyle 2002). It is considered to be a "species of concern" by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which smolts will enter the ocean at a size of approximately 160 mm (Fisher 1994). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

The historical distribution of the late-fall run Chinook salmon is hard to estimate, due to the paucity of historical data. Late-fall run Chinook salmon were not distinguished from fall run fish until 1966, when counts were initiated after the construction of the Red Bluff Diversion Dam (RBDD) in the mid 1960s (Yoshiyama et al. 1998). However, we know that ideal late-fall run Chinook salmon spawning habitat consists of year-round cold water allowing the rearing of yearlings, and that their current spawning range is from Red Bluff (480 river km (rkm) upstream from the Golden Gate Bridge) to the first barrier to anadromy, Keswick Dam (rkm 565) (Fisher 1994, Moyle et al. 1995, Yoshiyama et al. 2001). We assume that this run historically used the cold waters upstream of Keswick Dam, specifically the Upper

Sacramento, McCloud and Pit Rivers for spawning (Yoshiyama et al. 1998). Since these rivers are no longer accessible, the large majority of late-fall run Chinook salmon spawning grounds disappeared with the construction of Keswick and Shasta Dams.

Acoustic Telemetry

Acoustic tagging technology was used to acquire high-resolution movement and survival estimates. I used Vemco V7-2L acoustic tags (1.58g ± 0.03 S.D.; Amirix Systems, Inc., Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible monitors to track tagged fish. The monitor array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate). This array of approximately 300 monitors was maintained by the California Fish Tracking Consortium, and positioned to maximize detection probability at key sites along the outmigration corridor.

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subject to standardized quality control procedures to minimize the number of false detections. For example, detections that occurred before the release date-time of each tag, or detections that did not share a tag identification number (tagID) with any of the released fish, were excluded from analysis.

Tagging and Releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 300 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged fish (Table 1) was consistent with observed size frequency for this run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery-origin yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Approximately 85-90% of the hatchery smolts are the progeny of hatchery-origin adults trapped in Battle Creek (tributary to the Sacramento River); parents of the remaining hatchery smolts' are natural-origin adults trapped on the mainstem Sacramento River just below Keswick Dam (K. Niemela, USFWS, Red Bluff, CA 96080, unpubl. report).

Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized fish as described by two studies (Adams et al. 1998a, Martinelli et al. 1998). Tag weight did not exceed 5% of the total body weight to minimize potential affects on survival, growth, and behavior. This cutoff point was conservative, considering much of the literature shows tag-to-body ratios can be up to 6% and not affect growth (Moore et al. 1990, Adams et al. 1998a, Martinelli et al. 1998), and up to 8 % and not affect swimming performance (Brown et al. 1999, Anglea et al. 2004, Lacroix et al. 2004).

Tagged fish were kept in captivity for a minimum of 24 hr after surgery to ensure proper recovery. In the 2007 season, a portion of the tagged fish was released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

In the first year (2007), all 200 fish were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter two years, approximately 300 fish were tagged each year and simultaneously released from three release sites in the upper 150 rkm of the mainstem Sacramento River, allowing the lower release groups to reach the lower river and estuary in larger numbers. Fish were transported at low densities (~ 10 $g \bullet l^{-1}$) via coolers with aerators to the release sites. In years of multiple release sites, transport times were extended for closer sites to keep potential transport stress equal among all release groups.

Data Analysis

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 a fish is detected at one monitor site, but is never detected thereafter, we assume that the fish has died somewhere in the reach between the monitor where it was last detected and the next downstream monitor location.

Calculating mortality using fish absence as a proxy works if we assume detection efficiency is perfect. Unfortunately, detection efficiency is not 100% given current tagging technology. Therefore, to accurately calculate the mortality rates of the emigrating Chinook salmon while accounting for detection probability, I used the Cormack-Jolly-Seber (CJS) model for live recaptures within Program MARK (created by Gary White, Colorado State University(White and Burnham 1999). The CJS model was originally conceived to calculate survival of tagged animals over time, by re-sampling (recapturing individuals) an area and calculating survival and recapture probabilities using maximum likelihood models. For species that express an obligate migratory behavior, a spatial form of the CJS model can be used, in which recaptures (i.e., detected acoustically more than once) are structured spatially along a migratory corridor (Burnham 1987). The model determines if fish not seen at certain monitors were ever seen at any monitor downstream of that specific monitor, thus enabling calculation of maximum-likelihood estimates for detection efficiency of all monitor locations (p), all survival estimates (Φ), and 95% confidence intervals for both (Lebreton et al. 1992).

Detection efficiencies are calculated by assessing the number of tags missed by a monitor location. This can be done if a missed tag is seen at a downstream location and therefore assumed to have passed the upstream location. In addition, as sample size decreases further downstream, detection efficiencies have increasingly large errors until the final monitor location, where survival and detection efficiency at that station are not identifiable. Because accurate estimates of survival at ocean entry were important, parallel monitor lines were installed at the Golden Gate about 1 km apart to calculate both detection efficiency and survival at the inner Golden Gate line. Additionally, in the latter two tagging seasons, I benefitted from the installation of a monitor line at Point Reyes, seaward from the Golden Gate approximately 60 km to the north. This acoustic monitor curtain allowed an estimate of detection efficiency for the outer Golden Gate line, thereby further reducing error in the estimation of survival and detection efficiency to the inner Golden Gate line.

After the three-year study was completed, monitor locations were assessed for their detection probability and functional reliability over the three-year period, and their location within the watershed. Those that were consistently efficient monitor locations were chosen to delimit the river reaches that were used in spatially comparing mortality. A total of 19 monitor locations were chosen, spanning from just below the most upstream release site to the Golden Gate (Fig. 1; Table 2). Between them, I delineated 17 reaches in which mortality can be accurately estimated (the detection efficiency and survival of the 18th and last reach cannot be distinguished).

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes. Unfortunately, the downloadable detection files are not completely accurate, and occasionally, in areas with high densities of pinging tags or other acoustic noises, false detections are deemed correct by the monitor and saved in the detection files. Detection data was thus stored in a relational database (Microsoft SQL Server 2005, Microsoft Corporation) and analyzed for quality control. Detections that occurred before release date-time of each tag were then deleted. Next, single detections at locations that are not between valid upstream and downstream detections (a valid detection is defined as less than 10 days OR 50 rkm to prior or next detection) were deleted. Finally, if multiple consecutive detections of a tag at one location are greater than 216 minutes apart (10% less than the minimum observed time between consecutive known false detections of the same tag) the detections were considered for removal. These different conditions removed false detections to the best of my ability.

Hypothesis 1

Overall survival was first assessed from the release site to the Golden Gate for each release group. Using the 19 monitor locations, survival for 17 reaches was calculated, using the survival and detection probability linear model (in logit space) allowing for each reach to have a parameter ("full model"). This model, and all other models, allowed for full parameters for the estimation of detection efficiencies (i.e., allowing detection efficiencies to vary per monitor location). I calculated reach-specific survival for each release group separately. By multiplying these survival rates together, the cumulative survival per release group is estimated. Multiplying the cumulative survival rate by the release size produces an estimate of total fish per release group that reached the ocean. Standard error for the cumulative survival estimates were calculated using the delta method.

The influences of study design factors on survival rates were then assessed with Program MARK. To do this, a separate survival model was created for each factor. The influence of these factors was assessed by allowing each group (e.g., 3 groups for the release year model: 2007, 2008 and 2009) within each model to have its own set of survival parameters. Each survival model was added to some form of a base model (often representing a null hypothesis) one by one and then compared to the base model using model selection. The model selection criterion used was Akaike's Information Criterion (AIC), an excellent tool for model comparing and selection because it balances precision and accuracy by penalizing a model for the total amount of parameters it has. Therefore, we are effectively comparing model parsimony and not simply model goodness-of-fit. As suggested by Burnham and Anderson (2002), AIC values were corrected for small sample sizes (AICc), and corrected for over-dispersion (QAICc). If a test model improved the parsimony (lower QAICc) in relation to the base model by a difference of more than seven (Burnham and Anderson 2002), the test model was deemed substantially more parsimonious, and therefore supported over the base model.

The effects of reach (n=17), release year (n=3), release month (n=2), and release site (n=3) were tested. This was done by comparing the parsimony of each model to the parsimony of a "null model". The null model only allowed one parameter for survival (representing the null hypothesis: constant survival through space and time). To allow for these factors to express reach-specific variability in survival, each group (e.g., each year with the above example) has its own reach-specific survival estimates within the confines of one model. The most supported models (based on AIC scores) were then interpreted to determine if the tested factor could have a substantial influence on survival by comparing the models to their counterparts that did not include the factor in question.

Finally, the influence of individual covariates (fork length (mm) and weight (g)) on the parsimony of the survival model was assessed. This can be done by adding a parameter to the linear regression model for survival that represents the covariate. Program MARK then utilizes the parameter to include the individual contribution into the likelihood estimation of survival. The model selected *a priori* to add these covariates to is the reach-specific survival model. This model can then be compared to the simple reach-specific survival model without any individual covariates to determine whether parsimony increases.

Considering this study utilized hatchery-origin smolts for these analyses, the ability to suggest these smolts are adequate surrogates for wild (or natural-origin) smolts in terms of determining survival dynamics would be very useful. A pilot tagging project on natural-origin late-fall run Chinook salmon smolts was conducted in 2009 concurrent with hatchery-origin tagging. A total of 18 wild smolts were captured, acoustically tagged, and released in the mainstem Sacramento at Red Bluff (rkm 478) and in tributary Mill Creek (confluence with Sacramento River at rkm 460). Using the same methods as with hatchery-origin smolts, estimates of reach-specific survival were calculated for the natural-origin smolts. A survival model incorporating detection information from both wild-origin smolts and hatchery-origin smolts released in the 2009 season was created. This model allowed both smolt groups to have their own set of survival parameters. This model was compared to a survival model incorporating the same detection data but constructed as a reach-specific survival model, with both groups sharing the same survival parameters. Essentially, the comparison of the two models determined if natural-origin and hatchery-origin had similar or different survival estimates, based on which model was more supported. This permitted an approximate suggestion of how the hatchery-origin smolt survival estimates compare to a limited sample of the wild population.

Hypothesis 2

Data for environmental variables were compiled for the river reaches, from the release points to the upper limit of tidal influence on the river (rkm 189). They were grouped into two types: spatial-temporal natural variables and spatial natural and anthropogenic variables. All variables were chosen *a priori* based on salmon survival literature and data availability for the watershed. To formalize the approach on investigating the influence of the environment on survival, a conceptual model was constructed (Fig. 2). Riparian habitat and river morphology are spatial variables which influence water temperature, turbidity, and water dynamics. These variables likely govern the behavior of the smolts and their predators, and thus the smolts' susceptibility to predation. Due to the inability to directly measure predation, estimated mortality (using the above methods) was considered as a proxy for predation.

The spatial-temporal variables included water temperature (ºC) (Kjelson and Brandes 1989, Baker et al. 1995, Newman and Rice 2002, Smith et al. 2002, Connor et al. 2003), water flow ($m^3 \cdot s^{-1}$), channel water velocity ($m \cdot s^{-1}$) (Kjelson and Brandes 1989, Smith et al. 2002, Connor et al. 2003), water turbidity (Nephelometric Turbidity Units (ntu); Gregory 1993, Gregory and Levings 1998), maximum river depth (m), and the ratio of river width (m) to maximum river depth (m, WDR). The WDR will increase as the river becomes shallower and wider. Spatial-temporal variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 3). Measurements such as channel water velocity, depth and river width were simulated using actual flow recordings, high resolution bathymetric cross-sections and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers).

The spatial variables included water diversions (diversions$\cdot$km^{-1}) (Kjelson and Brandes 1989, Perry et al. 2010), riparian habitat type (% of riparian zone covered by either agricultural, natural, or urban land) (Gregory et al. 1991, Pusey and Arthington 2003), riprap (% of total shore reinforced with riprap) (Schmetterling et al. 2001), levees (% of total shore reinforced with leveed walls) and sinuosity (actual river length divided by the length of a direct line between the nodes delimiting each reach). All spatial variables were calculated using the geographic information system software program ArcGIS (ESRI, 1999). Spatial and spatial-temporal variables were associated to tag detections in a relational database.

Once data for the environmental variables were collected, they were averaged per appropriate unit. The spatial variables, not changing through time, were simply averaged per reach. The spatial-temporal variables were averaged per year, month of release, release site, and reach. Having the spatial-temporal variables averaged per smallest group denomination allowed for the maximum amount of spatial-temporal resolution associated to the mortality data.

Within Program Mark, riverine survival was modeled as a logit function of two linear predictors (Eqn 1), while detection efficiency was allowed to vary fully per reach (in the style of the full model). The survival model included an intercept (β_0), a parameter for the reach length (km), and a parameter for an environmental variable. This is a novel approach to relating environmental data to smolt survival, although the technique has been employed instead with detection efficiencies (Melnychuk 2009). The environmental parameter will also have an associated beta coefficient (β), allowing determination of the direction and slope of the relationship. Additionally, by standardizing the environmental variables (subtracting the mean value from each raw data point, then dividing by the standard deviation, essentially giving all standardized variable datasets a mean of zero and a standard deviation of one), standardized beta coefficients can be calculated, allowing for comparison of the strengths of beta coefficients for different models. For a change in one standard deviation unit of the environmental variable, survival will change by the amount specified by that model's standardized beta coefficient.

$$\text{Logit}\ (\Phi) = \beta_0 + \beta_1[\textit{Reach Length}] + \beta_2[\textit{Env. Variable}] \tag{1}$$

All environmental models were compared to a base model to test for a significant improvement in parsimony. The purpose of this base model is to include all sources of mortality that should not be attributed to the environment. The base model specified *a priori* included both reach length and initial mortality after release (Olla et al. 1994, Olla et al. 1995). I adopted reach length, needing to control for the large variation in lengths, but did not incorporate initial release mortality. This was determined after I compared survival models allowing for different survival estimates in the first one and two reaches after release in comparison to all other reaches to the "full model" (reach-specific survival model), and the initial release mortality models were not significantly more parsimonious. In essence, this compared survival through the same reaches of smolts released at that point and smolts released further upstream and found no significant evidence of different survival rates. Therefore, the final base model specified constant survival as a function of reach length.

Environmental models were also compared to the full model. The full model is widely used as the CJS model for calculating survival between, and detection probabilities at, each recapture event, and is typically the most parsimonious model. Comparing environmental models to the fully reach-varying model provided a rough estimate of the distance from potentially maximum parsimony.

Spatial and spatial-temporal environmental models cannot be compared to each other for causative and statistical reasons. In terms of causation, the spatial variables often govern the spatial-temporal variables (i.e., % leveed shoreline influences width and depth of river) (Fig. 2). Statistically, strictly spatial variables should not be added to the spatial-temporal varying base model due to the temporal grouping parameters (i.e., year, time) which would unnecessarily penalize the model for the superfluous parameters. Therefore, the different spatial and spatial-temporal environmental models were analyzed separately, and can only be compared to like models.

Once the environmental variables that had the strongest associations with survival estimates were determined, two sample *t-tests* were used to determine if variations existed between treatments that also exhibited significant variations in survival.

RESULTS

Hypothesis 1

Total survival through the entire studied migration corridor (rkm 518 to 2) per year varied from 3.1 to 6.1% (Table 4), with an all year total outmigration survival of 3.9% (± 0.6 S.E.). Release group-specific survival through the entire migration corridor averaged between 3 and 13%. In both 2008 and 2009, when three release sites were used, a consistent pattern emerged, such that the furthest upstream release group exhibited the lowest survival, the furthest downstream release group exhibited relatively moderate survival, and finally the middle release group had the best survival of the three.

Fish weight and fork length varied significantly among years ($P<0.001$), and pairwise hypothesis testing using Bonferroni and Tukey's HSD tests both indicate that fish sizes were statistically different between all years.

Survival on a reach-by-reach basis was quite variable. Through the three years of the study, the upper river reaches (reaches 1 through 8; rkm 518 to 325) had lower survival rates. The lower Sacramento River had relatively higher survival (reaches 9-12; rkm 325-169), whereas the delta and estuary had lower survival (reaches 13-17; rkm 169-2) (Fig. 3, Fig. 4). In the 2007 season, survival of tagged smolts within the Battle Creek tributary (rkm 534-518) was relatively very low, 63% (± 1.0 S.E.) per 10 km. Reach-specific survival rates throughout the three years in the Sacramento River-

San Francisco Estuary ranged from 67% per 10 km reach in the lower estuary reach (Richmond Bridge to Golden Gate; rkm 15-2) to 100% per 10 km reach in the last river reach before the delta (City of Sacramento to Freeport; rkm 189-169) (Table 5; Fig. 4). Detection efficiencies were also estimated grouping all three years of the study and were found to be satisfactory for CJS modeling, ranging from 0.52 to 1.00 (Table 5).

