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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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ABSTRACT

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

by

CYRIL J. MICHEL

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 ($\sim 10\ g\bullet l^{-1}$) 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·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·sec^{-1})	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel velocity (m·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·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.

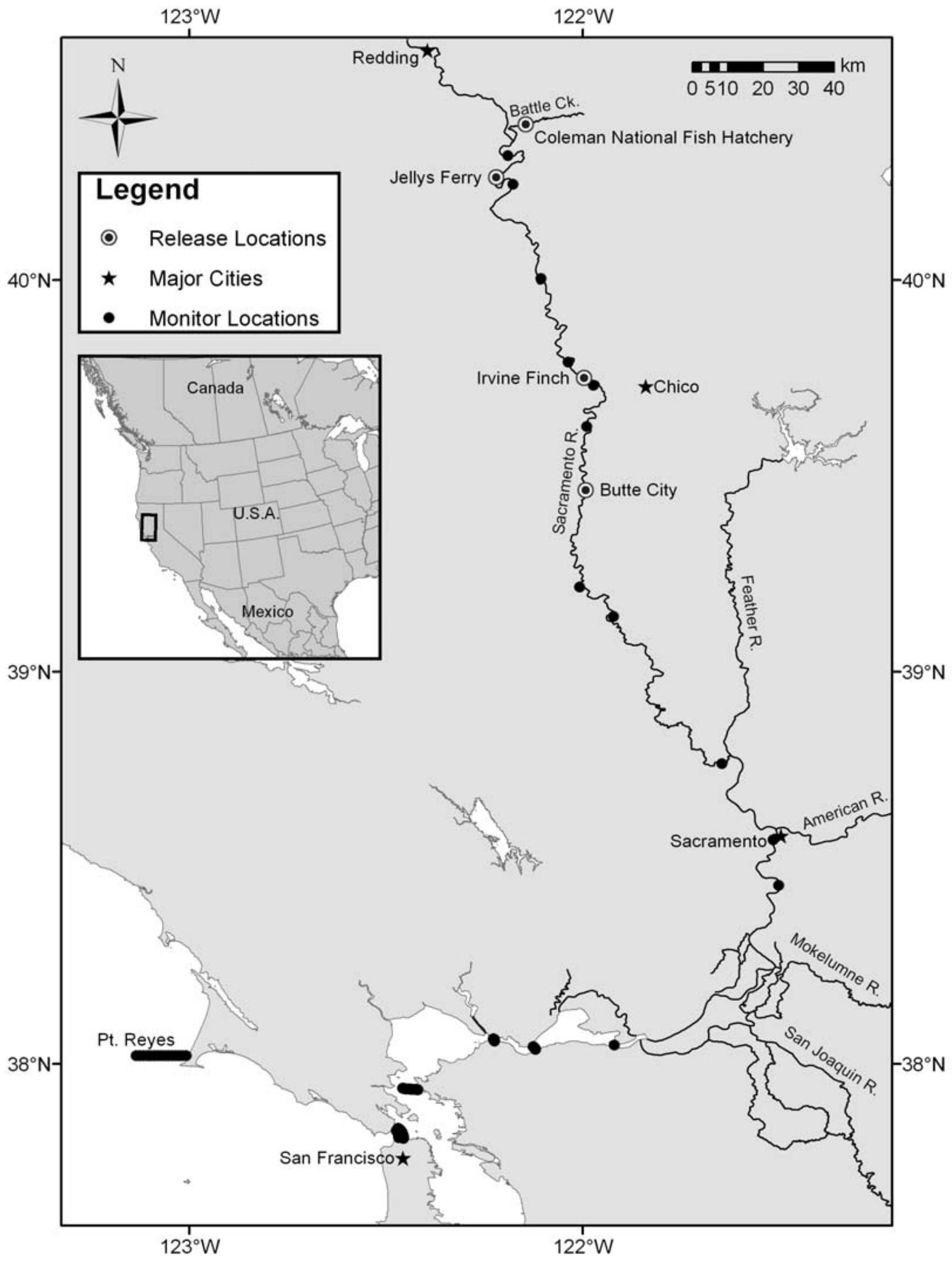

123°W
122°W
N
Redding
km
0 5 10 20 30 40
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
Legend
◉ Release Locations
★ Major Cities
● Monitor Locations
40°N
Canada
U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
39°N
American R.
Sacramento
Mokelumne R.
San Joaquin R.
Pt. Reyes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

Fig. 1

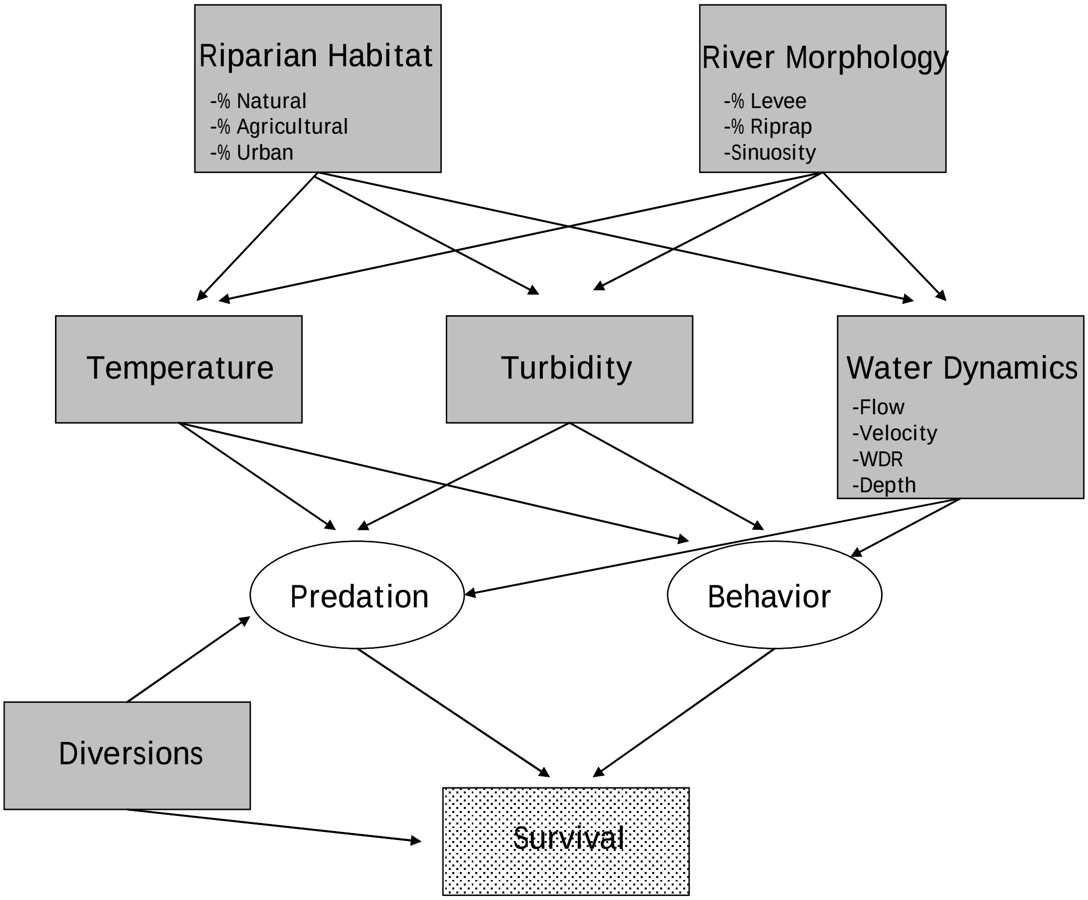

Riparian Habitat
-% Natural
-% Agricultural
-% Urban
River Morphology
-% Levee
-% Riprap
-Sinuosity
Temperature
Turbidity
Water Dynamics
-Flow
-Velocity
-WDR
-Depth
Predation
Behavior
Diversions
Survival