The influence of reach on survival rates was found to be significantly more parsimonious (ΔQAICc >7) than the Null Model (constant survival through space and time; Table 6). All the design structure factors were then added to the survival model including the influence of reach, and then tested for significance against the reach-specific survival and null model. The factors of year, month, release site, and the covariates of fork length and weight were all tested, entertaining every factorial possibility. The only model found to be statistically more parsimonious than the reach-specific model included month as a factor. That is, along with reach, month of release had a substantial effect on reach-specific survival. Specifically, in both 2008 and 2009 (2007 was omitted due to only one release month) smolts released in December had significantly higher survival rates in the upper river than smolts released in January (Fig. 5).

Wild (natural-origin) reach-specific survival rates were estimated and compared to study's hatchery-origin survival rates, and in most reaches, survival per 10 km per reach for both populations were not statistically different (Fig. 6). Furthermore, the parsimony of the survival model allowing for wild and hatchery smolts to have separate survival estimates was significantly less parsimonious (ΔQAICc=12) than the full model, further suggesting that reach-specific survival of wild smolts was not different than hatchery smolts.

Hypothesis 2

Riverine survival rates were then constrained to spatial environmental variables and compared to a base model of constant survival per km per reach. The environmental models found to be significantly more parsimonious were, in order of decreasing significance, % riprap shoreline, % levee shoreline, sinuosity, diversions per km, and finally % natural riparian habitat (Table 7). The fully reach dependent survival model (“full model”: constant survival per reach through time) is significantly more parsimonious than all spatial environmental models. The two most significant spatial variables, % riprap shoreline and % levee shoreline (Fig. 7), as well as sinuosity and diversions per km, had positive standardized beta coefficients, indicating that an increase in the variable produced an increase in survival. Natural riparian habitat had the opposite influence on survival rates.

Riverine survival rates were then constrained similarly with spatial-temporal environmental variables, and again compared to a base model of constant survival per km per reach. The models found to be significantly more parsimonious than the base model are, in order of decreasing significance, maximum river depth, turbidity, and WDR (Table 8). The fully reach-dependent survival model (“full model”) is indistinguishable from the best fit environmental model (maximum river depth). The standardized beta coefficients for the variable models are all positive with the exception of the WDR. Thus, survival is greater with deeper channels, greater turbidity, and channels that have increasing depth relative to width.

Two-sample *t-tests* were run to test for monthly differences in maximum river depth, turbidity, and WDR for both 2008 and 2009. Both turbidity and WDR were found to be significantly different by month in both years ($P<0.05$; Table 9).

DISCUSSION

Hypothesis 1

Overall survival of smolts to the ocean (3.9%) was low in this study relative to other large rivers along the west coast. Welch et al. (2008) found that yearling Chinook salmon smolts from the Snake River (tributary of the Columbia River) had an overall survival of 27.5% (± 6.9 S.E.) to the ocean (distance traveled 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 (distance traveled 330.8-395.2 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%. Additionally, Rechisky et al. (2009) found that outmigrating yearling Chinook salmon smolts from the Yakima River (another tributary of the Columbia River) had an overall survival of 28% (± 5 S.E.) to the ocean (distance traveled 655 km). Previous studies in the Sacramento River are limited, but indicate poor survival of Coleman Hatchery-origin late-fall run Chinook salmon smolts, similar to this study (1.3 to 2.3% overall survival to rkm 239 (Snider 2000b, a)), but never before has survival been calculated to ocean entry.

It could be hypothesized that the recent declines of California's Central Valley Chinook salmon populations (Lindley et al. 2009) reflect the low survival seen in this study. To put the overall outmigration survival in perspective of several life stages, I compared this study's outmigration survival to known smolt-to-adult return rates (SAR). SAR represents the percent of outmigrating Chinook salmon smolts that survive to return as adults to the original spawning reaches, and is calculated per cohort. Therefore, SAR incorporates the combination of mortality during the outmigration, mortality and harvest during the ocean phase, and finally pre-spawning ground mortality and harvest in the returning river stage. Smolt-to-adult return rates (SAR) for the Sacramento River, and specifically for Coleman hatchery-origin late-fall run Chinook salmon, are available, but not yet for the same cohorts as in this study. As a proxy, the long-term average SAR (brood years 1992-2005) for Coleman hatchery-origin yearling late-fall run Chinook salmon was 0.53% (± 0.04 S.E.) (Regional Mark Information System, http://www.rmpc.org/). If the cohorts of this study were assumed to have similar SAR as the long-term average, overall outmigration mortality for late-fall run Chinook salmon smolts released (or native) to Battle Creek (and potentially the upper Sacramento River and tributaries) could be responsible for a considerable portion of salmon mortality for such a short life stage (Fig. 8).

Survival in the 2007 season was surprisingly low in the short nine kilometer passage through Battle Creek to the Sacramento River. Poor survival in Battle Creek was likely due to high densities of Sacramento pikeminnow (*Ptychocheilus grandis*) observed there (CJM pers. observation; K. Brown, USFWS - Coleman National Fish Hatchery, Anderson, CA 96007, pers. comm.), potentially caused by hatchery-subsidized prey abundance. Sacramento pikeminnow are one of the main predators of salmonid smolts in the Sacramento River (Brown and Moyle 1981), along with striped bass (*Morone saxatilis*) (Stevens 1966), largemouth bass (*Micropterus salmoides*), and several avian species. Efforts to reduce the seemingly unnatural high densities of predators in Battle Creek could be an effective strategy for maximizing survival of the large number of outmigrating hatchery and wild-origin smolts.

Due to the resulting low numbers of fish reaching lower reaches in 2007, survival estimates had such wide confidence intervals that understanding changes in reach-specific mortality was difficult. The release strategy was therefore changed for the 2008 and 2009 seasons to potentially increase the number of fish reaching downstream sections, thus reducing survival estimate confidence intervals. Additionally, only fish that successfully reached the Sacramento River in 2007 (131 individuals after Battle Creek) were included for comparative survival analysis with the two following years.

In the latter two years of the study, three simultaneous release sites were used, and appeared to have an effect on overall survival to the ocean. The furthest upstream release group had the lowest survival and the middle release group had the highest survival in both years. Although the release site interaction with reach model was less parsimonious than the base model (reach), and the 95% confidence intervals around the cumulative survival estimates at the entrance to the ocean do not indicate significant differences, it is noteworthy that the pattern was consistent through both years. One explanation for this could stem from the fact that late-fall run Chinook salmon smolts take longer to outmigrate the further downstream they are released (Michel unpubl. data). There could consequently be a tradeoff between bypassing the high mortality of the upper river with additional temporal exposure to predation further downstream. Currently, a large portion of hatchery produced Chinook salmon smolts are released downstream of their native nurseries, in an attempt to minimize riverine mortality, but at a cost of increased straying rates of returning adults (Quinn 1993). Considering the lack of evidence suggesting an improvement in survival with this release strategy, the cessation of this practice should be considered by fisheries managers.

The year of release did not have a significant influence on reach-specific survival rates. The study occurred during three dry years (low rainfall and snowpack) in northern California, with 2008 deemed as critically dry (Department of Water Resources 2009). Therefore, the survival dynamics and environmental associations found in this study represent those for years of relatively low freshwater flow and may be different during wet years.

The rates of survival were relatively low in the reaches of the upper river and higher in the reaches of the lower river. Total river survival was 23.5% (± 1.7 S.E.), considerably higher than previous studies on the Sacramento River (Snider 2000a, b). River survival on the Columbia River varied from 26.6% (± 1.5 S.E.) to 61.2 % (± 1.6 S.E.) depending on the year or release group (Welch et al. 2008). Potential reasons for the bipartite survival dynamics in the Sacramento River will be discussed in the environmental influence section.

The rate of survival was relatively low in the Sacramento – San Joaquin River Delta. Survival of outmigrating Sacramento River Chinook salmon smolts has been known to be low in the delta (Baker and Morhardt 2001, Brandes and McLain 2001), reportedly due to low river flow, lethally high water temperatures and entrainment into the predator-rich interior delta by water pumping for agriculture (Kjelson and Brandes 1989). Perry et al. (2010) found delta survival of Coleman hatchery-origin late-fall run Chinook salmon smolts to be 35% (± 10 S.E.) and 54% (± 7 S.E.) in December 2006 and January 2007 respectively. These estimates are similar to this study's estimate of delta survival (93.7% per 10km, corresponding to a total delta survival of 52.6% (± 3 S.E.)).

Salmonid smolt survival rates in the San Francisco Estuary do not exist in the literature (only indices allowing temporal comparisons exist (Brandes and McLain 2001)), an unfortunate information gap considering that this region had the lowest survival rates of the outmigration corridor. Welch et al. (2008) found yearling Chinook salmon smolts to have a survival of 61.8% (± 1.9 S.E.) through the lower river and estuary of the Columbia River while this study found smolt survival through the estuary alone to be 31.4%, considerably lower. Possible reasons for the low survival through the estuary include the physiological stresses of acclimatizing to salt water, the increased presence of some predators such as marine mammals, and the poor condition of the estuary (Nichols et al. 1986).

The significant effect of reach was informative, and in one case, counterintuitive (Fig. 3). Possibly due to the biased management focus on salmon survival in the delta (in large part motivated by concerns of the detrimental effects of water exports for agriculture), many believe that mortality during the river migration is greatest in the delta. Moreover, it is alleged by many that the more anthropogenically modified lower river has lower survival rates than the more natural upper river for outmigrating salmonids. However, this study demonstrated that not only does the upper river have significantly lower survival than the lower river, but the poor survival in the upper river is comparable in magnitude to the poor survival seen in the delta and estuary.

Although the sample size of the tagged wild (natural-origin) population was too small (n=18) for useful confidence intervals, and the tag weight-to-body weight ratio was generally above the 5% threshold, survival for both wild and the study's hatchery populations were not different in most reaches. Survival rates seemed to follow the same pattern of lower upstream survival and higher downstream survival. Moreover, model comparison confirmed that there is no evidence that the 18 natural-origin smolts and the study's hatchery-origin smolts had different survival estimates. Because none of the wild fish were detected below the lower river reaches, survival comparisons for the delta and estuary were not possible. This evidence suggests, though very cautiously, that hatchery-origin late-fall run Chinook salmon smolts may be used as surrogates for studying wild late-fall run Chinook salmon smolt survival in the Sacramento River.

Fish weight and fork length varied significantly among years, however, the survival models including size covariates were not found to be more parsimonious than the base model. Specifically, I did not detect a substantial effect of weight and fork length were not found to influence survival in a significant way. This seems counterintuitive considering gape-limited predators almost certainly have a significant impact on smolt survival and because larger smolts are likely superior at evading predators. However, having a minimum size limit on smolt tagging to enforce the 5% tag weight-to-body weight ratio restricted this study's smolt size range to about 145 mm to 180 mm (10th percentile to 90th percentile). This may have reduced size variability sufficiently to mask any size effects.

The month of release had a significant influence on survival in the two latter years when two release months were implemented. In the 2008 and 2009 tagging season, the December release groups had higher survival than the January release groups, especially in the upper river. This could be evidence for environmental change between months. Perry et al. (2002) found a monthly variation in survival in the Sacramento - San Joaquin Delta in the 2006/2007 winter with Coleman hatchery yearling late-fall run Chinook salmon smolts, except he found higher survival in December rather than January. This variation was thought to be in part due to variation in environmental conditions such as temperature and turbidity.

While creating a base model that would incorporate all sources of mortality that are not attributable to the environment, I found that there seemed to be no initial release mortality effect (i.e., immediately following release) on survival. This suggests that there is no evidence for hatchery “naïveté”-induced or handling stress-induced mortality of smolts soon after release.

In conclusion, hypothesis 1 is supported. There is evidence for both spatial (by reach) and temporal (by month) variation in survival rates for the three years of this study and it is likely that environmental variability is a contributor. Environmental variability is influential on the survival of outmigrating Chinook salmon smolts because they transit a wide range of environmental conditions during their extensive journey, all of which may have different impacts on their survivability.

Hypothesis 2

Of the spatial variables, significant relationships with riverine survival were found with, in order of decreasing significance, % riprap shoreline, % levee shoreline, sinuosity, diversions per km, and finally % natural riparian habitat (Table 7). With the exception of sinuosity, the four other variables are correlated to each other by a Pearson’s correlation coefficient of at least 0.64. This is because, in the Sacramento River, riprap often accompanies levees and the river is leveed in the lower, more populated reaches (therefore, less natural habitat) with more need for water diversions. It is difficult to understand which of these correlated variables is having a dominating influence on survival without controlling for the others. However, the overall channelization of the river (entailing both the levee and riprap riverbank factors) seems to have the most influential effect on smolt survival, and the relationships between natural riparian habitat and water diversions with survival may be spurious. Sinuousity is less correlated with the other variables and will be discussed separately.

Traditionally, levees, riprap, and channelization have been considered to be detrimental for salmon populations due to their degradation of spawning grounds (reduced input of gravel) (Buer et al. 1989), lack of prey and cover, and increased predators on juveniles (Chapman and Knudsen 1980, Schmetterling et al. 2001, Garland et al. 2002). However, a positive effect of channelized reaches on smolt survival was found in the present study. This might be because smolts actively migrate through channelized reaches, thus reducing the period of exposure to sources of mortality. In the Sacramento River, channelized reaches often have higher turbidity that acts as cover. Furthermore, the presence of predators may be restricted to only the immediate vicinity of the riprap, lowering the potential detrimental effects of channelization. Channelization of rivers leads to increased depth and uniformity of bathymetry and flows, all of which reduce predator habitat and ambush areas, and ease downstream migration. Similarly, smolt survival in the Columbia River was higher in deep impoundments compared to shallower undammed reaches (Welch et al. 2008). In contrast, if we are to consider the non-channelized upper reaches that exhibit low survival, it could be that the shallow run-riffle structure of the river has created many opportunities for predators to ambush passing smolts.

Sinuosity was negatively correlated with indices for channelization, and positively correlated with natural riparian habitat, suggesting at first that the river is most sinuous in the upper reaches. However, unlike most other variables, sinuosity does not follow a strict downstream gradient. Sinuosity must consequently co-vary with small-scale fluctuations in indices for channelization and natural riparian habitat. Given that sinuosity had a positive beta coefficient, suggesting that the more sinuous the river, the better the survival, sinuosity may be having an influence on survival independent of other measured variables.

As expressed in the conceptual model, spatial variables control spatial-temporal variables that theoretically influence riverine survival rates. Therefore, I have concluded that channelization and sinuosity influence survival, but have not determined the mechanisms. Of the spatial-temporal variables tested, I found significant relationships with riverine survival for maximum river depth, turbidity, and width-to-depth ratio (WDR). The beta coefficients for depth and WDR both suggested similar information: the greater the absolute depth or relative to the width of the reach, the greater the survival. Deep rivers with a low WDR are defining characteristics of channelized reaches of a large river, in agreement with the results in this study that channelized river reaches improved smolt survival.

Turbidity was also found to have a significant influence on survival rates, and the positive beta coefficient indicated that more turbid water improved survival. This theory, explained by decreased predator efficiency in turbid water, has been established in previous research in other large rivers of the west coast, the Fraser and the Columbia (Gregory and Levings 1998, Anderson et al. 2005). In the present study, the concept that smolts use cryptic techniques was corroborated by the finding that smolts exhibited a nocturnal migratory behavior in the clear upper river. As smolts entered the more turbid water of the lower river reaches, the nocturnal pattern became less defined, suggesting that smolts substituted turbidity for nocturnal cover to avoid predation (Michel unpubl. data). In the Sacramento River, water clarity in the lower reaches is reduced in part by tributaries contributing suspended sediment.

Diversions have been known to have an important negative influence on smolt survival, in part due to being physically drawn into the pumps, but also as a location of high predation in response to the aggregation of smolts (Brown and Moyle 1981). However, diversions were not found to have a significant influence on survival rates in this study. In the river reaches used for this analysis, there were a total of 352 water diversions, the majority being found in the lowest river reaches. These same reaches were found to have high survival, and so it seems that the potentially detrimental direct effects of the diversions were not important to outmigrating late-fall run Chinooks salmon smolts within the Sacramento River under the environmental conditions found in 2007-2009. Perhaps the larger size of the late-fall run smolts relative to other salmon populations decreases their susceptibility to entrainment by water diversions. Many diversions are now screened in an attempt to limit the number of smolts that are drawn into the pumps. It should be noted that very large water diversions within the Sacramento – San Joaquin River Delta are thought to have strong influences on smolt survival (Brandes and McLain 2001), a region in which the analysis of the influence of diversions did not extend in the present study.

Although channelization, turbidity, and sinuosity have accounted for a considerable amount of variation in survival rates, other factors also appear to be significant. As an example, the maximum river depth survival model alone was as parsimonious as the fully reach dependent survival model, meaning maximum river depth alone could account for the majority of the spatial-temporal variation in survival in these years. Furthermore, given that month of release significantly affected survival (in 2008 and 2009), two-sample *t-tests* were run and found that both turbidity and WDR were significantly different by month in both years. This is an indication that two of the three important spatial-temporal environmental factors could theoretically be responsible for the monthly variation in survival. In conclusion, attempting to associate environmental variables to survival rates has produced compelling information, reinforcing its merit in understanding survival dynamics in this system, and thus hypothesis 2 is supported.