Fig. 2

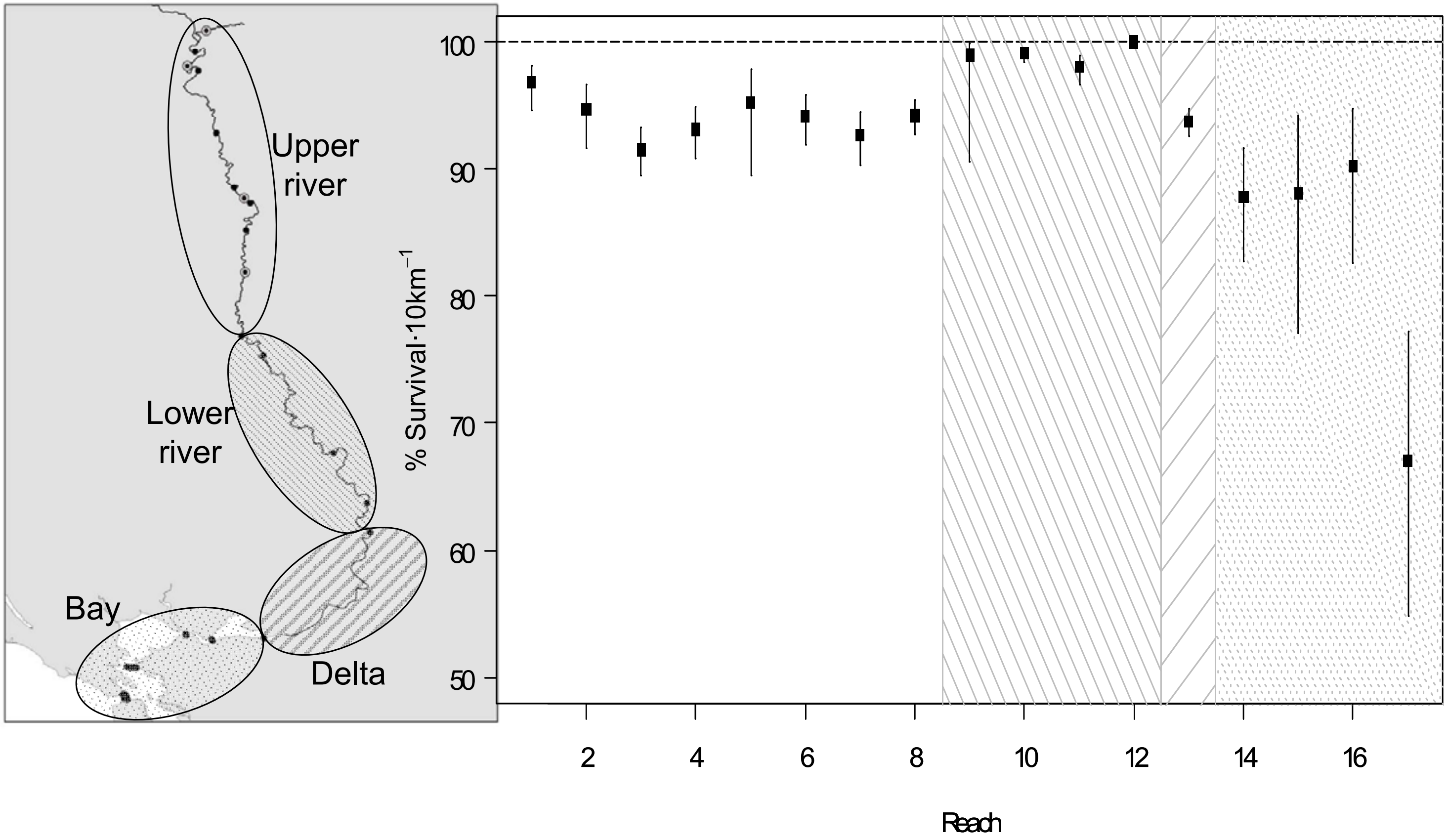

Upper river
Lower river
Bay
Delta
100
90
80
70
60
50
% Survival·10km^{-1}
2
4
6
8
10
12
14
16
Reach

Fig. 3

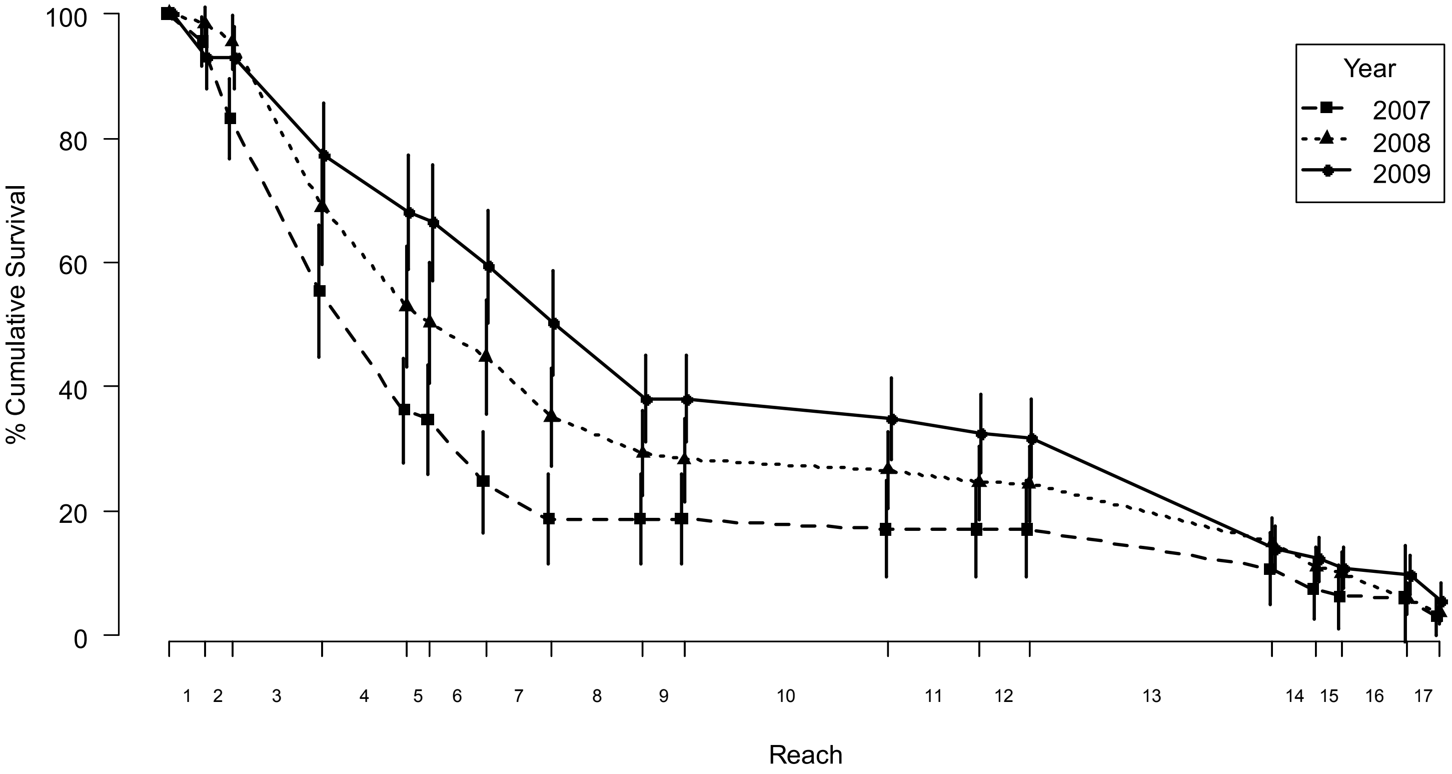

Year
2007
2008
2009
% Cumulative Survival
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Reach

Fig. 4

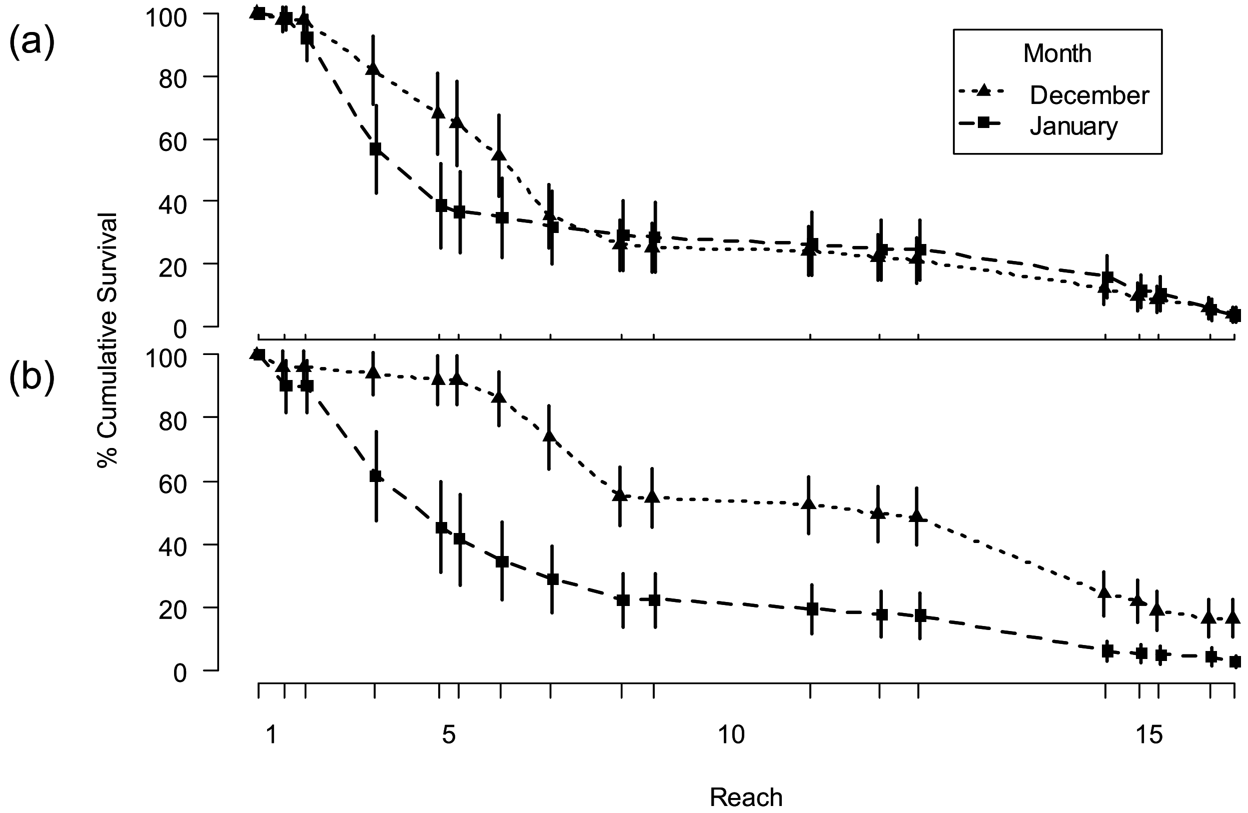

(a)
(b)
% Cumulative Survival
100
80
60
40
20
0
Month
December
January
1
5
10
15
Reach

Fig. 5

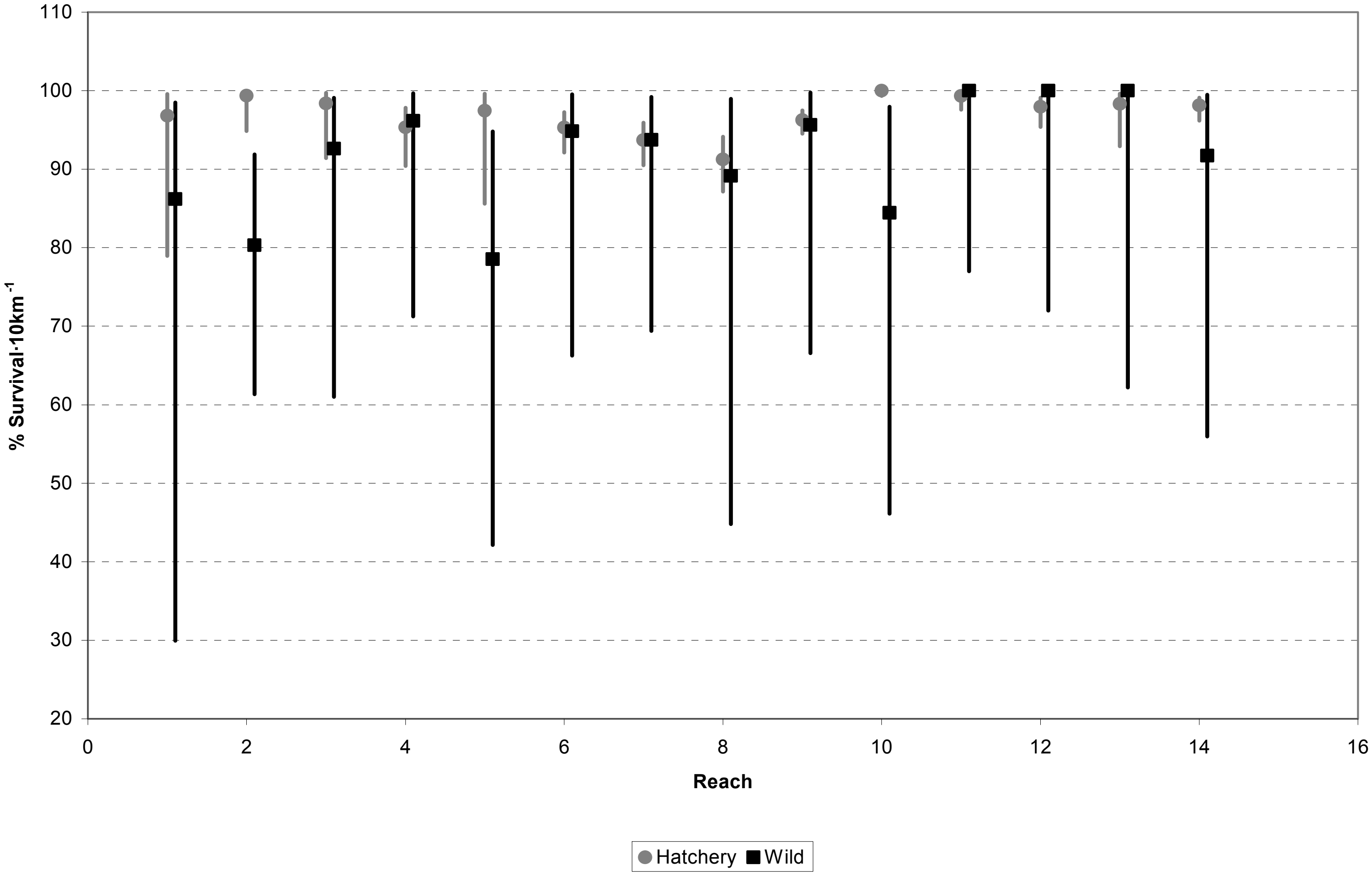

110
100
90
80
70
60
50
40
30
20
% Survival·10km-1
0
2
4
6
8
10
12
14
16
Reach
● Hatchery ■ Wild