CONCLUSIONS

This study is one of the first telemetry studies to correlate survival rates with riverine characteristics. Indeed, there were strong associations between environmental variables (such as channel depth) and survival rates. Furthermore, no other salmonid survival study has been able to measure smolt migration survival at such a high spatial resolution. However, some key assumptions and limitations are worth mentioning to promote the continuation and improvement of these studies.

Skalski (1998) determined seven key assumptions related to study design of a single release-multiple recapture study; here I have addressed the three that apply to this study:

Marked individuals are representative of the larger population of interest: This study was limited to hatchery fish due to their increased size and availability over wild fish, and therefore I can theoretically only extrapolate this study's findings to hatchery populations with confidence. However, being that the wild (natural-origin) and hatchery-origin populations share similar individual sizes and migration times, the two populations are likely both encountering the same sources of mortality during their migration. Furthermore, results from the natural-origin late-fall run Chinook salmon smolt pilot study suggest reach-specific survival estimates in the Sacramento River are the same as for the hatchery-origin smolts used in this study.

Survival and detection likelihood are not influenced by tagging or sampling: To address these issues, a series of tagging effects experiments were conducted concurrently with the study on smolts from the same population, late-fall run Chinook salmon smolts from Coleman National Fish Hatchery. Results show that tagging had no effect on survival within the first 34 days (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data), a timeframe allowing for the majority of tagged smolts to migrate completely out of the Sacramento river and estuary (Michel unpubl. data). Additionally, swimming performance tests showed no statistical difference in maximum swimming speeds between tagged and control fish (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data).

All tagged fish are correctly identified as either alive or dead: The first situation that could violate this assumption is if a fish is deemed dead when it is actually alive. This could happen if a fish sheds its tag and is therefore deemed dead. During the above mentioned survival experiments, there was not a single recorded case of tag ejection. The reciprocal is when a fish is deemed alive when in fact it is dead. This could happen when a predator eats a tagged fish and proceeds to migrate while having the tag in its gastric system. With the technology available today, there is no definitive way of knowing if you are tracking the predator instead of your study species (Vogel 2010). For this study, the migration path was plotted over time and space for each individual fish and visually inspected, and all suspicious migratory behaviors (such as a fish moving continuously downstream then suddenly turning around and moving back upstream, sometimes past the original release location) were removed. However, it is likely minor inaccuracies occurred in the survival estimates. Perhaps advances in tag technology will allow for a system for detecting when a tagged smolt has been consumed in the near future.

Due to the limited availability of environmental data in the Sacramento – San Joaquin Delta and San Francisco Estuary, environmental factors were only associated with survival in the regions beyond tidal influence. Nevertheless, while such a study has already been attempted (Kjelson and Brandes 1989), future work should explore these relationships in the delta and estuary using the methodology presented in this paper.

The use of the seaward Golden Gate line to calculate the detection efficiency of the river-ward line has some shortcomings. Tidal currents are notoriously strong at the Golden Gate, and these currents do affect detection probabilities (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data). Due to the close proximity of the two Golden Gate lines (within 2 km), strong tides affect the lines' detection probabilities similarly, which could result in fish being detected by neither line, leading to the under-estimation of survival to ocean entry. Thus, survival estimates for the last reach (reach 17), from Richmond Bridge to the Golden Gate, represent minimum estimates of survival, and true survival could be significantly higher.

One conclusion that could be extrapolated from this study is the apparent need to channelize the entire Sacramento River and artificially raise turbidity. While such modifications may improve survival of outmigrating yearling late-fall run Chinook salmon smolts, many other Chinook salmon life stages would be negatively impacted (Buer et al. 1989), potentially resulting in further declines in already dwindling salmonid populations.

The reach-specific survival estimates provide resource managers with the first high-resolution survival information for the Sacramento River watershed, allowing the identification of high mortality reaches for Chinook salmon smolts and the factors that may cause mortality. For the most part, ongoing efforts to improve Chinook salmon smolt survival have concentrated on anthropologic influences within the delta.

While the findings presented here do not disagree with this emphasis, more attention toward low survival in the upper river and estuary is warranted. This suggests the need to not overlook natural processes in influencing survival of a species.

This study also provides insight into how survival dynamics might be structured for U.S. Endangered Species Act (ESA) listed Sacramento River Chinook salmon populations, which could facilitate conservation measures. Specifically, the Sacramento River winter run Chinook salmon population is considered to be endangered by the ESA, and smolts from this population are known to outmigrate from the Sacramento River over the same time window, at similar sizes (approximately 120 mm), using the same routes. It is likely that the survival dynamics and environmental associations are similar for the late-fall run and winter Chinook salmon populations.

Finally, analytic exploration of possible environmental causes are valuable not only for ecological understanding of the smolt life-history stage, but also to increase capabilities of improving survival and making stock predictions incorporating environmental conditions.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for eventual recovery, and this can not be achieved without understanding the survival dynamics and causal mechanisms of arguably the most vulnerable life stage. This study provides novel information on the small scale temporal and spatial survival dynamics, on the total survival throughout the entire migration, and finally provides suggestions on what environmental factors could be driving these dynamics, and how.

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

Year	Weight ± SE (g)*	Fork length ± SE (mm)*	Sample size
ALL	46.0 ± 0.4	161.5 ± 0.5	804
2007	46.6 ± 0.7^a	164.6 ± 0.8^a	200
2008	52.6 ± 0.8^b	168.7 ± 0.8^b	304
2009	38.9 ± 0.5^c	152.1 ± 0.5^c	300

*Size distributions with different superscripts are significantly different ($P < 0.05$)

Table 2. Locations of acoustic monitors and tagged fish release locations.

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
I-80/50 Bridge Sacramento	189	Monitor location
Freeport	169	Monitor location
Chipps Island	70	Monitor location
Benicia Bridge	52	Monitor location
Carquinez Bridge	41	Monitor location
Richmond Bridge	15	Monitor location
Golden Gate East Line	2	Monitor location
Golden Gate West Line	1	Monitor location

Table 3. Sources of environmental data for this study.

Environmental variables	Data source*	Data Location
Water temperature (ºC)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow ($m^3 \cdot sec^{-1}$)	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel velocity ($m \cdot sec^{-1}$)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †
Channel depth (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †
River surface width (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †
Water diversions ($diversions \cdot km^{-1}$)	CalFish Passage Assesment Database	http://nrm.dfg.ca.gov/PAD/Default.aspx
Riparian habitat type (% of total)	DWR Land Use Survey	http://www.water.ca.gov/landwateruse/lusrvymain.cfm
Riprap (% of total shore)	DWR, USACE, USFWS Sacramento River Bank Survey	Adam Henderson, James Oliver *pers. comm.* †
Levees (% of total shore)	DWR	Alison Groom *pers. comm.* †

*Agency Acronyms: UCD= University of California - Davis, BOR= United States Bureau of Reclamation, DWR= California Department of Water Resources, USGS= United States Geological Survey, USFWS= United States Fish and Wildlife Service, USACE= United States Army Corps of Engineers

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Table 4. Survival to ocean entry by release group for each year, including an estimate for survival for all release groups combined for both 2008 and 2009 (representing total survival from rkm 518 to ocean), and a total estimate for a release groups and years combined. The column "# at Golden Gate" represents actual detected smolts, while "% of release ± SE (modeled)" represents the product of reach-specific survival for all reachs using estimates from CJS model (and therefore accounting for detection efficiency). "*ALL*" in release column represents the total studied watershed survival, combining release group survival for each reach. In some cases (2008), comparatively lower survival in lower reaches for 412 and 363 release groups accounted for "*ALL*" survival to ocean being lower than survival for 518 release group over the same distance.

Year	Release (rkm)*	# released	# at Golden Gate	% survival to ocean ± SE (modeled)
2007	518[†]	131[†]	4	3.1 ± 1.5
2008	518	102	6	6.1 ± 2.4
	412	101	9	8.9 ± 2.8
	363	101	7	7.2 ± 2.6
	ALL			3.8 ± 0.9
2009	518	100	4	4.3 ± 2.1
	412	100	12	13.2 ± 3.8
	363	100	8	8.1 ± 2.7
	ALL			5.5 ± 1.2
ALL	*ALL*			3.9 ± 0.6

*distance (kilometers) from Golden Gate

[†] smolt mortality in Battle Creek not included

Table 5. Survival rates and detection probabilities by reach for all years combined.

Region	Reach #	Rkm from Golden Gate	% Survival·10km^{-1} ± SE	Detection probability ± SE (of downstream station)
Upper Sacramento River	1	518 - 504	96.8 ± 0.8	0.93 ± 0.01
	2	504 - 492	94.7 ± 1.3	1.00 ± 0.00
	3	492 - 456	91.5 ± 0.9	0.90 ± 0.02
	4	456 - 421	93.1 ± 1.0	0.93 ± 0.02
	5	421 - 412	95.2 ± 1.9	0.93 ± 0.02
	6	412 - 389	94.1 ± 0.9	0.87 ± 0.02
	7	389 - 363	92.6 ± 1.1	0.92 ± 0.02
	8	363 - 325	94.2 ± 0.7	0.52 ± 0.03
Lower Sacramento River	9	325 - 309	98.9 ± 1.2	0.58 ± 0.03
	10	309 - 226	99.1 ± 0.3	0.71 ± 0.03
	11	226 - 189	98.1 ± 0.6	0.75 ± 0.03
	12	189 - 169	100 ± 0.0	0.82 ± 0.02
Sacramento/San Joaquin Delta	13	169 - 70	93.7 ± 0.5	0.89 ± 0.03
San Francisco Estuary	14	70 - 52	87.8 ± 2.2	0.86 ± 0.03
	15	52 - 41	88.0 ± 4.2	0.81 ± 0.04
	16	41 - 15	90.2 ± 3.0	0.68 ± 0.07
	17	15 - 2	67.0 ± 5.8	0.85 ± 0.06*

*Calculated using the Pt. Reyes Ocean Monitor Line and Golden Gate West Monitor Line

Table 6. Survival models for different study design factors, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities (reach-specific).

Survival (Φ) treatment	**Δ AIC**	**# Parameters**
Reach x Month	0.00	53
Reach + Fork length + Weight	21.20	37
Reach + Fork length	22.30	36
Reach x Year	24.30	71
Reach	24.60	35
Reach + Weight	25.40	36
Reach x Month x Year	31.70	107
Reach x Release site	47.10	59
Reach x Release site x Month	60.00	101
Reach x Release site x Year	87.00	119
Reach x Release site x Month x Year	185.70	203
Null model (constant survival)	263.93	19

Table 7. Survival models for spatially varying environmental data, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities.

Model	QAICc	Δ QAICc	# Parameters	Standardized β coefficient ± SE
Full model	2634.8	0	22	
% Riprap shoreline	2687.6	52.8	14	1.04 ± 0.22
% Levee shoreline	2697.9	63.1	14	0.61 ± 0.13
Sinuosity	2703.1	68.3	14	0.46 ± 0.10
Diversions·km^{-1}	2707.0	72.2	14	0.55 ± 0.15
% Natural riparian habitat	2714.3	79.5	14	-0.45 ± 0.13
% Agriculture riparian habitat	2721.3	86.5	14	
% Urban riparian habitat	2725.4	90.6	14	
Base model (constant survival·km^{-1})	2725.5	90.7	13	

Table 8. Survival models for spatially and temporally varying environmental data, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities.

Model	QAICc	Δ QAICc	# Parameters	Standardized β coefficient ± SE
Full model	1975.1	0.0	17	
Max channel depth (m)	1978.4	3.3	24	1.91 ± 0.28
Turbidity (ntu)	2001.4	26.3	24	1.52 ± 0.27
Width/Depth (WDR)	2012.2	37.1	24	-0.64 ± 0.12
Flow ($m^3 \cdot sec^{-1}$)	2039.0	63.9	24	
Base model (constant survival·km^{-1})	2039.5	64.4	23	
Channel velocity ($m \cdot s^{-1}$)	2040.2	65.1	24	
Temperature (ºC)	2041.5	66.4	24	

Table 9. Comparisons of spatial-temporal environmental variables by year and month of release that had a significant effect on late-fall run Chinook salmon smolt survival using a two-sample T-test.

2-sample T-test		Depth		Turbidity		WDR	
Year	**Month**	**Mean**	**P**	**Mean**	**P**	**Mean**	**P**
2008	Dec	5.4	0.43	9.0	< 0.01	37.2	0.02
	Jan	5.2		6.7		34.7	
2009	Dec	5.3	0.03	4.4	< 0.01	37.0	< 0.01
	Jan	5.9		6.0		33.0	

Figure Captions

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

Fig. 2. Conceptual model of ecosystem influences on late-fall run Chinook salmon smolt survival in the Sacramento River.

Fig. 3. Percent survival per 10 km per reach for all three study years combined. Figure is delimited based on the regions identified on the associated map. Error bars represent 95% confidence intervals.

Fig. 4. Cumulative survival of all smolt release groups by study year. Reach 1 represents the uppermost reach, and reach 17 represents the lowest reach, at the ocean entry at the Golden Gate. Error bars represent 95% confidence intervals.

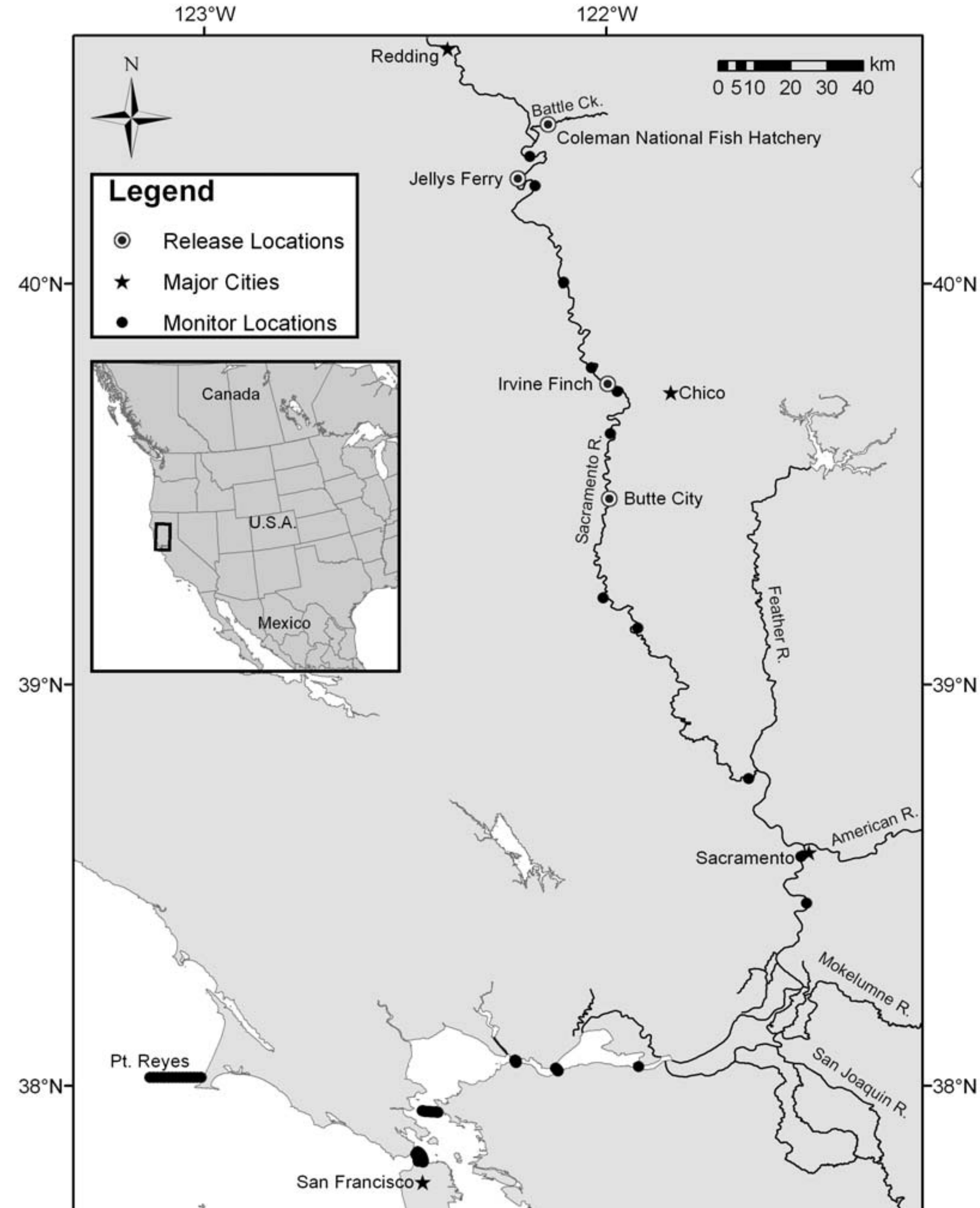
Fig. 5. Cumulative survival of outmigrating smolts by month of release in (a) 2008 and (b) 2009 study years. Reach 1 represents the upper-most reach, and reach 17 represents the lowest reach, in the San Francisco Bay Estuary. Error bars represent 95% confidence intervals.