Fig. 6

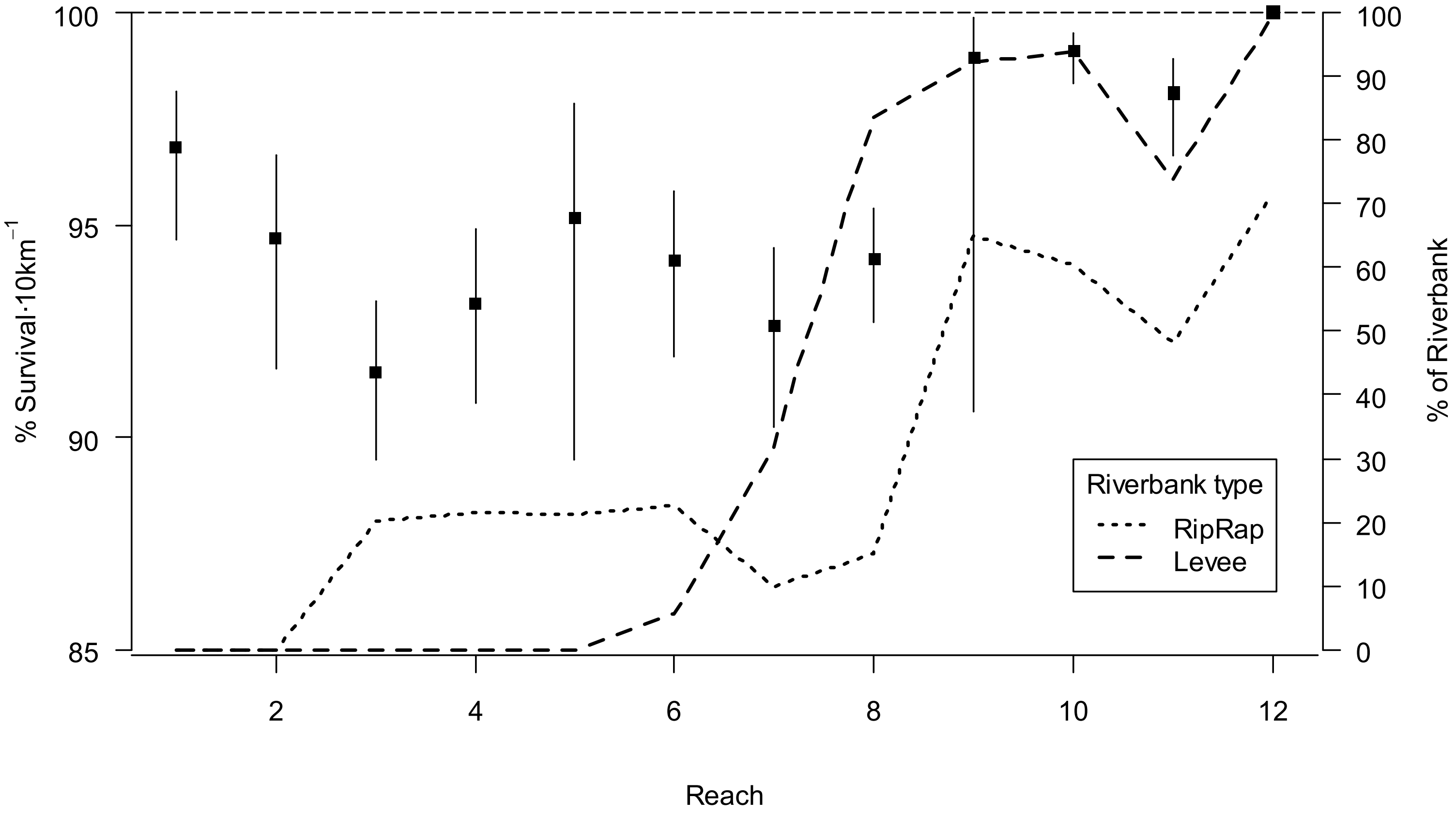
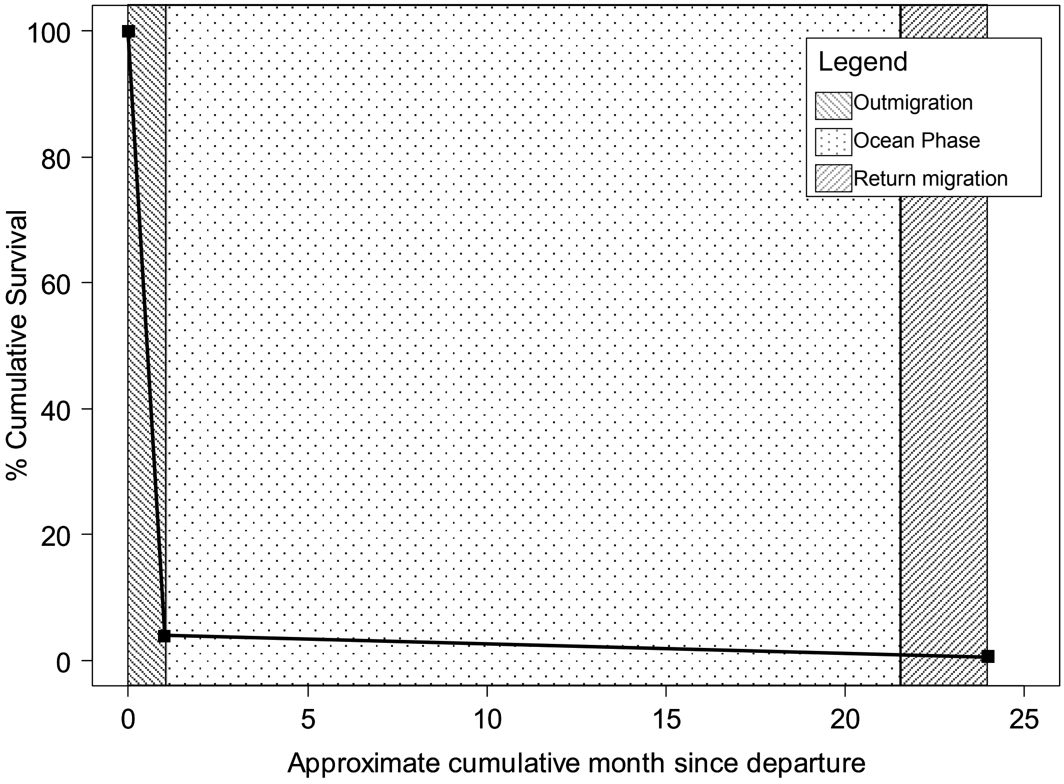

100
95
90
85
% Survival·10km^{-1}
100
90
80
70
60
50
40
30
20
10
0
% of Riverbank
2
4
6
8
10
12
Reach
Riverbank type
RipRap
Levee

Fig. 7



% Cumulative Survival
100
80
60
40
20
0
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 $g \bullet l^{-1}$) 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. 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 $km \cdot day^{-1}$ (± 1.32 S.E.) for the 2009 Butte City release group (rkm 363) to 23.53 $km \cdot day^{-1}$ (± 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 km·day^{-1} in the Sacramento-San Joaquin River Delta to 89.1 km·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 $\text{km}\cdot\text{day}^{-1}$) 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 $\text{km}\cdot\text{day}^{-1}$, 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 $\text{km}\cdot\text{day}^{-1}$ (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 $\text{km}\cdot\text{day}^{-1}$ (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·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).

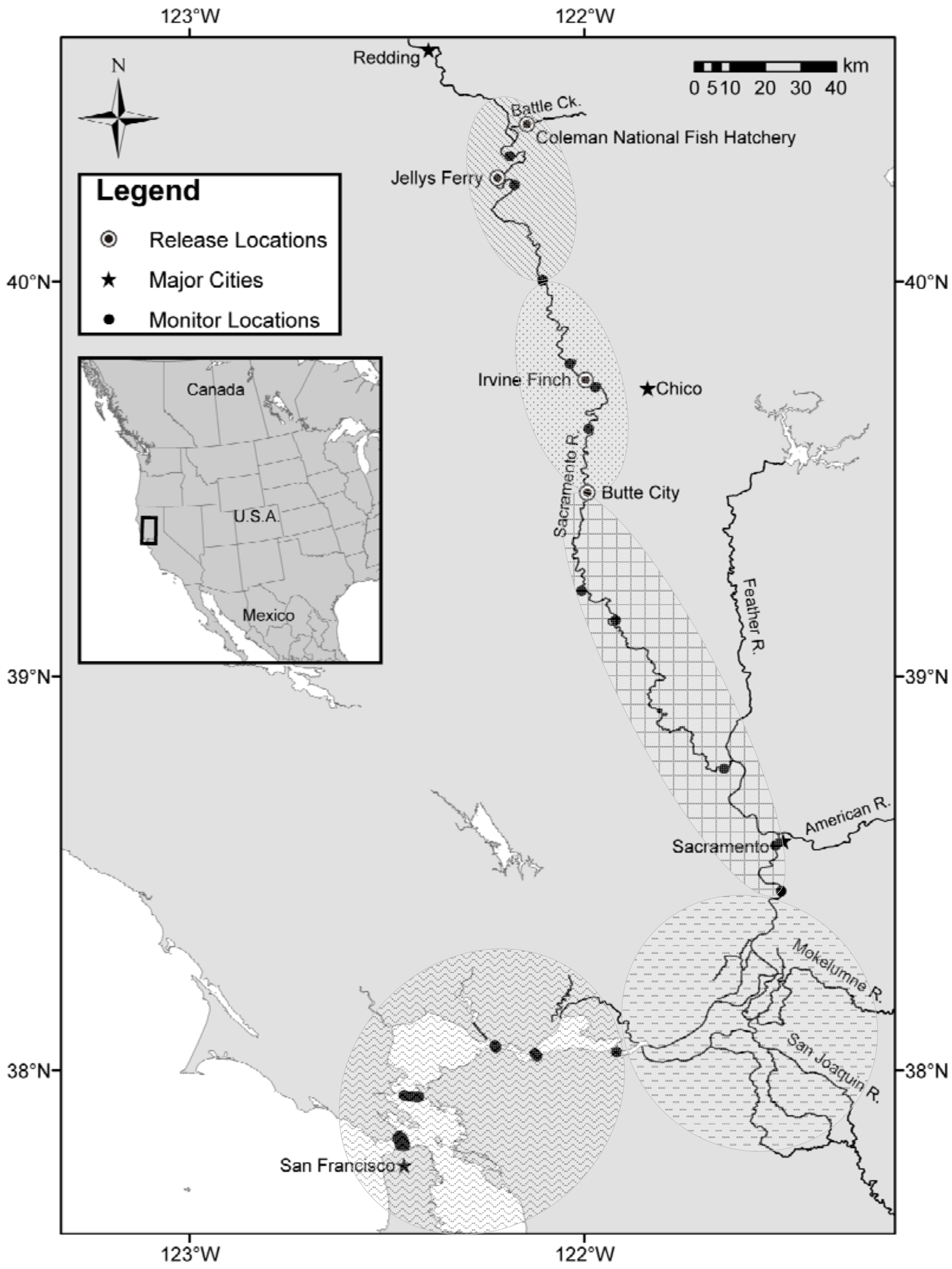
123°W
122°W
40°N
39°N
38°N
N
km
0 5 10 20 30 40
Legend
Release Locations
Major Cities
Monitor Locations
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
Irvine Finch
Chico
Butte City
Sacramento R.
Feather R.
American R.
Sacramento
Mokelumne R.
San Joaquin R.
San Francisco
Canada
U.S.A.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

Fig. 1

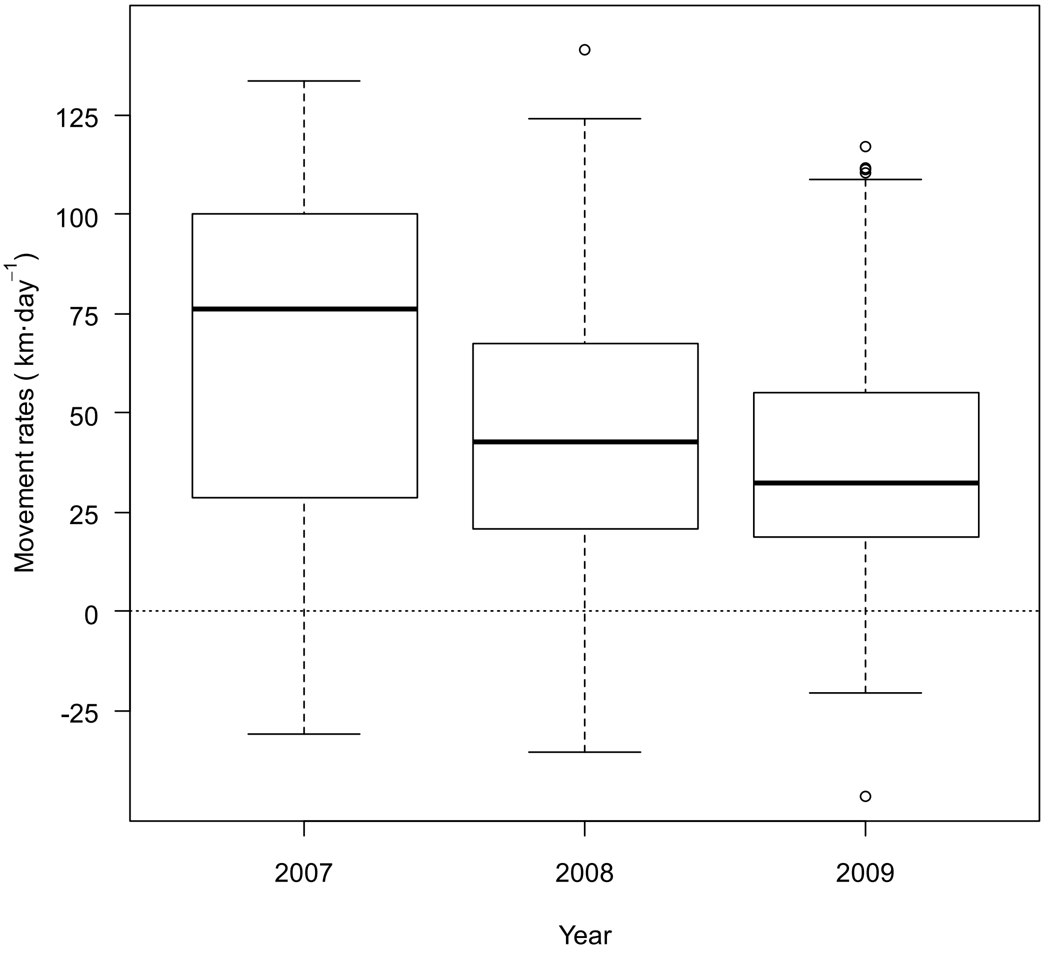
Movement rates (km·day^{-1})
125
100
75
50
25
0
-25
2007
2008
2009
Year

Fig. 2

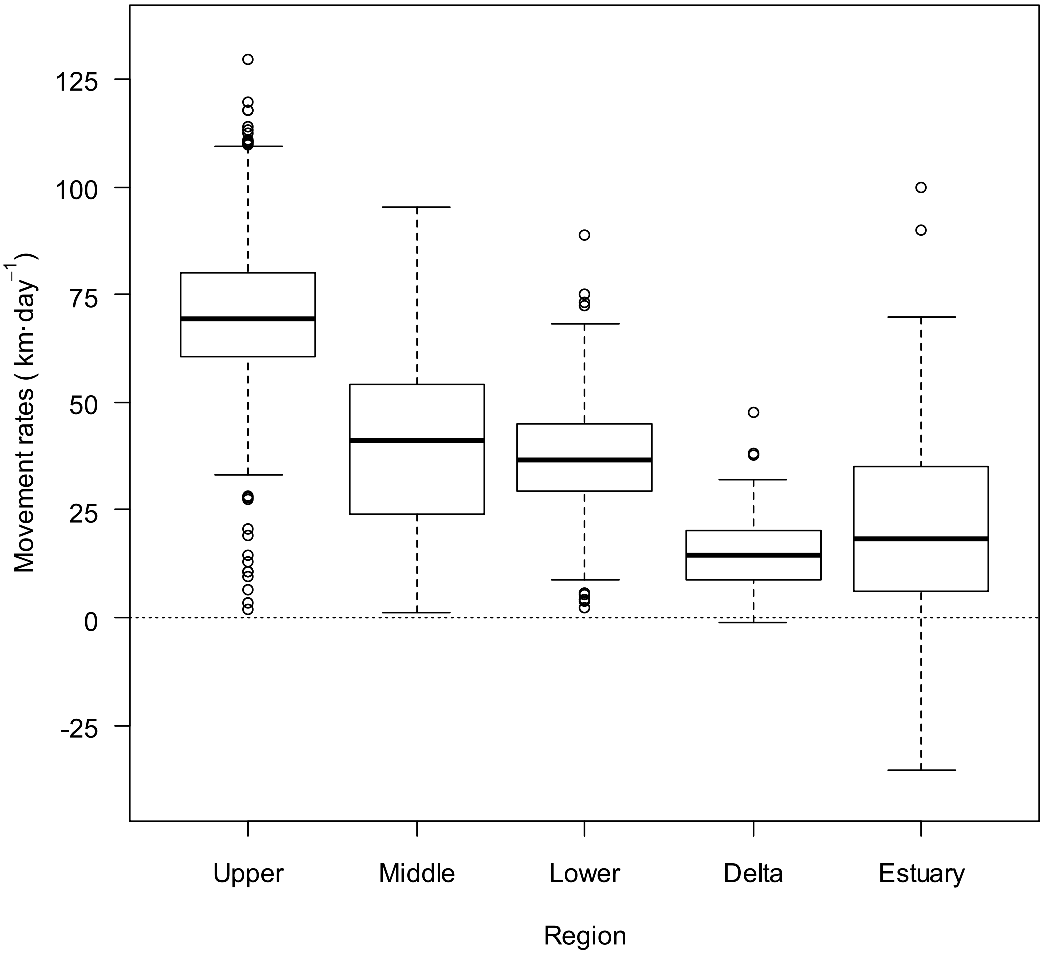
Movement rates (km·day⁻¹)
125
100
75
50
25
0
-25
Upper
Middle
Lower
Delta
Estuary
Region

Fig. 3


2007
2008
2009
Movement rates ($\mathrm{km\,day^{-1}}$)
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