Fig. 6. Percent survival per 10 km per reach for the wild and hatchery smolt groups over 15 river reaches (rkm 475-169 (Freeport)). Reach numbering is not the same as employed in remainder of paper, 2009 year allowed for the use of more monitor locations due to increased detection efficiencies. Black square symbols represent wild survival, and gray circle symbols represent hatchery survival. Associated error bars represent 95% confidence intervals.

Fig. 7. Percent survival per 10 km per reach (squares) for all three study years combined for the non-tidally influenced reaches of the Sacramento River (reaches 1-12), plotted with the % of total riverbank per reach that is either riprapped (dotted line) or leveed (dashed line). Survival error bars represent 95% confidence intervals.

Fig. 8. Percent cumulative survival of hatchery released smolts to adult return (to the spawning grounds). This represents a hypothetical example of the contribution of outmigration mortality (value used is all year survival of 3.9%) to the total smolt-to-adult rate (long term average for Coleman hatchery late-fall run Chinook salmon smolts 0.53%). Cumulative months since departure represents the approximate life stage timeline for adult late-fall run Chinook salmon returning as age 3 fish, the most common returning age class (Fisher 1994). The line between

3.9% and 0.53% does not represent true survival rate by month or per life stage, it assumes constant survival.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U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
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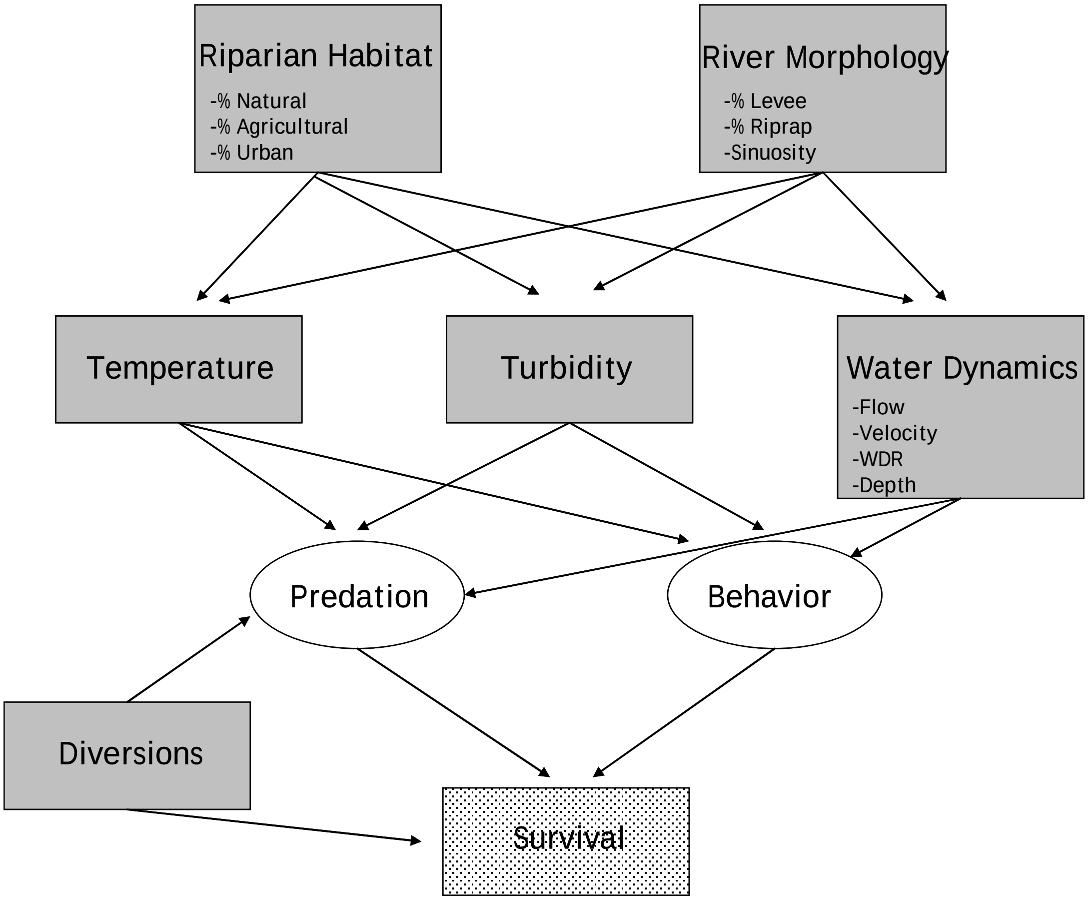
San Joaquin R.
Pt. Reyes
San Francisco
40°N
39°N
38°N

Fig. 1


Riparian Habitat
-% Natural
-% Agricultural
-% Urban
River Morphology
-% Levee
-% Riprap
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Water Dynamics
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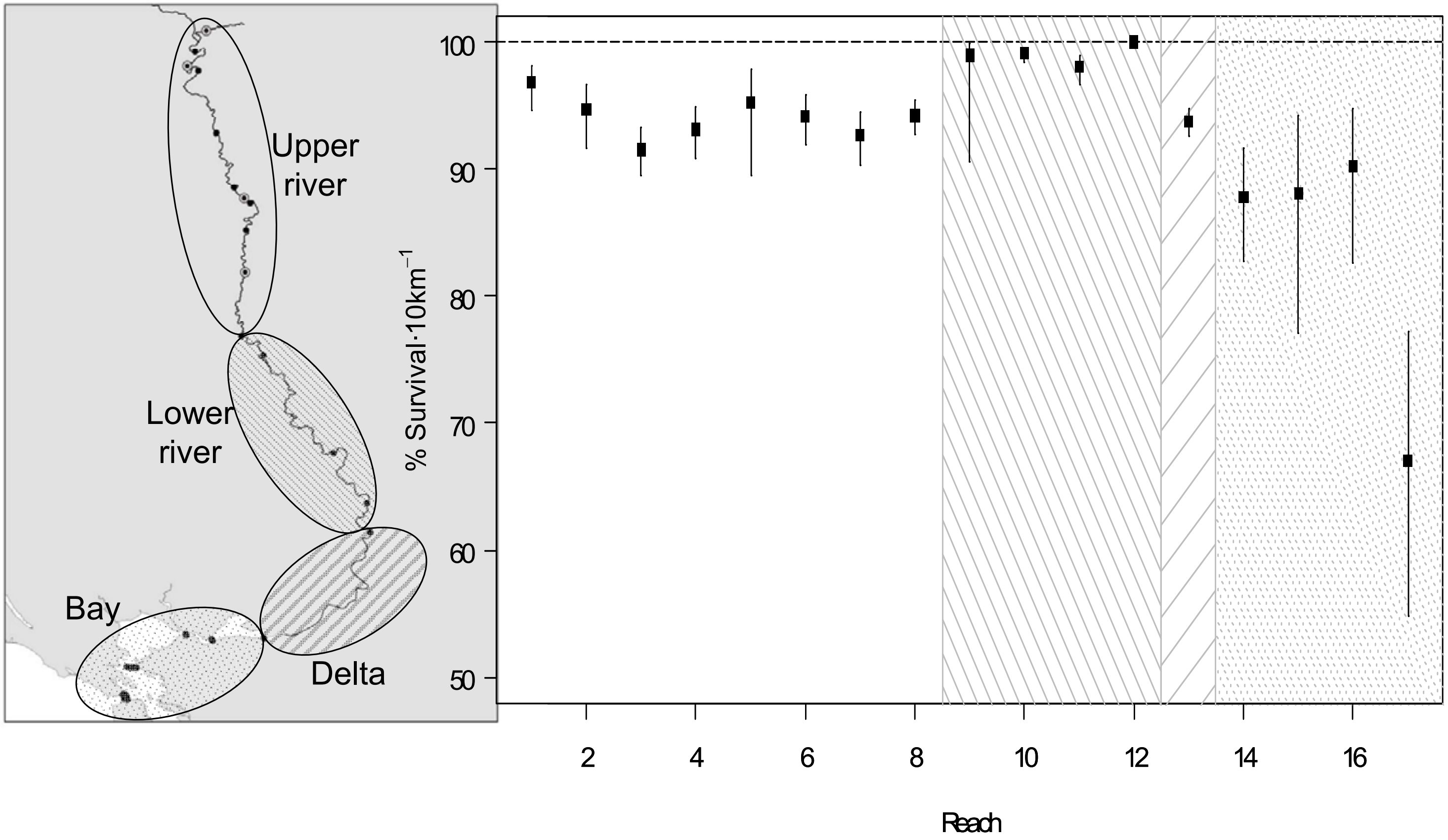
-WDR
-Depth
Predation
Behavior
Diversions
Survival

Fig. 2


Upper river
Lower river
Delta
Bay
% Survival·10km^{-1}
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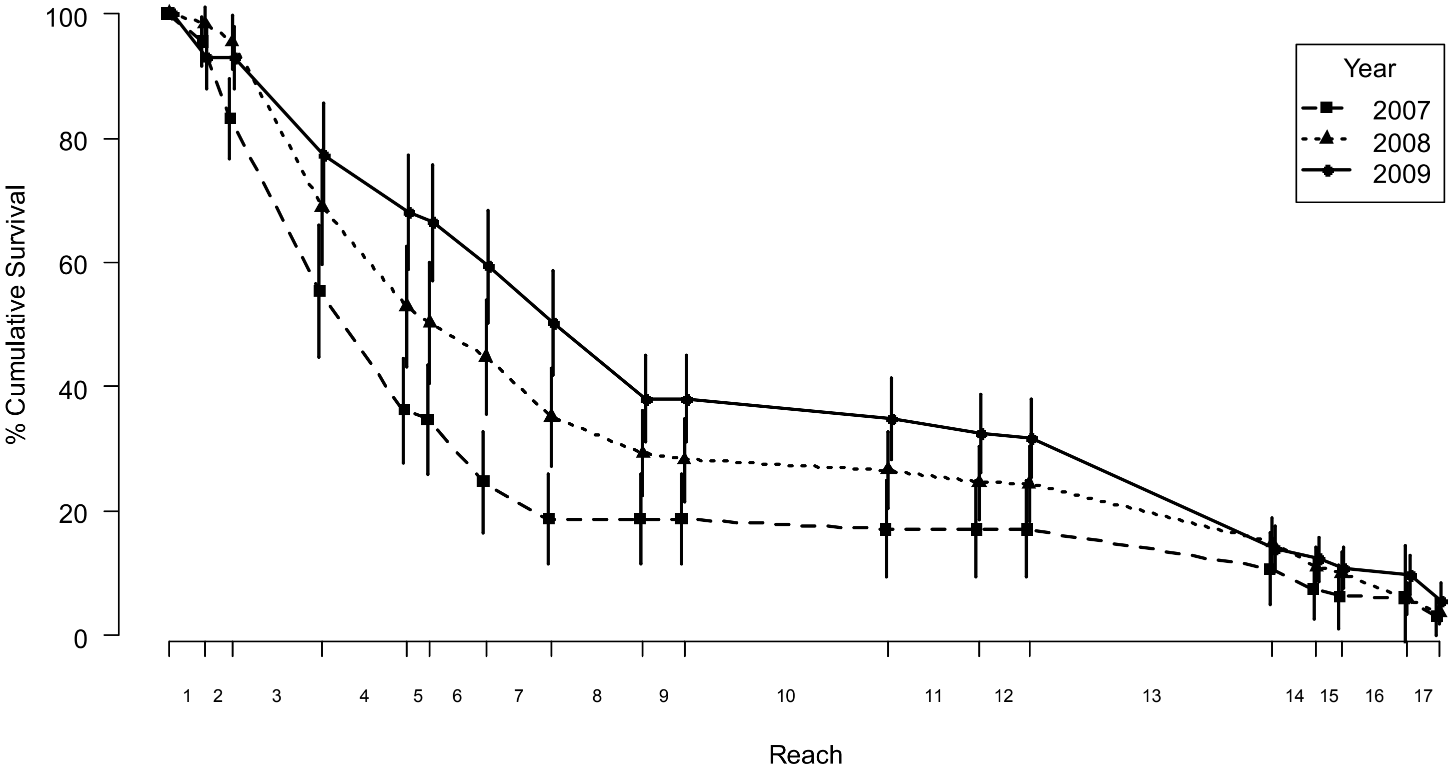
16
Reach