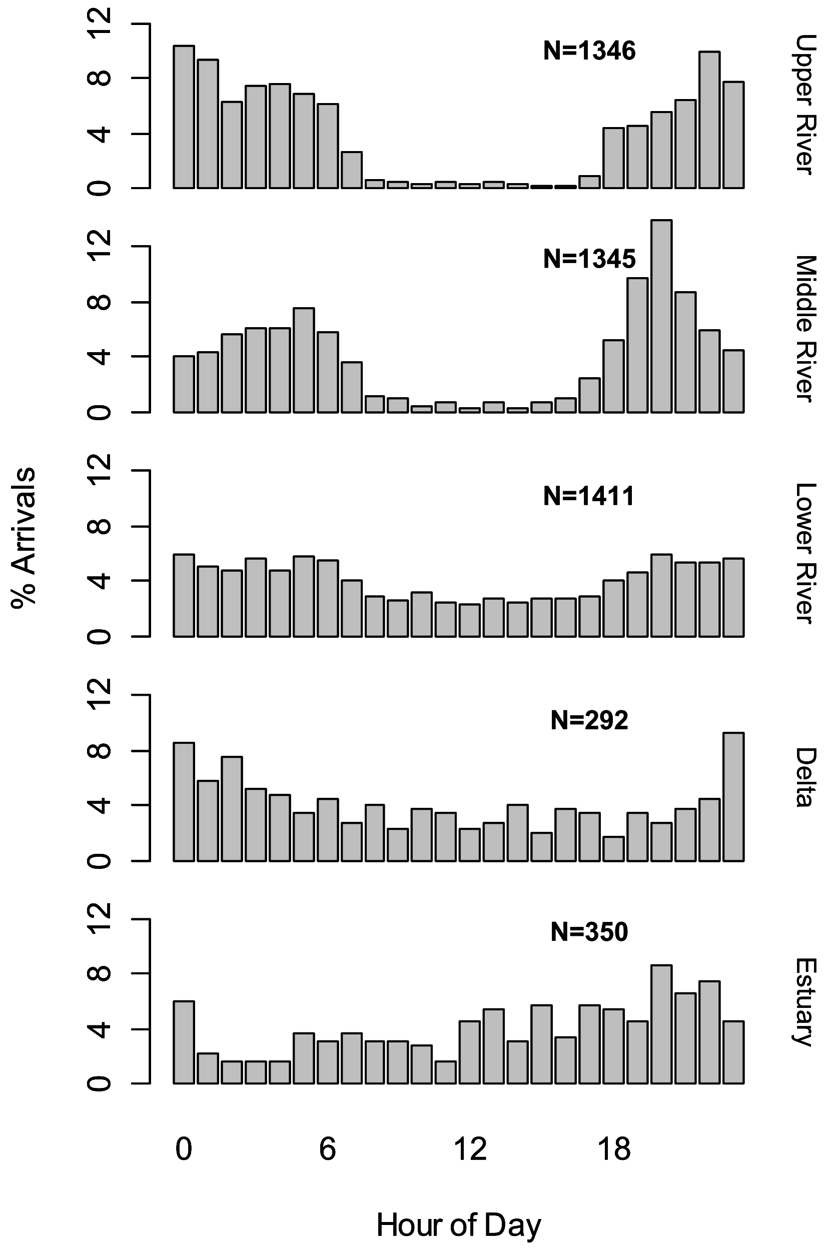
N=1346
Upper River
N=1345
Middle River
N=1411
Lower River
N=292
Delta
N=350
Estuary
% Arrivals
0
4
8
12
0
6
12
18
Hour of Day

Fig. 5

REFERENCE EXHIBIT G

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[Article]

Hierarchical Modeling of Juvenile Chinook Salmon Survival as a Function of Sacramento–San Joaquin Delta Water Exports

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Abstract.—A multiyear study was carried out in the Sacramento–San Joaquin Delta system to examine the relationship between the survival of out-migrating Chinook salmon *Oncorhynchus tshawytscha* and the amount of water exported from the system by the two major pumping stations in the southern portion of the delta. Paired releases of groups of coded-wire-tagged juvenile late-fall-run Chinook salmon were made at two locations in the delta, one in the main-stem Sacramento River and one in the interior portion of the delta where they were more likely to be directly affected by the pumping stations. Shortly after release, the fish were recovered downstream by a midwater trawl, and over a 2–4-year period the fish were recovered in ocean fishery catches and spawning ground surveys. A Bayesian hierarchical model for the recoveries was fit that explicitly accounted for the between-release variation in survival and capture probabilities as well as the sampling variation in the recoveries. The survival of the interior delta releases was considerably lower than that of main-steam releases (mean ratio of survival probabilities, 0.35). The ratio of survival probabilities was negatively associated with water export levels, but various model selection criteria gave more (or nearly equal) weight to simpler models that excluded exports. However, the signal-to-noise ratio, defined in terms of the export effect relative to environmental variation, was very low, and this could explain the indeterminacy in the results of the model selection procedures. Many more years of data would be needed to more precisely estimate the export effect. Whatever the factors that adversely affect survival through the interior delta, the fraction of out-migrants that enter the interior delta needs to be estimated in order to determine the overall effect of water exports on out-migrating Sacramento river Chinook salmon.

Survival experiments with juvenile Chinook salmon *Oncorhynchus tshawytscha* have been conducted in the Sacramento–San Joaquin Delta of California since the early 1970s (Kjelson et al. 1981, 1982; Kjelson and Brandes 1989; Brandes and McLain 2001). The experiments have involved the release, at multiple locations throughout the delta, of marked and tagged hatchery-reared juvenile Chinook salmon followed by later recovery of these fish. The survival of juvenile salmon through the delta is of particular interest because of the delta's role in water management in California. Two large pumping facilities, the Central Valley Project's C. W. "Bill" Jones Pumping Plant (CVP) and the State Water Project's Harvey Banks Pumping Plant (SWP), are located in the southern part of the delta (Figure 1) and provide water for municipal, agricultural, and domestic purposes to more than 23 million people throughout central and southern California. The delta is critical for the survival of salmon of Sacramento–San Joaquin origin, as all juvenile salmon must migrate through it to reach the Pacific Ocean. Two races of Central Valley Chinook salmon are listed under the Endangered Species Act (the winter run as endangered [NMFS 1997] and the spring run as threatened), and two others (the fall and late-fall runs) are considered species of concern. The role of CVP and SWP water exports on the survival of juvenile salmon through the delta is of great interest to managers and stakeholders, and this was the primary reason for the survival experiments.

Previous analyses of survival experiments involving juvenile fall-run Chinook salmon (Kjelson et al. 1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003), which out-migrate through the delta from March through June (Yoshiyama et al. 1998), have suggested that survival is negatively associated with water exports. These analyses included data from a very spatially dispersed set of release locations, at which many variables other than export levels may have affected survival.

In this paper we analyze release–recovery data from a more narrowly focused study of the effects of water exports, in which factors other than exports were to some degree controlled for by the temporal pairing of releases. Paired releases of juvenile late-fall-run Chinook salmon were made simultaneously in the interior delta and the main stem of the Sacramento River downstream from the Delta Cross Channel and Georgiana Slough (Figure 1). The interior delta is an area that out-migrating juvenile salmon can enter from the Sacramento River through either the Delta Cross

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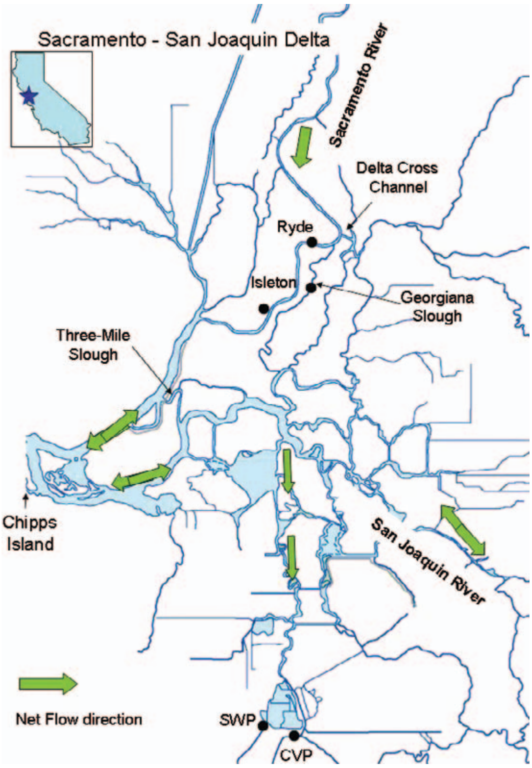


FIGURE 1.—Map of the Sacramento–San Joaquin Delta showing the Ryde and Georgiana Slough release locations, the Chipps Island recovery location, and the locations of two pumping stations with fish salvage facilities (SWP and CVP).

Channel (when the gates are open) or Georgiana Slough. Fish released directly into the interior delta are presumably more vulnerable to the influence of the CVP and SWP pumping facilities than fish released into the main stem. Unlike in the fall-run experiments (Newman and Rice 2002), the temporal pairing of releases controlled for the effects of all factors other than release location and exports on survival. One limitation of the study, however, is that the levels of exports cannot be fixed or controlled by researchers because water demands take precedence. Another limitation is that the overall effect of exports on out-migrating salmon cannot be determined without knowing the proportion of such salmon that enter the interior delta.

Brandes and McLain (2001) analyzed paired release–recovery data that involved releases of late-fall-run and fall-run fish. Their analytical procedure was to calculate freshwater recovery fractions (adjusted for estimates of capture efficiency) and regress those fractions against export levels. Based on the data available at the time, they found a statistically significant negative association between the survival of releases at Georgiana Slough (relative to that of releases at Ryde on the main-stem Sacramento River) and export levels (Figure 1).

One purpose of this paper was to update the analysis of Brandes and McLain (2001) incorporating more recent data but only using the late-fall-run stock. Late-fall-run fish are potential surrogates for winter-run Chinook salmon (Brandes and McLain 2001) since both runs out-migrate from November through May (Yoshiyama et al. 1998). A second purpose was to compare the results of the Brandes and McLain approach with those based on Bayesian hierarchical models (Carlin and Louis 1996; Gelman et al. 2004; for a fisheries release–recovery application, see Newman 2003). Hierarchical models offer several potential advantages for analyzing multirelease studies. One advantage is parsimony: rather than estimating release-pair-specific effects independently (e.g., n independent estimates of relative survival for n release pairs), one can specify a single distribution for the effects underlying the results for all release pairs. Another advantage is that such a "random effects" distribution characterizes the environmental variation in survival probabilities and the hierarchical approach makes this variation distinct from the sampling variation. A third advantage is that a hierarchical model provides a sensible means of combining data from multiple-year studies, in this case multiple sets of paired releases and recoveries (giving, for example, release pairs for which fewer fish were released less weight than those for which more fish were released).

Methods

Data

The paired release–recovery data, including the numbers of fish released, the numbers recovered at various locations, and the water export levels at the times of release, are given in Table 1. Fifteen paired groups of juvenile late-fall-run Chinook salmon yearlings (mean size, >100 mm) reared at Coleman National Fish Hatchery were released between 1993 and 2005 during the months of December and January. At the hatchery, each fish had its adipose fin clipped and a coded wire tag inserted into its snout; to read such tags after implantation requires sacrificing the fish. The tag codes were batch specific, that is, the same codes were used for thousands of fish, with unique tag codes for each release location. The fish were trucked from the hatchery to the interior delta (Georgiana Slough) and the main-stem Sacramento River (Ryde or Isleton) and releases at both locations made within a day or two.

Within a few weeks of release, recoveries were made

TABLE 1.—Release and recovery data for juvenile Chinook salmon in the Sacramento–San Joaquin Delta. Abbreviations are as follows: *R* is the number of fish released, CI and $\widehat{\mathrm{Oc}}$ are observed recoveries at Chipps Island and expanded recoveries in the ocean fisheries, $\widehat{\mathrm{FF}}$ is expanded recoveries at fish salvage facilities, and $\widehat{\mathrm{IL}}$ is expanded inland recoveries. Exports are 3-d averages (cfs) of the water exported from SWP and CVP, and *E*/*F* is the export–flow ratio over the same period.

		Georgiana Slough					Ryde						
Release date	Pair	*R*	CI	$\widehat{\mathrm{Oc}}$	$\widehat{\mathrm{FF}}$	$\widehat{\mathrm{IL}}$	*R*	CI	$\widehat{\mathrm{Oc}}$	$\widehat{\mathrm{FF}}$	$\widehat{\mathrm{IL}}$	*E*/*F*	Exports
Dec 2, 1993	1	33,608	5	79	248	12	34,650	37	293	10	36	0.68	10,434
Dec 5, 1994	2[a]	31,532	4	11	87	8	30,220	15	28	6	13	0.22	5,988
Jan 4–5, 1995	3[a]	31,328	2	102	837	53	31,557	13	266	231	138	0.40	10,403
Jan 10–11, 1996	4	33,670	5	146	768	9	30,281	21	239	12	23	0.55	9,523
Dec 4–5, 1997	5	61,276	2	7	153	4	46,756	22	42	18	11	0.51	10,570
Jan 13–14, 1997	6	66,803	18	240	24	51	49,059	48	167	0	70	0.06	3,887
Dec 1–2, 1998	7	69,180	12	172	28	44	48,207	30	183	0	102	0.04	1,868
Dec 29–30, 1998	8	68,843	12	151	48	54	48,804	17	156	0	88	0.09	1,984
Dec 10–11, 1999	9[a]	65,517	3	43	24	9	53,426	16	129	0	20	0.18	3,237
Dec 20–21, 1999	10[a]	64,515	21	149	82	32	49,341	19	160	4	66	0.26	4,010
Jan 3–5, 2002	11	77,053	18	240	390	116	52,327	34	521	18	418	0.12	7,789
Dec 5–6, 2002	12	90,219	1	68	700	11	49,629	18	148	42	34	0.46	5,007
Dec 9–10, 2003	13	68,703	5	51	306	8	45,981	13	127	24	69	0.18	4,016
Dec 8–9, 2004	14	72,082	10	11	0	1	50,397	28	20	0	0	0.25	6,092
Dec 8–9, 2005	15	70,414	6	35	165	1	51,017	23	49	12	1	0.68	10,837

[a] Ryde releases made at Isleton (see Figure 1).

in freshwater by a midwater trawl operating near Chipps Island (Figure 1). The trawl was towed at the surface almost daily for 4–6 weeks after the fish were released. Typically, ten 20-min tows were made each day between roughly 0700 and 1200 hours. Juvenile fish were also recovered at fish facilities located in front of the CVP and SWP pumping plants. These Chinook salmon were transported by truck and released at locations north of the pumps and nearer to the main stem of the Sacramento River upstream of Chipps Island, where they could be caught by the midwater trawl at Chipps Island. Then, over a 3–4-year period, adult fish were recovered from the landings of ocean fisheries. The total number of ocean fishery recoveries, summed over many landing areas and years, was estimated from a spatially and temporally stratified random sample of the landings and catches. The percentage of ocean catch sampled was roughly 20–25%. Additional recoveries of adult fish were made in freshwater fisheries, at hatcheries, and on spawning grounds (inland recoveries). The expanded ocean and inland recoveries were retrieved from a Web-based database query system administered by the Pacific States Marine Fisheries Commission (www.rmpc.org). The straying proportions for the Georgiana Slough and Ryde releases (i.e., the fractions of inland recoveries that were not recovered at Coleman National Fish Hatchery) varied considerably between release pairs, but within release pairs they were quite similar.

The combined water export levels (hereafter referred to as exports) from both the SWP and CVP facilities were averaged over a 3-d period starting the day after the release in Georgiana Slough. The choice of 3 d was somewhat arbitrary, although linear correlations of 3-d average export levels with those for 10 and 17 d were quite high (0.94 and 0.91, respectively). There is a certain degree of imprecision in defining an export variable with regard to fish out-migration because some fish take longer to out-migrate than others and the degree of exposure to the area influenced by the pumps will vary (for example, in group 1 of the Georgiana Slough release there was one recovery at the SWP fish facility 3 months after release). Furthermore, export levels are not necessarily constant, even within a 3-d period, and the day-to-day variation in export level is not captured by an average. The water volumes entering the interior delta are also affected by the position of the Delta Cross Channel gates, which when open increase the flow of water from the Sacramento River into the interior delta. The gates were open on the day of the Georgiana Slough releases in the first 2 years of the study (1993 and 1994) and for one of the 1999 releases (group 10), but otherwise closed. Recognizing that the amount of exports relative to total inflow from the Sacramento River (at Freeport) could be more important than absolute exports, we also examined the export-to-flow ratio as a covariate; the relationship between the ratios and the absolute values, however, was positive and linear ($r = 0.83$).

Assumptions and Notation

Within and between releases, the fate of an individual fish (live or die, be caught or not) was assumed to be independent of that of any other fish. For all fish released from a given location at a given time, the survival and capture probabilities were assumed to be identical. In recognition of the paired-release aspect of the study, we further assumed that within a release pair the probability of capture at Chipps Island and the recovery probabilities (complicated combinations of the survival and capture probabilities) in the ocean fishery and inland areas were identical. For example, for release pair 1 (Table 1) the capture probability is the same for a Ryde fish and a Georgiana Slough fish that has survived to Chipps Island, but that probability can differ from the probability for release pair 2.

We further assumed that only fish released in Georgiana Slough were affected by exports. Ryde is located 2.5 mi (1 mi = 1.61 km) downstream of the location on the main stem where water is diverted into Georgiana Slough, and releases at Ryde are further removed geographically from the export facilities. However, for 2 years sizeable numbers of Ryde fish were recovered at the fish facilities (Table 1); it may be that flood tides carried some of the Ryde releases into the interior delta at some upstream or downstream locations such as Three Mile Slough (Figure 1), a channel several miles downstream that connects the Sacramento and San Joaquin rivers.