Fig. 3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Year
2007
2008
2009

Fig. 4

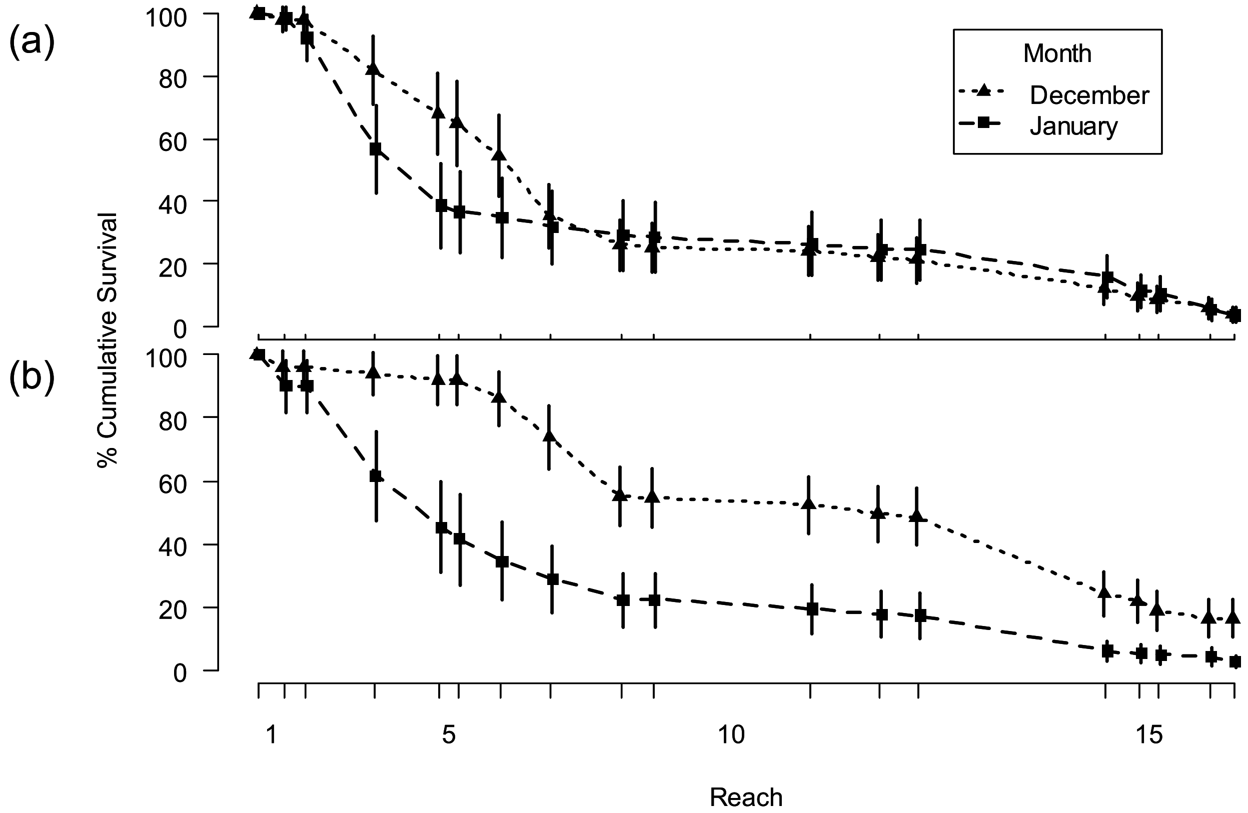
(a)
(b)
% Cumulative Survival
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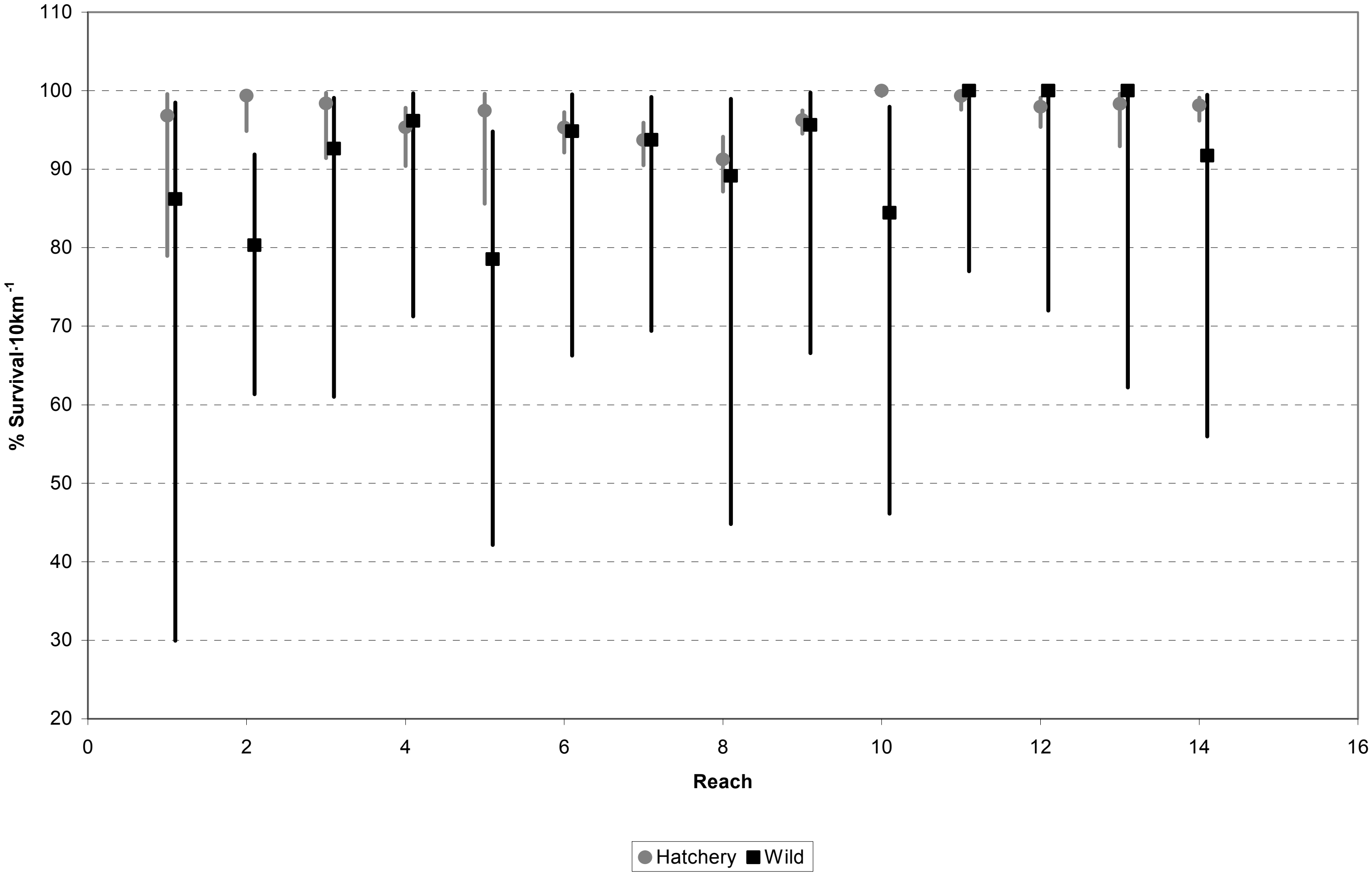
Fig. 5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% Survival·10km^{-1}
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Reach
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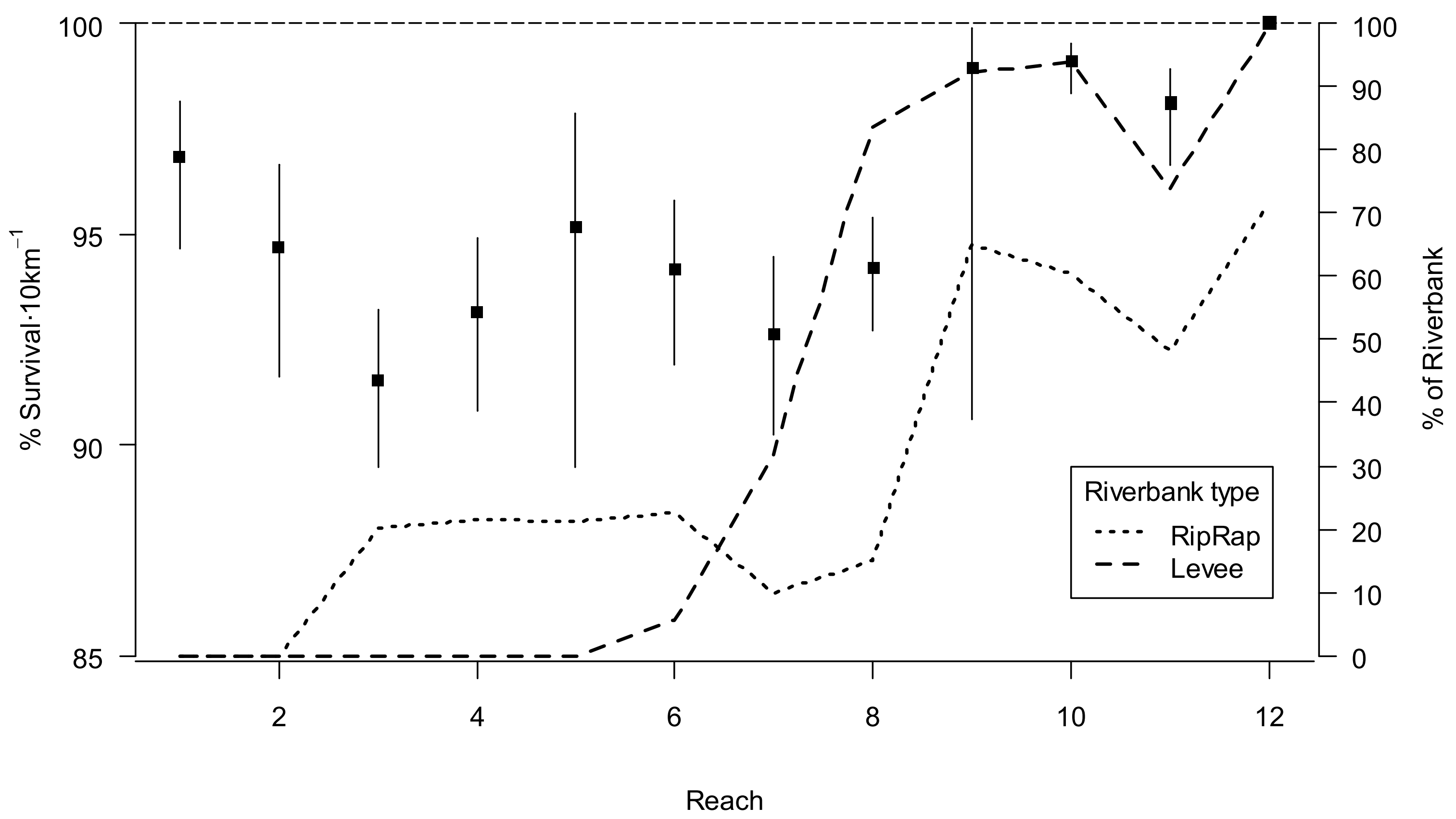
Fig. 6



100
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85
% Survival·10km^{-1}
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12
Reach
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40
30
20
10
0
% of Riverbank
Riverbank type
RipRap
Levee

Fig. 7

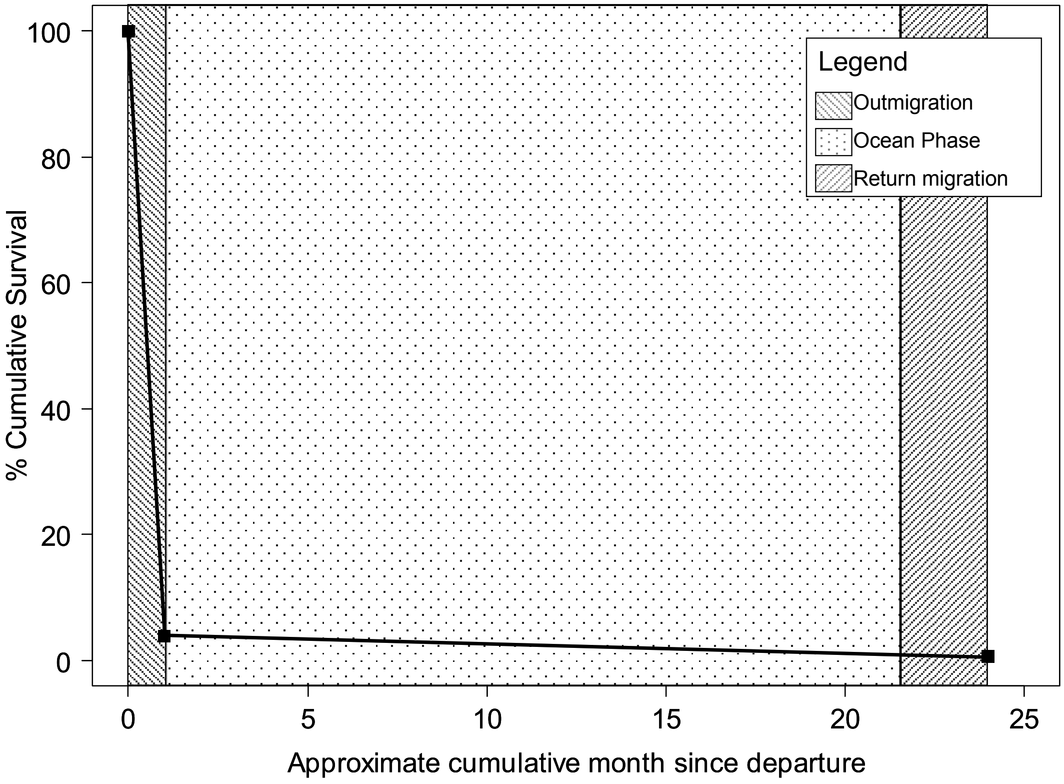
100
80
60
40
20
0
% Cumulative Survival
0
5
10
15
20
25
Approximate cumulative month since departure
Legend
▨ Outmigration
Ocean Phase
▨ Return migration

Fig. 8

Chapter 2

The effects of environmental factors on the migratory patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*)

INTRODUCTION

Migrations in the animal kingdom have fascinated humans for centuries, and their associated folklore is intrinsically tied to many different cultures and beliefs. Perhaps none are more written about or culturally important than the Pacific salmon migrations. Specifically, the Chinook or “king” salmon have fascinated people for ages due to their sheer size, power and determination.

The term migration can have a multitude of definitions, but with respect to salmonids, perhaps migration is best defined by Dingle and Drake (2007) as “a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable or unfavorable (including one region in which breeding occurs)”. In this paper I attempt to better understand the beginning half of this migration, the migration of juvenile salmon from their riverine nursery to the food-rich ocean, often considered one of the most vulnerable stages in a Chinook salmon’s life (Healey 1991). During this life stage, juvenile salmon undergo many morphological, physiological, and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River’s Chinook salmon populations, this freshwater journey may be as long as 600 kilometers, transiting many different habitats, all with varying natural conditions. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed.

Studies have been investigating the timing and patterns of juvenile salmonid migrations on a large-scale focus for decades. Thorpe and Morgan (1978) tracked juvenile Atlantic salmon (*Salmo salar*) fry periodicity during outmigration in Scottish Rivers. Raymond (1968) calculated migration rates by marking and recapturing yearling Chinook salmon smolts traveling through the Snake and Columbia Rivers and their impoundments. However, to best comprehend the intricacies of the migration, one must understand that a migration is determined by the fine scale movements that constitute it. New fish tracking technologies have allowed the exploration of small-scale movement during migration. These technologies have already yielded high-resolution migration data on steelhead (*Oncorhynchus mykiss*) smolts in the Cheakamus River in British Columbia, Canada (Melnychuk et al. 2007), and on sockeye salmon (*Oncorhynchus nerka*) smolts in the Fraser River in British Columbia, Canada (Welch et al. 2009). Once small-scale movement information is attainable, our knowledge of salmon migrations can begin to delve into what might be governing variability in movement patterns.

A few studies have explored how environmental conditions might be influencing migration dynamics (Giorgi et al. 1997, Smith et al. 2002), but at large spatial and temporal scales. These relationships are therefore usually limited to inter-annual and inter-population comparisons, thereby only uncovering the strongest and most persistent of patterns. Smaller-scale, more subtle environmental factors may also exert significant influences on salmonid movement patterns, which may have higher order population consequences. Elucidating these require incorporation of high-resolution movement data.

I have structured this study to answer the two following hypotheses:

(1) Total migration and reach-specific movement rates of outmigrating late-fall run Chinook salmon smolts vary spatially and temporally in the Sacramento River, Sacramento-San Joaquin Delta and San Francisco Estuary.

(2) Environmental variables can explain a substantial portion of variation in reach-specific movement rates.

This study aims to capitalize on one of the largest networks of acoustic monitors in the world developed by the California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu/), and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to provide the first high-resolution analysis of the spatial and temporal variation of Chinook salmon movement and migration in the Sacramento River and San Francisco Estuary. Using this information, I will provide insight into which environmental variables (natural and anthropogenic) explain variations in movement patterns. Finally, relating migration and movement dynamics to smolt survival will be the important final step in understanding the intricacies of this life stage.

This work is essential for improving both our basic ecological understanding and management of salmon. It represents an advancement in our awareness of the environmental factors that likely influence the out-migration of late-fall run Chinook salmon smolts. Without this type of information, resource managers are unable to consider the consequences of anthropogenic activities that may have detrimental effects on salmon populations, or predict migration dynamics of future cohorts facing environmental changes. Finally, assessing what environmental conditions influence variation in late-fall run Chinook salmon movement will provide guidance into factors affecting the movement dynamics of other valued salmon runs in California.

METHODS

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river to be fully contained within the state of California, and is the third largest river that flows in the Pacific Ocean in the contiguous United States (Fig. 1). The headwaters are located slightly south of Mount Shasta in the lower Cascade Range, and the river enters the ocean through the San Francisco Estuary at the Golden Gate Bridge. The total catchment area spans approximately 70,000 km^2.

The Sacramento River and its tributaries have been heavily dammed, and it is estimated that approximately 47% of the historic area that was used for spawning, migration and/or rearing of Chinook salmon is no longer accessible (Yoshiyama et al. 2001). The Sacramento River watershed includes diverse habitats, from a pristine run-riffle meandering river, to a heavily channelized and impacted waterway further south, to an expansive tidally-influenced freshwater delta at its confluence with the San Joaquin River, and finally to the San Francisco Bay Estuary, the largest and most modified estuary on the West Coast of the United States (Nichols et al. 1986). The annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 $m^3 \cdot s^{-1}$ (Interagency Ecological Program 2004), however, it is estimated that today, water discharge of the Sacramento and San Joaquin Rivers combined amounts to approximately 40% of the historical, pre-colonization 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, notably reducing the historical winter high flows and flooding (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 Battle Creek (534 km upstream from the Golden Gate) is only 47 km downstream from Keswick Dam, the first impassable barrier to anadromy (Table 1).

Central Valley late-fall run Chinook salmon

The California Central Valley, which includes the Sacramento and San Joaquin Rivers and their tributaries, has four distinct Chinook salmon populations (runs) that migrate at different times of the year. Additionally, these populations demonstrate one of two early life history strategies: "ocean-type" and "stream-type" (Gilbert 1912). Ocean-type Chinook salmon are born in the lower reaches of large rivers and spend very little time (days to weeks) in the river before migrating to the ocean. Stream-type juveniles are born in the headwaters of large rivers or tributaries and spend up to a year in the river (yearling) before migrating to the ocean at a relatively large size. Among the different runs and early life history strategies, it becomes clear that different populations have found different migration strategies to maximize survival (Taylor 1990).

The late-fall run is one of the four runs found in the Sacramento River drainage, and is the only run to exhibit a predominately stream-type life history (Moyle 2002). Coupled with the fall run, the pair form an evolutionary significant unit (ESU) deemed a "species of concern" by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which smolts will enter the ocean at a size of approximately 160 mm (Fisher 1994). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

The historical distribution of the late-fall run Chinook salmon is hard to estimate, due to the paucity of historical data. Late-fall run Chinook salmon were not distinguished from fall run fish until 1966, when counts were initiated after the construction of the Red Bluff Diversion Dam (RBDD) in the mid 1960s (Yoshiyama et al. 1998). However, we know that ideal late-fall run spawning habitat consists of year-round cold water allowing the rearing of yearlings, and that their current spawning range is from Red Bluff (480 river km (rkm) upstream from the Golden Gate) up to the first barrier to anadromy, Keswick Dam (rkm 565) (Fisher 1994, Moyle et al. 1995, Yoshiyama et al. 2001). We assume that this run historically used the cold waters upstream of Keswick Dam, specifically the Upper Sacramento, McCloud and Pit Rivers for spawning (Yoshiyama et al. 1998). Since these rivers are no longer accessible, the large majority of late-fall run Chinook salmon spawning grounds disappeared with the construction of Keswick and Shasta Dams.

Acoustic Telemetry

I used Vemco V7-2L acoustic tags (1.58g ± 0.03 S.D.; Amirix Systems, Inc. Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible monitors to track tagged fish. The monitor array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate) (Fig. 1). This array of approximately 300 monitors was maintained by the California Fish Tracking Consortium (a group of academic, federal and state resources agencies, and private consulting firms) and positioned to maximize detection probability at key sites along the outmigration corridor.

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subjected to standardized quality control procedures to minimize the number of false detections. For example, detections that occurred before the release date-time of each tag or detections that did not share a tag identification number with any of the released fish were excluded from analysis.

Tagging and Releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 300 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged fish (Table 2) was consistent with the observed size frequency for this Chinook salmon run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery origin yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Approximately 85-90% of the hatchery smolts are the progeny of hatchery-origin adults trapped in Battle Creek (tributary to the Sacramento River); the remaining hatchery smolts' parents are natural-origin adults trapped on the mainstem Sacramento River just below Keswick Dam (K. Niemela, USFWS, Red Bluff, CA 96080, unpubl. report).

Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized fish as described by two studies (Adams et al. 1998a, Martinelli et al. 1998). To minimize potential effects on survival, growth and behavior, tag weight did not exceed 5% of the total body weight. This cutoff point was conservative, considering much of the literature shows tag-to-body ratios can be up to 6% and not effect growth (Moore et al. 1990, Adams et al. 1998a, Martinelli et al. 1998), and up to 8% and not affect swimming performance (Moore et al. 1990, Adams et al. 1998b, Brown et al. 1999, Anglea et al. 2004, Lacroix et al. 2004).

Post-surgery, the fish were kept in captivity for a minimum of 24 hours to ensure proper recovery from surgery. In the 2007 season, a portion of the tagged fish were released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

Fish were transported at low densities (~ 10 $g \cdot l^{-1}$) via coolers with aerators to the release sites. In years of multiple release sites, transport times were extended for closer sites to keep potential transport stress equal among all release groups. In the first year of the tagging effort (2007), all 200 fish were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter two years, 300 fish a year were tagged and released simultaneously from three release sites in the upper 150 rkm of the mainstem Sacramento River, allowing the lower release groups a greater likelihood of reaching the lower river and estuary in large numbers (to improve statistical confidence intervals).

Data Analysis

After the three-year study was completed, monitor locations were assessed for their tag detection probability and functional reliability over the three-year period (Michel unpubl. data) and their location within the watershed. Detection efficiencies are calculated by assessing the number of tags missed by a monitor location. This can be done if a missed tag is seen at a downstream location and therefore we can assume it had to pass the upstream location. Detection probabilities were calculated using the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) within Program MARK (created by Gary White, Colorado State University (White and Burnham 1999)). Those monitor locations that had consistently high tag detection probabilities and that were strategically located were chosen to delimit the river reaches that were used in spatially comparing movement. A total of 19 monitor locations were chosen, from just below the most upstream release site to the Golden Gate (Table 1).

Hypothesis 1

Total elapsed time from release site to the Golden Gate was calculated for each smolt that survived to the Golden Gate (3-13% of all smolts, depending on release group and year (Michel unpubl. data)) and averaged per release group (by year and release site), representing mean total outmigration time. Respective fish movement rates ($km \cdot day^{-1}$) from release site to ocean entrance at the Golden Gate monitoring location were also calculated and averaged per release group, representing the mean successful migration movement rate (MSMMR). A two-factor (year and release site) analysis of variance (ANOVA) was performed to determine the influence of year and release site on total movement rate. Reach-specific and smolt-specific movement rates were then calculated using the last detection time from the upstream monitor locations and the first detection time from the downstream monitor locations. Distances between monitor locations were calculated in kilometers using the geographic information system software program ArcGIS (ESRI, 1999), giving a movement metric of kilometers per day over ground. Reach-by-reach movement rates were also averaged among all detected smolts, and then associated to the detection probabilities of each reach's upstream and downstream node. The product of the two detection probabilities equals the proportion of individual movement rates sampled out of all the individual smolts that are estimated to have traversed each reach.

Once movement rates were calculated, I tested for the influence of the study design factors. The outmigration corridor was then delimited into 5 different regions for the ensuing ANOVA. The regions were the run-riffle upper Sacramento River, the deeper and more uniform middle Sacramento River, the deep and channelized lower Sacramento River, the tidally influenced Sacramento-San Joaquin River Delta, and finally the San Francisco Estuary. I averaged reach-specific and smolt-specific movement rates per region. I then tested for the assumption of homogeneity of variance and of normal distributions among the groups of observations. If these assumptions were true, I then used a mixed-effect ANOVA, which allows for both fixed factors (such as year and region) and random factors (in this case individual fish) to test for the effect of year, month, release site, and region. Including region as a factor can be a source of non-independence of measurements. An individual will travel through different regions, and could theoretically express individual variation in movement rates. The mixed-effect ANOVA can statistically test for fixed factor effects while controlling for individual variation.

As fish were only released from one location during one month in the first year (three locations and two months in the other two years), the preliminary linear mixed-effect ANOVA did not test for the influence of release location on movement rates. Therefore, the analysis tested for year, region, the interaction of the two, and for the random factor.

To determine the influence of release location and month on movement rates, a second mixed-effect ANOVA was then performed excluding data from the 2007 season. This ANOVA included the factors of year, region, release site, release month, all interaction terms, and the random factor.

While these analyses will test for large-scale variation in movement rates (by year and by month), small-scale variation in movement was also calculated. An hourly reach-specific metric of movement was calculated, consisting of the frequency of novel smolt arrivals per hour of the day for each monitor location. Novel reach arrivals per hour were then summed for each region, giving a frequency distribution of hourly fish movement per region.

A contingency table was then constructed to test if any discernable hourly arrival pattern varies across regions. This was used to determine if there is contingency (non-independence) between the two factors, region and hour of arrival (or a binning of these). For this, Pearson's chi-squared test of independence was used (tests the null hypothesis that the two factors are not related).

Hypothesis 2

Environmental data were collected for this study for the majority of the river reaches, from the release points to the upper limit of tidal influence on the river (river km (rkm) 189; Table 3). Environmental variables collected can be grouped into two types: several spatial-temporal variables and one purely spatial variable. All variables were chosen *a priori* based on salmon migration literature and data availability for the watershed.

The single spatial variable was river sinuosity (actual river length divided by the length of a direct line between the nodes delimiting each reach). The temporally varying spatial variables included water temperature (ºC), river flow ($m^3 \cdot s^{-1}$), water turbidity (Nephelometric Turbidity Units (ntu); McCormick et al. 1998), channel water velocity ($m \cdot s^{-1}$), and a ratio of river surface width (m) to maximum river depth (m) (WDR; Tiffan et al. 2009). The WDR will increase as the river becomes shallower and wider. Spatial-temporal variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 3). Measurements such as water velocity and WDR were simulated incorporating actual flow recordings, high resolution bathymetric cross-sections and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers 1995). All spatial variables were calculated using the program ArcGIS.

All reach-specific spatial-temporal environmental variables were then averaged by reach and by day. Spatial variables were averaged per reach. All reach-specific spatial and spatial-temporal environmental variables were then associated with their respective reach-specific movement rates in a relational database (Microsoft SQL Server 2005, Microsoft Corporation). When a specific smolt movement spanned several days, weighted averages of the appropriate daily spatial-temporal environmental variables were used. A Pearson's correlation test was then performed to calculate correlation coefficients for each environmental variable, similar to Smith et al. (2002). Additionally, the statistical significance of each environmental correlation coefficient on movement was calculated.

Different environmental variables are frequently correlated with one another, and caution must be employed to minimize spurious conclusions. I therefore calculated all Pearson's correlation coefficients between variables that had strong influences on movement rates. When there was a significant relationship between two environmental variables ($r^2 > 0.7$ and $P < 0.05$ (Giorgi et al. 1997)), the lesser of the two movement-correlated variables was dropped from further analysis.

Once the more influential environmental variables were determined, their means and standard errors were calculated to the resolution of each significant study design factor (e.g. if year was significant, mean and standard error were calculated for each year). Using this information, I suggest hypotheses for how the environmental variables may have influenced spatial and temporal variability in movement rates.

RESULTS

Hypothesis 1

The mean successful migration movement rate (MSMMR) and total outmigration time per release group varied by release site and by year (Table 4). Mean total movement rates decreased the further downstream the release group was released. Movement rates varied from 14.32 $\text{km}\cdot\text{day}^{-1}$ (± 1.32 S.E.) for the 2009 Butte City release group (rkm 363) to 23.53 $\text{km}\cdot\text{day}^{-1}$ (± 3.64 S.E.) for the 2007 Battle Creek release group (rkm 534). Total outmigration time increased the further downstream the release group was released, varying from approximately 39 days for the 2008 Butte City release group to approximately 24 days for the 2007 Battle Creek release group. Analysis of variance confirmed this pattern: release location had a significant effect on MSMMR ($P < 0.05$), while year did not (P 0.2).

Reach-specific movement rates varied substantially from 15.3 $\text{km}\cdot\text{day}^{-1}$ in the Sacramento-San Joaquin River Delta to 89.1 $\text{km}\cdot\text{day}^{-1}$ in a reach of the upper river region (Table 5). The proportion of fish sampled varied due to differences in detection efficiencies throughout the watershed.

The distributions of movement rates per year and per region did not violate the assumptions of homogeneity of variances and of normal distributions were not violated, and therefore the mixed-effect ANOVA was performed. Results from the initial all-years mixed-effect ANOVA, including region and year factors, showed that region had a significant influence ($P < 0.001$) on the variation in movement rates, as well as the interaction between region and year (i.e. the relative movement rates among regions differed among years; Table 6). Year did not have a significant effect on movement rates (P 0.07), but still warrants further investigation (Fig. 2). Movement rates decreased as fish moved from upstream regions downstream toward ocean entry, with the fastest movement rates found in the upper river region, and the slowest in the Sacramento-San Joaquin River Delta (Fig. 3). The interaction between region and year suggested a similar trend in 2007 and 2008 of generally decreasing movement rates the further downstream the region is, but in 2009, movement rates were generally slower and more uniform among regions (Fig. 4). As expected, the random factor, individual fish, was significant ($P < 0.001$), suggesting that there was great variation in movement rates among individual fish.

Results from the 2008 and 2009-effect ANOVA included the additional factors of release month and release site (Table 7). Results from this analysis indicate a significant influence of region and the interaction between year and region (P <0.001) as was the case for the three-year analysis. The large majority of interactions including the region factor were significant. The influence of year, release site, and release month on the variation in movement rates was not significant, although again year had a strong, but statistically insignificant, influence on movement rates (P 0.07).

Smolt movement varied substantially per hour, notably in the upper and middle river regions, where the majority of daily movement occured between midnight and 700 hours, then again from 1700 hours and midnight, suggesting a nocturnal movement (Fig. 5). The nocturnal pattern in arrivals seemed to lessen in strength the further downstream the region is found, to the point where in the estuary, smolts moved at all times of the day. To determine if the nocturnal pattern truly varied in strength per region, a Pearson's chi-squared test of independence was performed. Hour of arrival was therefore binned into two groups, day hours (arrival hours 7-17) and night hours (arrival hours 0-6, and 18-23) based on average sunrise and sunset during the time period of the study. A five-by-two contingency table of arrivals was created with the categorical factors of day/night and region. A Pearson's chi-squared test of independence indicated that the night/day arrival factor was significantly dependent on region (P <0.001).

Hypothesis 2

Several variables tested had significant relationships with movement rate ($P < 0.001$; Table 8). Reach sinuosity had the strongest association with movement rates, suggesting that the more sinuous a river reach is, the faster a fish will travel through it. Width-to-depth ratio (WDR) had a negative relationship with movement rates, suggesting that the deeper and narrower reaches (low WDR) will have faster movement rates. Water velocity and river flow were both positively related to movement rates. Temperature was also positively related to movement rates, but was a relatively weak predictor of variability in movement rates. This suggests that smolts moved faster through faster flowing water, greater volume of water flow, and narrower-deeper channels.

All selected environmental variables were then tested for correlations among each other. No variables were found to be overly correlated using previously mentioned cutoff ($r^2 > 0.7$ and $P < 0.05$). However, while not significant, the negative relationship between WDR and sinuosity ($r^2=0.27$, $P < 0.001$) was the strongest correlation.

Mean sinuosity was seen to vary among region in a generally decreasing trend from the upper river down to the lower river (Table 9). Mean water velocity also followed this trend, with a sizeable decrease in regional mean velocity between the middle river and the lower river. Mean water velocity also varied among years, with a generally decreasing trend from 2007 to 2009.

DISCUSSION

Hypothesis 1

Mean successful migration movement rate (MSMMR) varied significantly by release location but did not vary significantly among the three years of the study. Effectively, movement rates were consistently slower the further downstream a group was released. Consequently, the mean total outmigration time for each group reflected this strong pattern: the further downstream a group was released, the longer the group took to reach the ocean. Therefore, smolts released further upstream, closer to their native nurseries, are exhibiting behavioral differences relative to the downstream released smolts with regard to migration that suggest that environmental cues that trigger migration are subdued or absent from the lower, more distant sites from their evolutionary migration origin.

Migration rates from the Battle Creek release site to the ocean in 2007 (23.53 km·day^{-1}) were very similar to migration rates of late-fall run Chinook salmon smolts released at the same site and recaptured at the beginning of the San Francisco Estuary in a previous study (20.63 km·day^{-1}, USFWS data 1998-2003, www.delta.dfg.ca.gov/usfws/maps/index.htm). The mean migration rate for yearling Chinook salmon smolts on the Columbia River, another large West Coast river, was 21.5 km·day^{-1} (Giorgi et al. 1997). Although migration rates of yearling Chinook salmon on the Fraser River are not available in the literature, similarly sized sockeye salmon (*Oncorhynchus nerka*) smolts navigated the watershed at a rate of 15 to 30 km·day^{-1} (Welch et al. 2009). The results for late-fall Chinook salmon smolts presented here in combination with those of yearlings from other studies strongly suggest that like-sized smolts exhibit very similar migration rates regardless of river they reside in.

Reach-specific movement rates displayed substantial variation among reaches and within reaches for some of the lower reaches. Specifically, the movement rates within the estuary have the largest variability. This is likely due to the influence of tidal dynamics on movement rates, as seen by Lacroix and McCurdy (1996) with Atlantic salmon (*Salmo salar*) smolts.

While mean movement rates appeared to be fastest in 2007, slower in 2008, and slowest in 2009, movement rates did not differ significantly among years (although there were greater differences than observed in most other factors). Coupled with the fact that MSMMR did not differ significantly among years, this could be misconstrued to suggest that yearly environmental variation has little effect on movement rates in general. However, the three years of the study were all similarly dry years resulting in low freshwater flows (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). Therefore, movement rates and environmental associations found in this study may only be indicative of variation among similarly dry years.

The large majority of movement, particularly in the river regions, was nocturnal, which has been seen by other studies (McCormick et al. 1998, Ibbotson et al. 2006). This has often been suggested to be a predator avoidance strategy, particularly from visual predators like some fish and birds (McCormick et al. 1998, Ibbotson et al. 2006).

In addition to stealth by night movement, water turbidity has been shown to reduce predation (Gregory and Levings 1998), and warmer water temperatures allow for more efficient predator evasion in salmonid smolts due to increased neuromuscular escape responses. Also seen by Ibbotson et al. (2006), this is particularly interesting because the nocturnal migration pattern dissipates in the lower river region, which had higher turbidity and warmer water temperatures, suggesting smolts may only use night travel as a predator avoidance strategy until water turbidity and water temperature is protective enough to allow migration at all hours.

In conclusion, I find that hypothesis 1 is supported. There is evidence for both spatial (by region) and temporal (by hour and by year (although not significantly)) variation in movement rates for the three years of this study and it is likely that environmental variability is a contributor.

Hypothesis 2

River sinuosity had the strongest relationship with movement rates among the measured environmental variables. The relationship suggested that the more sinuous river reaches exhibited faster smolt movement rates. Sinuosity is associated with channel complexity and diverse flow velocities. In the Sacramento River, the most sinuous river reaches are also the most natural and unmodified reaches. Therefore, if a smolt were to seek the fastest water velocities in the river's cross-section, it would benefit from more energy-efficient movement (Kemp et al. 2005) and expedite transit. Since some of the greatest river velocities occurred in the reaches with the greatest sinuosity, where late-fall run smolts moved the fastest, this association may be operative.

Width-to-depth ratios (WDR) were found to have a moderately strong negative relationship with movement rates, meaning that the narrower and deeper reaches would exhibit faster smolt movement. This relationship is counter-intuitive when considering that the lower river region had the slowest river movement rates and also had the lowest WDR. However, the upper river region did not have the highest mean WDR, suggesting that the fast movement rates in this region may be associated to medium to low WDR values, driving this relationship. Additionally, WDR was also found to associate negatively with sinuosity, suggesting that the narrower and deeper reachs (low WDR) are relatively more sinuous. The correlation between WDR and sinuosity (Pearson's correlation coefficient (r) -0.52), and between sinuosity and movement rates (r 0.53), were both substantially stronger than the correlation between WDR and movement rates (r -0.26), leading me to the conclusion that the counter-intuitive direction of the correlation between WDR and movement rates may be an indirect effect through the intermediary of the much stronger relationship between sinuosity and movement rate.

Flow has often been suggested to influence movement rates (Giorgi et al. 1997). In this study, flow was found to be positively related with movement rates. Flow generally increases in the downstream direction, in large part due to the progressive addition of flow from the numerous tributaries in this system. However, the mean flows experienced by smolts in this study were very similar across regions.

One possible interpretation of the relationship between flow and movement could be that it is the temporal (and not the spatial) variability in flow that drives this relationship. Salmonid smolts are known to initiate their downstream migration during storm events (McCormick et al. 1998), analogous with high flows. Additionally, there was evidence of increased watershed-wide smolt movements during particularly strong storm events. I therefore conclude that the relationship between flow and movement rate is potentially due to drastic increases in flow.

Movement rates and velocity were found to be positively correlated. Faster water velocities can help a smolt move downstream at faster rates by increasing passive transport. This relationship was believed to be the most important environmental factor *a priori,* however, the strength of the correlation was not as strong as some of the other relationships. A reason for this could be that the nocturnal behavior of smolts in the upper river decreases the total number of hours that smolts devote to migration. Although smolts moved the fastest in the upper regions of the river, movement rates would likely have been faster if the smolts travelled at all times of the day and benefitted from the maximum potential of the substantially faster water velocities.

Variation in water velocities and nocturnal movement were assessed in an attempt to explain regional differences in movement rates. I found that nocturnal movement decreases progressively as smolts moved further downstream toward the ocean, with smolts moving more continuously. However, lower river reaches also exhibit slower movement rates, probably in part due to the substantially slower water velocities. This could suggest a trade-off between predator avoidance via nocturnal travel upstream and increased continuous daily movement downstream when velocities do not provide relatively efficient passive transport. Although turbidity was not seen to influence movement rates directly in this study, turbidity may increase survival by decreasing predator efficiency (Michel unpubl. data). Thus, increased daylight migration (increasing daily travelled distance, thereby reducing temporal exposure to predators) coupled with increased turbidity may act in concert to improve predator avoidance during seaward migration.

Of the environmental variables found to have a significant relationship with movement rates, only water velocity was found to fluctuate similarly to the yearly fluctuations in movement rates. Mean water velocity declined between 2007 and 2009, while mean and region-specific movement rates followed the same trend. This evidence supports the *a priori* theory that water velocity may be one of the key factors influencing yearly differences in movement rates.

The evidence that fluctuations in river sinuosity and water velocities could explain spatial and temporal variation in movement rates, I find that hypothesis 2 is supported.

CONCLUSIONS

The relationship between movement patterns and migration strategies with environmental factors allows hypothesizing on which factors have the most important effect. Relating these same movement and migration patterns to immediate survival provides invaluable information on the success of the different strategies, and in turn provides evidence for how those strategies might have evolved.

Survival data from these same late-fall run individuals, with respect to release location shows that the furthest upstream release site group (rkm 518) experienced the worst survival, but the middle release site group (rkm 413) experienced the highest survival (Michel unpubl. data). Additionally, the smolts experienced relatively low survival in the upper and middle river regions, and high survival in the lower river region. When considered with the MSMMR of these same release groups, it becomes apparent that there could be tradeoff between the benefit of bypassing the upper river region and its high associated mortality, and the detriment of additional temporal exposure to predation of the groups released further downstream. It should be added that while releasing smolts downstream improves survival in some cases, it also increases straying of returning adults, which has been known to be detrimental to natural reproductive success (Quinn 1993).

This low survival in the upper reaches of the Sacramento River coincided with the location of the primarily nocturnal migration, while the high survival coincides with the temporally uniform timing of migration seen in the lower river reaches. Additionally, turbidity was found to have one of the strongest associations with survival rates (Michel unpubl. data). Taken together, these results suggest that the relatively clear waters of the upper and middle river regions have much higher predation rates, which in turn may have formed the nocturnal migration strategy to minimize mortality. The lower river region, being more turbid and therefore more hospitable to smolt survival (Gregory and Levings 1998), eased the nocturnal strategy to a more temporally uniform migration allowing smolts to travel larger distances per day.

The slowest movement rates were seen in the Sacramento-San Joaquin River Delta, a highly modified and complex system of sloughs and channels. Furthermore, water diversions in the southern delta remove nearly 40% of the historic flows through the delta, resulting in substantial modifications in flow dynamics and directions (Nichols et al. 1986). The result is a region in which smolts have a high susceptibility of entering the interior delta, predisposing them to longer routes, higher predation from invasive predators, and the risk of entrainment into water pump, inevitably leading to higher mortality rates (Perry et al. 2010). Interestingly, although movement rates were relatively slow compared to other regions, suggesting many smolts were diverted into the interior delta, the survival rate for these same smolts was still higher than in the San Francisco Estuary, and on par with survival rates from the upper river regions.

The delta has long been known to have an important nursery function, especially for subyearling fall run Chinook salmon (Kjelson et al. 1982). However, smolts in this study were in the delta for an average of 6.5 days, a period too short for significant nursery function. This may be because delta and estuarine residency is known to be shorter for yearling Chinook salmon smolts than for subyearlings in many watersheds along the West coast of North America (Healey 1991), but could also be an adaptation due to the above mentioned sources of mortality and the human modification of the delta, leading to dramatically decreased wetlands (Frayer et al. 1989) and potentially as a result, decreased benefits from foraging there.

This study has presented the spatial and temporal variability in movement rates and migration strategy, and supplied evidence that water velocity and nocturnal travel work cohesively in explaining yearly and regional variation in movement rates.

This study has also provided novel information on salmonid smolt migration, and will be valuable to resource managers. However, the study had some limitations that should not be overlooked. Perhaps most importantly, the study occurred during three years of very low precipitation and river flows for the Sacramento River Valley, with 2008 being deemed critically dry (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). Therefore the movement dynamics and environmental associations may be different during years of substantially greater flow.

Another limitation of acoustic telemetry data is that one cannot positively know when a smolt has been eaten by a predator (Vogel 2010). While I attempted to filter the receiver detections to the best of my abilities, it is possible that some minor inaccuracies in movement rates exist from data recorded from predators retaining the tag gastrically. These data, if present, would not change mean calculated movement rates substantially, but does stress the need for tag technology that will allow detection of when a tagged smolt, or any tagged animal, has been consumed.

Finally, due to the limited availability of environmental data in the Sacramento – San Joaquin Delta and San Francisco Estuary, movement dynamics were associated with only environmental factors in the river reaches beyond tidal influence. Future work should explore these relationships in the delta and estuary using the methodology presented in this paper.

The results found in this study provide resource managers with valuable information that can be used to improve survival for the imperiled Sacramento River Chinook salmon populations. This study is the first in the Sacramento River watershed to provide reliable information on the total migration time and high-resolution reach specific movement rates for late-fall run Chinook salmon smolts. This information allows resource managers to better comprehend when and for how long smolts will be migrating, as well as smolt transit times in specific areas in the watershed, thus efficiently guiding the timing and scope of water and riparian development activities.

This study found significant evidence for an increasingly long total outmigration time and MSMMR for groups released progressively further from their native nurseries. This information is especially germane to the release strategies employed by Chinook salmon hatcheries in the Central Valley. A large portion of these hatchery-produced smolts are trucked and released in the estuary to reduce pre-ocean mortality and therefore maximize returns. However, if these smolts react similarly to this study's smolts when released downriver of their natal origins, they may be subject to high predation rates as they slowly acclimate and begin their outmigration. This may be evidence to discontinue the aforementioned hatchery release strategy.

This study also elucidated a strong nocturnal migration pattern during a portion of the outmigration. While other examples of nocturnal migration in salmonids exists in the literature (McCormick et al. 1998, Ibbotson et al. 2006), and may not be novel information to resource managers, the added complexity that the nocturnal migration pattern dissipates as the smolts progressively near the ocean is valuable information. Many detrimental anthropogenic impacts such as pile driving and dredging occur during the day based on the assumption that the fish migrate nocturnally (D. Hampton, NMFS Protected Resources Division, Sacramento, CA 95814, pers. comm.). This study shows that this assumption is not supported in the lower region of the river, as well as in the delta and estuary.

Finally, the hypothesis that water velocity and turbidity co-vary with (and perhaps govern) the extent to which smolts migrate nocturnally will be a useful tool in predicting the migrations of future cohorts facing environmental changes.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for any hope of an eventual recovery, and this cannot be achieved without understanding the movement and migration dynamics and causal mechanisms of emigrating smolts, arguably the most vulnerable life stage. This study provides new insights on small scale temporal and spatial movement dynamics, the migration through the entire watershed, and finally provides suggestions on what and how environmental factors are influencing these dynamics.

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Table 1. Locations of acoustic monitors and tagged fish release locations.

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
I-80/50 Bridge Sacramento	189	Monitor location
Freeport	169	Monitor location
Chipps Island	70	Monitor location
Benicia Bridge	52	Monitor location
Carquinez Bridge	41	Monitor location
Richmond Bridge	15	Monitor location
Golden Gate East Line	2	Monitor location
Golden Gate West Line	1	Monitor location

Table 2. Means and standard errors for weight and fork length of acoustically-tagged smolts by year and for all years combined.

Year	Weight ± SE (g)*	Fork length ± SE (mm)*	Sample size
ALL	46.0 ± 0.4	161.5 ± 0.5	804
2007	46.6 ± 0.7^a	164.6 ± 0.8^a	200
2008	52.6 ± 0.8^b	168.7 ± 0.8^b	304
2009	38.9 ± 0.5^c	152.1 ± 0.5^c	300

*Size distributions with different superscripts are significantly different ($P < 0.05$)

Table 3. Sources of environmental data for this study.

Environmental variables	Data source *	Data Location
Water temperature (ºC)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow ($m^3 \cdot sec^{-1}$)	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel water velocity ($m \cdot sec^{-1}$)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]
Maximum river depth (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]
River surface width (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]

*Agency Acronyms: UCD= University of California - Davis, BOR= United States Bureau of Reclamation, DWR= California Department of Water Resources, USGS= United States Geological Survey, USFWS= United States Fish and Wildlife Service, USACE= United States Army Corps of Engineers

[†] Ricky Doung (rdoung@water.ca.gov); Todd Hillaire (hillaire@water.ca.gov)

Table 4. Mean total outmigration time in days and mean successful migration movement rate (MSMMR) for all years and all release groups.

Year	Release (rkm)*	# released	Mean total outmigration time (days) ± SE	MSMMR ($km \cdot day^{-1}$) ± SE
2007	534	200	24.2 ± 3.3	23.5 ± 3.6
2008	517	102	28.9 ± 2.8	18.9 ± 1.9
	413	101	30.2 ± 5.5	18.1 ± 3.3
	363	101	39.4 ± 3.0	15.6 ± 1.8
2009	517	100	24.5 ± 4.3	22.7 ± 3.1
	413	100	24.7 ± 2.4	18.1 ± 1.3
	363	100	27.1 ± 2.7	14.3 ± 1.3

*distance (river km (rkm)) from Golden Gate

Table 5. Mean movement rates (km·day^{-1}) and the respective proportions of fish sampled for each of the 17 reaches. Proportion sampled is the product of the detection efficiencies from the monitoring stations above and below each specific reach.

Region	Reach	Rkm from Golden Gate	Mean movement rate (km·day^{-1}) ± SE	Proportion sampled ± SE
Upper Sacramento River	1	518 - 504	69.5 ± 1.5	0.93 ± 0.01
	2	504 - 492	89.1 ± 1.7	0.93 ± 0.01
	3	492 - 456	41.2 ± 1.3	0.90 ± 0.02
Middle Sacramento River	4	456 - 421	35 ± 1.7	0.84 ± 0.03
	5	421 - 412	55.3 ± 2.6	0.86 ± 0.03
	6	412 - 389	36.9 ± 1.5	0.81 ± 0.03
	7	389 - 363	35.7 ± 1.7	0.80 ± 0.03
Lower Sacramento River	8	363 - 325	36 ± 1.4	0.48 ± 0.03
	9	325 - 309	56.4 ± 2.1	0.30 ± 0.02
	10	309 - 226	40.9 ± 1.3	0.41 ± 0.03
	11	226 - 189	34.1 ± 1.1	0.53 ± 0.03
	12	189 - 169	26.2 ± 1	0.62 ± 0.03
Sacramento/San Joaquin Delta	13	169 - 70	15.3 ± 0.8	0.73 ± 0.03
San Francisco Estuary	14	70 - 52	18.5 ± 2	0.77 ± 0.04
	15	52 - 41	31.2 ± 4.7	0.70 ± 0.04
	16	41 - 15	26.2 ± 4.2	0.55 ± 0.06
	17	15 - 2	32.8 ± 5.5	0.58 ± 0.07*

*Calculated using the Pt. Reyes Ocean Monitor Line and Golden Gate West Monitor Line

Table 6. Results from the 3-year linear mixed-effect ANOVA looking at the influence of region, year, the interactive term and individual fish on movement rates.

Source	Numerator df	Denominator df	F-Ratio	P
Region	4	534	2.696	<0.001
Year	2	956.953	107.462	0.07
Year x Region	8	534	6.875	<0.001
Individual Fish (random factor)	615	534	1.562	<0.001

Table 7. Results from the 2008-2009 linear mixed-effect ANOVA looking at the influence of region, year, release month, release site, all the interactive terms and individual fish on movement rates.

Source	Numerator df	Denominator df	F-Ratio	P
Region	4	453	3.224	<0.001
Year	1	787.872	1.398	0.07
Month	1	787.872	0.03	0.24
Site	2	807.501	100.287	0.97
Year x Region	4	453	0.223	<0.001
Month x Region	4	453	1.36	0.13
Site x Region	5	453	10.509	0.04
Month x Year	1	789.894	1.765	0.64
Site x Year	2	807.501	1.775	0.37
Site x Month	2	807.501	2.357	0.26
Month x Year x Region	4	453	0.281	0.11
Site x Year x Region	5	453	1.902	0.03
Site x Month x Region	5	453	2.538	0.10
Site x Month x Year	2	807.501	1.887	0.76
Site x Month x Year x Region	5	453	0.454	0.81
Individual Fish (random factor)	484	453	1.244	0.01

Table 8. Results from the Pearson's correlation analysis between all environmental variables and movement rates. P represents whether the correlation's slope is significantly different from zero.

Environmental Variable	**Pearson's Correlation coefficient with Movement Rate (km·day^{-1})**	**P**
Sinuosity	0.53	<0.001
WDR	-0.26	<0.001
Water Velocity (m·s^{-1})	0.21	<0.001
Flow (m^{3}·s^{-1})	0.21	<0.001
Temperature (Cº)	0.06	0.02
Turbidity (ntu)	0.03	0.18

Table 9. Mean and standard error by river region and by year for river sinuosity, river width-to-depth ratio (WDR), water velocity ($m \cdot s^{-1}$), and water flow($m^3 \cdot s^{-1}$). Sinuosity is a spatial variable only, so there are no year values.

Variable	Upper River	Middle River	Lower River	2007	2008	2009
Sinuosity	2.23 ± 0.02	1.57 ± 0.01	1.53 ± 0.01			
WDR	36.4 ± 0.7	42.0 ± 0.3	23.9 ± 0.3	24.0 ± 0.0	47.5 ± 0.5	30.8 ± 0.4
Velocity	0.91 ± 0.01	0.84 ± 0.00	0.29 ± 0.01	0.98 ± 0.01	0.84 ± 0.00	0.50 ± 0.01
Flow	161 ± 1	163 ± 1	159 ± 2	168 ± 1	161 ± 1	159 ± 1

Figure Captions

Fig. 1. Map of the study area, including the Sacramento River, Sacramento – San Joaquin River Delta, San Francisco Estuary, and Pacific Ocean. Bull's-eye icons signify a release locations, stars symbolizes major cities, and black dots symbolizes monitor locations used in final analysis. Shaded regions delimit (from North to South) the upper river, middle river, lower river, delta, and estuary.

Fig. 2. Movement rate distributions per year for all regions combined. These boxplots depict the general decrease in movement rates from 2007 to 2009. The bold horizontal lines that dissect the boxes represents the median values, while the upper and lower edges of the boxes represent the 75th and 25th percentiles of the movement data, respectively. The upper and lower ends of the vertical lines represent the maximum and minimum values of the movement data, unless outliers are present. Outliers are data points that are above the 75th percentile or below the 25th percentile by more than 1.5 times the inter-quartile range (the range from the 25th to 75th percentile) of each specific boxplot.

Fig. 3. Movement rate distributions per region for all years. These boxplots depicts the general decrease in movement rates from the upper river region to the delta. The boxplots are constructed in the same fashion as Fig. 2.

Fig. 4. Stacked boxplot of movement rate distributions per region by year. These boxplots depict the interaction of region and year. The boxplots are constructed in the same fashion as Fig. 2.

Fig. 5. Individual smolt arrivals to new monitor locations per hour, grouped by region. Each plot is a histogram, representing the percent of arrivals for each hour bin out of all arrivals for that region (N).

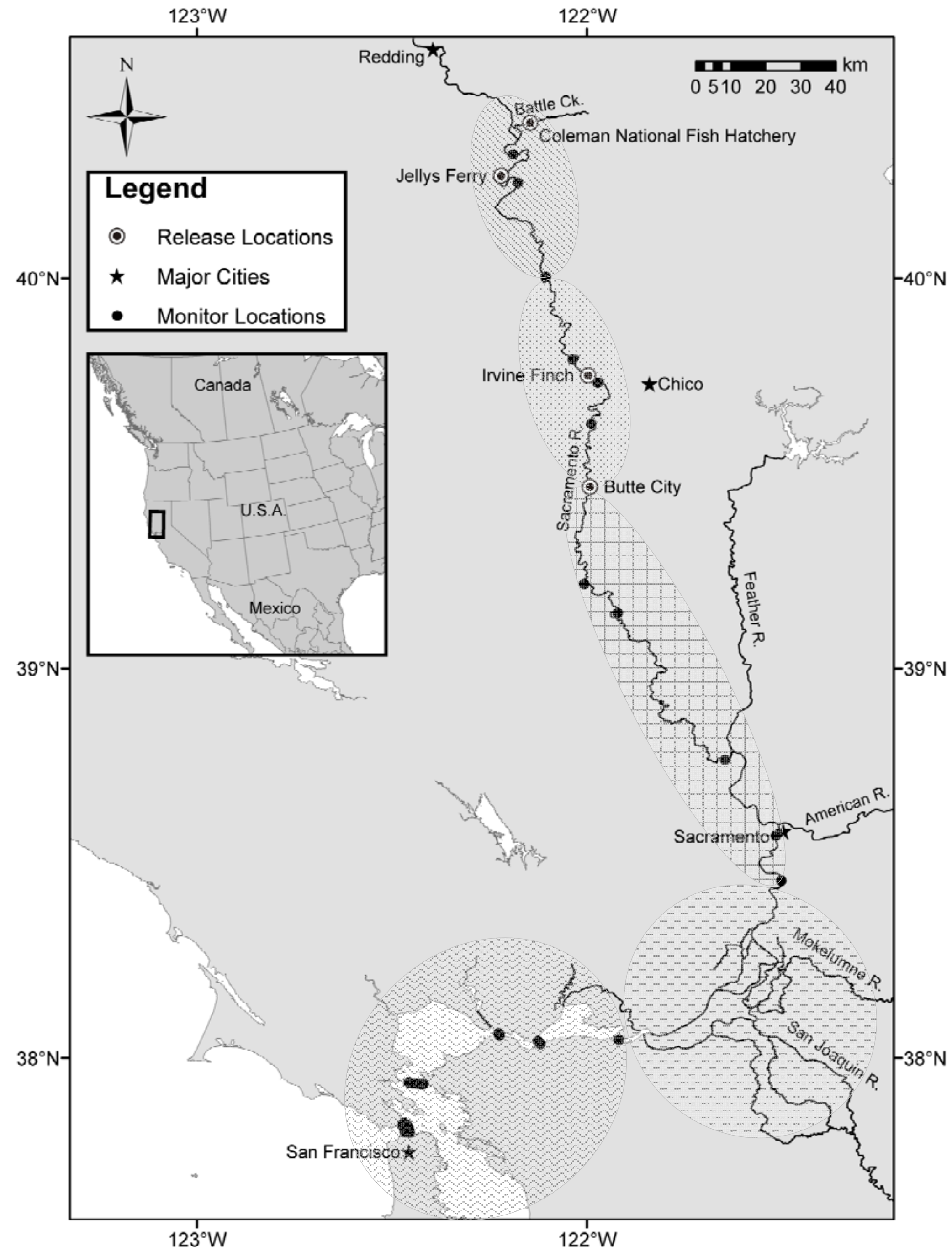

123°W
122°W
N
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
km
0 5 10 20 30 40
Legend
Release Locations
Major Cities
Monitor Locations
40°N
40°N
Canada
U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
39°N
39°N
American R.
Sacramento
Mokelumne R.
San Joaquin R.
38°N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

Fig. 1

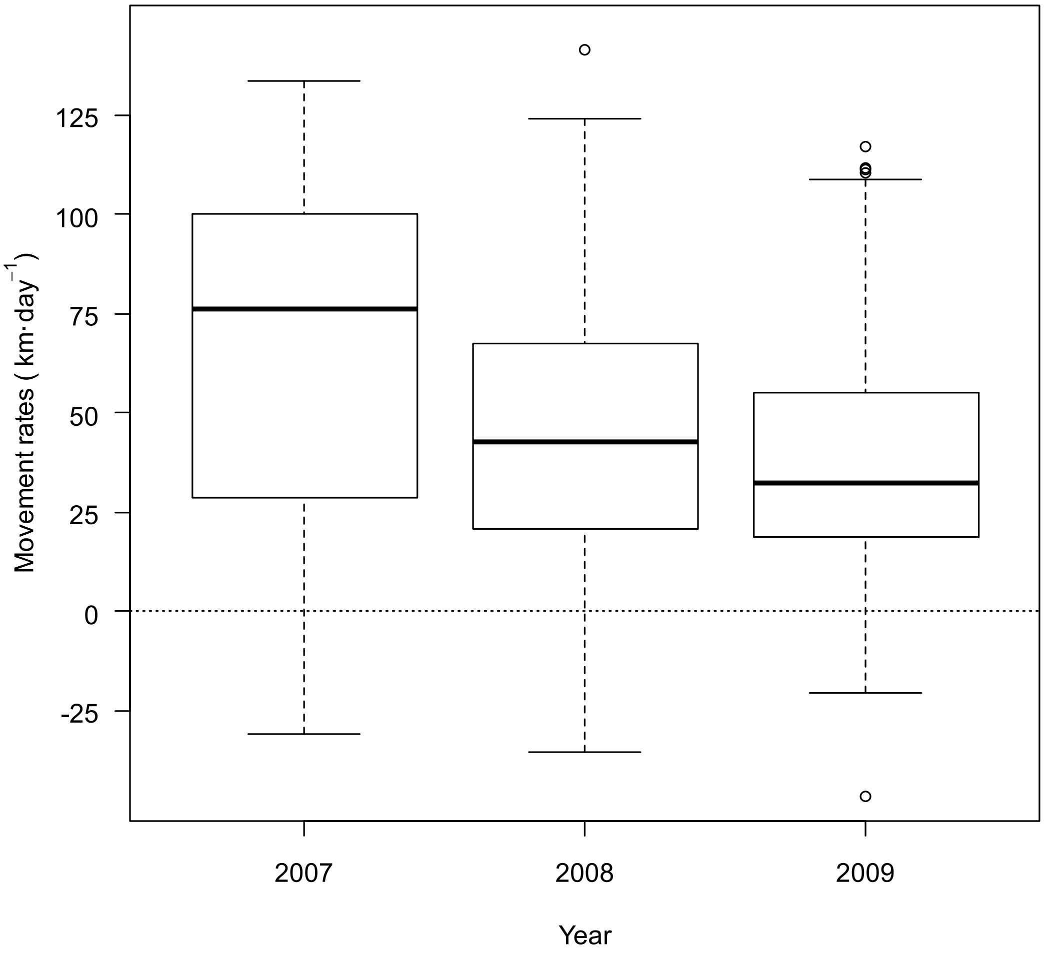

125
100
75
50
25
0
-25
Movement rates ($\mathrm{km \cdot day^{-1}}$)
2007
2008
2009
Year

Fig. 2

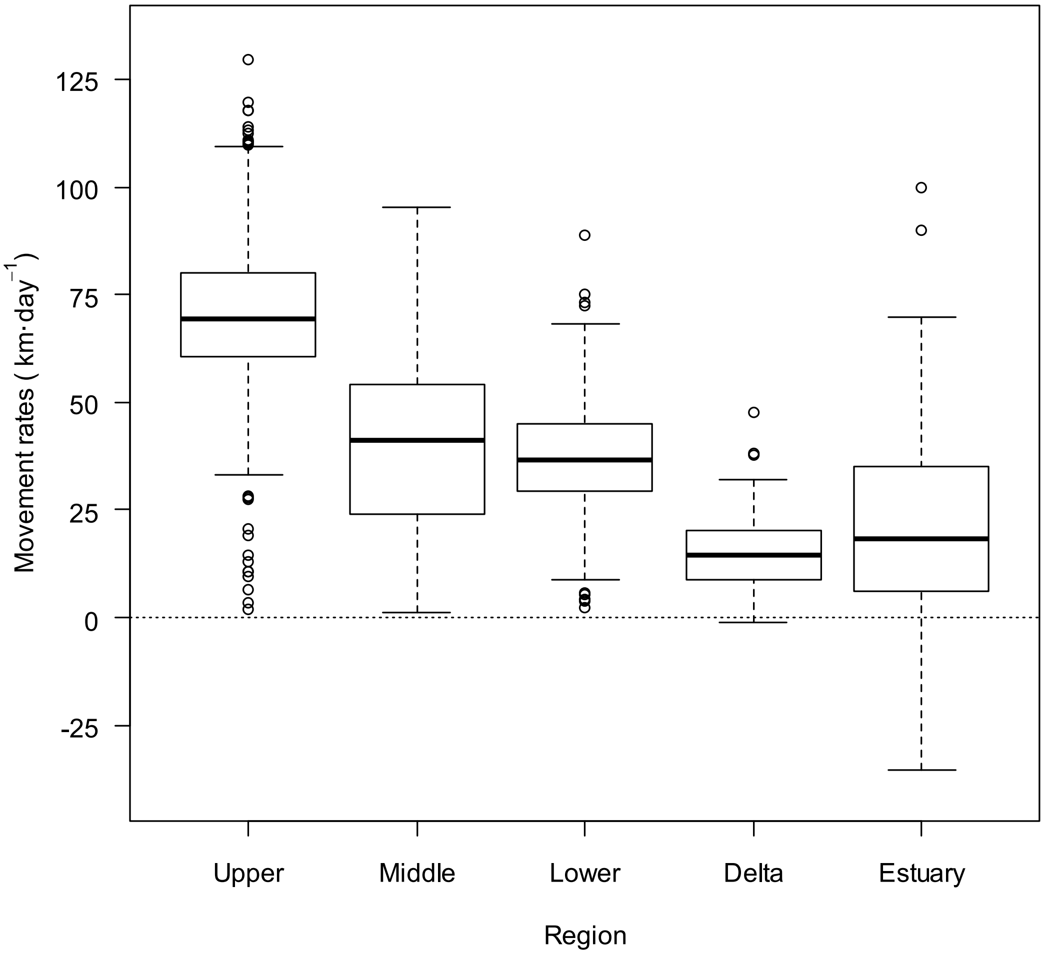

Movement rates (km·day^{-1})
125
100
75
50
25
0
-25
Upper
Middle
Lower
Delta
Estuary
Region

Fig. 3

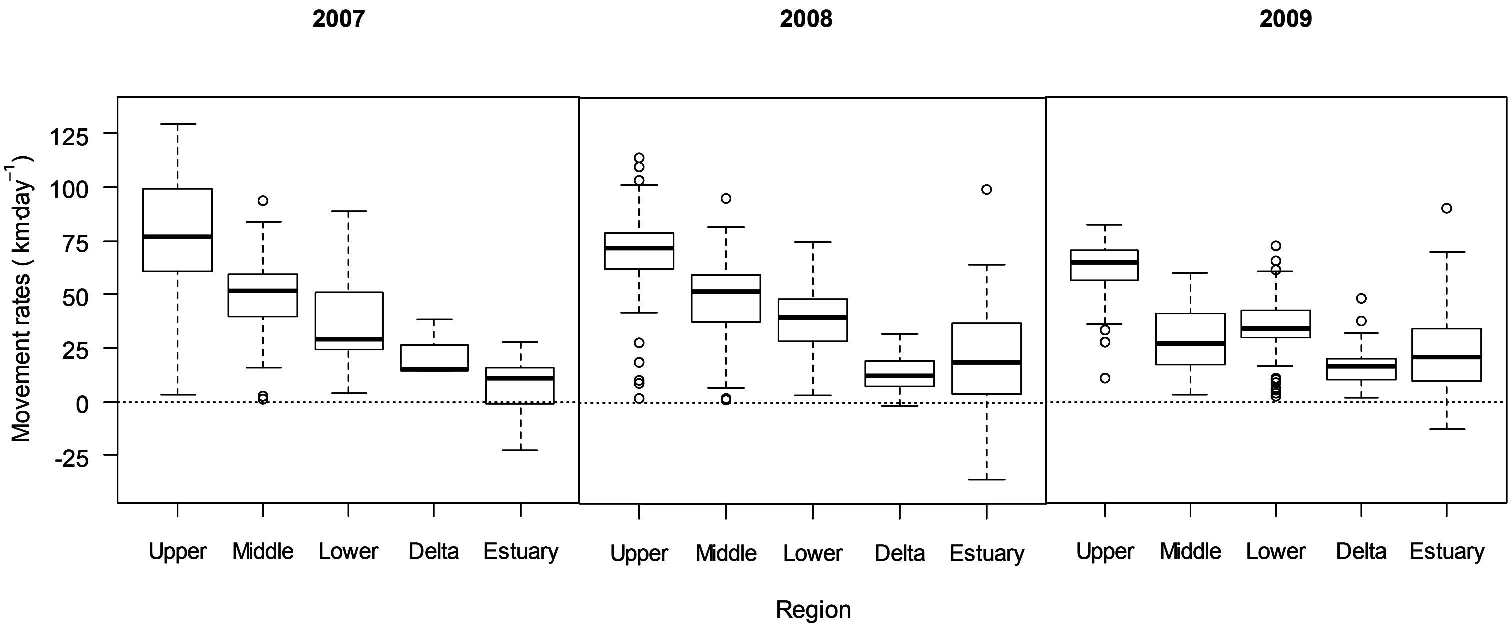
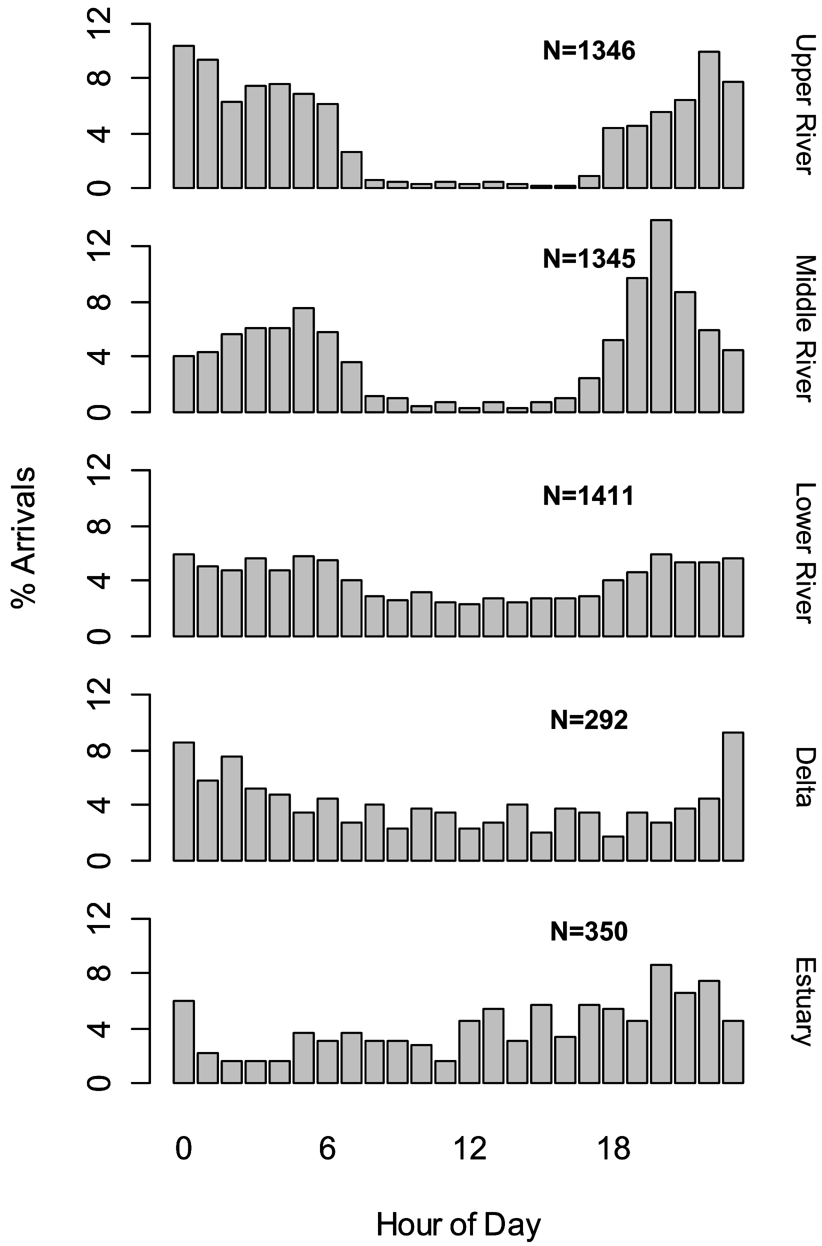

2007
2008
2009
Movement rates (kmday^{-1})
125
100
75
50
25
0
-25
Upper
Middle
Lower
Delta
Estuary
Upper
Middle
Lower
Delta
Estuary
Upper
Middle
Lower
Delta
Estuary
Region

Fig. 4



% Arrivals
0
4
8
12
N=1346
Upper River
N=1345
Middle River
N=1411
Lower River
N=292
Delta
N=350
Estuary
0
6
12
18
Hour of Day

Fig. 5