For a given release pair t, the numbers released at Ryde and Georgiana Slough are denoted $R_{\mathrm{Ry},t}$ and $R_{\mathrm{GS},t}$ and the associated recoveries at Chipps Island $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $y_{\mathrm{GS}\rightarrow\mathrm{CI},t}$. Expanded ocean recoveries are denoted $\hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}$ and $\hat{y}_{\mathrm{GS}\rightarrow\mathrm{Oc},t}$ and expanded inland recoveries $\hat{y}_{\mathrm{Ry}\rightarrow\mathrm{IL},t}$ and $\hat{y}_{\mathrm{GS}\rightarrow\mathrm{IL},t}$. The recovery fractions, defined as the ratios of the number of recoveries to the number released, are denoted $\hat{r}$, the subscripts indicating the release and recovery locations (e.g., $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t} = \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}/R_{\mathrm{Ry},t}$). The combined recovery fractions for more than one recovery location are denoted similarly (e.g., $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI+Oc+IL},t} = [y_{\mathrm{Ry}\rightarrow\mathrm{CI},t} + \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t} + \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{IL},t}]/R_{\mathrm{Ry},t}$).

The notation for the probability that a Ryde release will be recovered at Chipps Island is $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and that for the probability that it will be recovered in either the ocean fisheries or inland recoveries is $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$. The corresponding probabilities of recovery for Georgiana Slough releases are denoted $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}$, where θ_t is a release-pair-specific constant. Given the assumption that within a release pair the capture probabilities at Chipps Island are the same, θ_t is the ratio of the survival probability between Georgiana Slough and Chipps Island and the survival probability between Ryde and Chipps Island. How it relates to export levels is the primary management question.

Non-Bayesian, Nonhierarchical Models

Two nonhierarchical models were fit. Both somewhat mimic Brandes and McLain's (2001) analysis in that a two-step procedure was used, that is, an estimate of θ_t was first calculated and then regressed against exports. The first model is quite similar to Brandes and McLain's in that only recoveries at Chipps Island were used, that is, θ_t was estimated as the ratio of the recovery fractions at Chipps Island for the Georgiana Slough and Ryde releases,

$$\hat{\theta}_{1,t} = \frac{\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI},t}}{\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI},t}} \qquad (1)$$

In contrast to Brandes and McLain (2001), recoveries were not scaled by estimated gear efficiency because of the assumption that the capture probabilities were identical within a release pair. A simple linear regression model using standardized exports was fit, namely,

$$\hat{\theta}_{1,t} \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma^2), \qquad (2)$$

where $\mathrm{Exp}_t^* = (\mathrm{Exp}_t - \overline{\mathrm{Exp}}/s_{\mathrm{Exp}}$, Exp_t is exports at time t, $\overline{\mathrm{Exp}}$ is the average export level, and s_{Exp} is the standard deviation of exports. Assuming independence and identical probabilities of survival and capture for all fish in a single release, the number of fish recovered at Chipps Island is a binomial random variable, that is, $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t} \sim \mathrm{Binomial}(R_{\mathrm{Ry},t}, r_{\mathrm{Ry}\rightarrow\mathrm{CI},t})$. Given $R_{\mathrm{Ry},t}$ and $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$, $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ is the maximum likelihood estimate (mle) of $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$; similarly, $\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI},t}$ is the mle of $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $\hat{\theta}_{1,t}$ is the mle for θ_t based on Chipps Island recoveries alone.

For the second nonhierarchical model, θ_t was estimated from Chipps Island, ocean, and inland recoveries combined, that is,

$$\hat{\theta}_{2,t} = \frac{\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI+Oc+IL},t}}{\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI+Oc+IL},t}}. \qquad (3)$$

Implicit in this calculation is the assumption that within a release pair the Chipps Island capture, ocean recovery, and inland recovery probabilities are identical. If the total ocean and inland recoveries were known exactly and not estimated, the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries would be multinomial, and $\hat{\theta}_{2,t}$ would be the mle for θ_t. However, with the expanded recoveries, the distribution is more complex. To account for the differences in sampling variation and to somewhat duplicate the hierarchical model, a weighted regression of the log of $\hat{\theta}_{2,t}$ against standardized exports was fit, that is,

$$\log_e(\hat{\theta}_{2,t}) \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \mathrm{se}^2_{\log_e[\hat{\theta}_{2,t}]}\sigma^2). \qquad (4)$$

The weights were the inverses of the squares of the standard errors of $\log_e(\hat{\theta}_{2,t})$, $\mathrm{se}_{\log_e[\hat{\theta}_{2,t}]}$, which were calculated using the delta method (see section 10.5 in Stuart and Ord 1987). The log transformation ensures that $\theta_{2,t}$ remains nonnegative.

The primary inferential aim for both models (equations 2 and 4) is to estimate the slope coefficient (β_1) and its standard error.

Hierarchical Models

Hierarchical models (Carlin and Louis 1996) consist of two or more levels, each level accounting for a different type of variation. For our data, the first level accounts for the sampling variation in the recoveries conditional on the survival and capture probabilities, the second level for the variation in the survival and capture probabilities between release pairs. The second level reflects what is sometimes referred to as random effects. The prior distributions for the fixed and unknown parameters of the model (in the second level) make up the third level of the model.

Bayesian hierarchical model.—A Bayesian hierarchical model (BHM) was formulated for the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries. The statistical distributions for the different levels of the hierarchical model are shown below. The first-level distributions are conditional on the second-level variables, and similarly for the second-level distributions.

Level 1:

$$y_{\mathrm{GS}\rightarrow\mathrm{CI},t}, \hat{y}_{\mathrm{GS}\rightarrow\mathrm{Oc+IL},t} \sim \mathrm{Multinomial}(R_{\mathrm{GS},t}, \theta_{3,t} r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, \theta_{3,t} r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \tag{5}$$

$$y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t} \sim \mathrm{Multinomial}(R_{\mathrm{Ry},t}, r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \tag{6}$$

Level 2:

$$\log_e(\theta_{3,t}) \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}^*, \sigma_\theta^2) \tag{7}$$

$$\mathrm{logit}(r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}) \sim \mathrm{Normal}(\mu_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}, \sigma^2_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}) \tag{8}$$

$$\mathrm{logit}(r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \sim \mathrm{Normal}(\mu_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}}, \sigma^2_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}}) \tag{9}$$

Level 3:

$$\beta_0, \beta_1, \mu_{\mathrm{Ry}\rightarrow\mathrm{CI}}, \mu_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}} \sim \mathrm{Normal}(0, 1.0\mathrm{E}+6) \tag{10}$$

$$\sigma_\theta, \sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}, \sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}} \sim \mathrm{Uniform}(0, 20) \tag{11}$$

As noted previously, the joint distributions for the Chipps Island recoveries and the combined expanded ocean and inland recoveries cannot be multinomial owing to estimation error in the expansions; thus, the level 1 formulation is an approximation. The log transformation of $\theta_{3,t}$ (in the level 2 model) ensures that $\theta_{3,t}$ is nonnegative. The logit transformations in level 2 force $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$ to lie between 0 and 1; however, the resulting probabilities are so small that log transformations would have the same practical effect.

Unlike in the likelihood framework, the inferential objective in the Bayesian setting is to calculate the posterior distribution for the unknown parameters (Gelman et al. 2004), that is, to calculate

$$p(\Theta|\mathrm{Data}) \propto p(\mathrm{Data}|\Theta)p(\Theta),$$

where Θ is the vector of unknown constants (such as β_0 and β_1) and unknown random variables (such as θ_t) and $p(\Theta)$ is the prior distribution (here defined by level 3). In this case the primary interest is in the posterior distribution for β_1, and the probability that β_1 is negative is a measure of the degree of the negative association between exports and the relative survival of Georgiana Slough releases.

Sensitivity analysis.—The sensitivity of the BHM to the choice of distributions and functional forms was assessed by alternative formulations for each level. At level 1, to allow for the possible dependence between fish within a release as well as extramultinomial variation due to the fact that the ocean and inland recoveries are sample expansions, negative binomial distributions were used for the Chipps Island and expanded ocean and inland recoveries from a given release. For example, the negative binomial model for the recoveries at Chipps Island of releases from Ryde is

$$y_{\mathrm{Ry}\rightarrow\mathrm{CI}} \sim \text{Negative binomial}\left(k_{\mathrm{CI}}, \frac{k_{\mathrm{CI}}}{R_{\mathrm{Ry}} r_{\mathrm{Ry}\rightarrow\mathrm{CI}} + k_{\mathrm{CI}}}\right),$$

where k_{CI} is a nonnegative constant that affects the degree of overdispersion (relative to a Poisson, or indirectly a binomial, random variable). The larger it is, the less the overdispersion.

At level 2, several alternative models were fit. One model removed exports from the model for $\log_e(\theta_{3,t})$. A second used a logistic transformation of $\theta_{3,t}$, ensuring that $0 \leq \theta_{3,t} \leq 1$ (i.e., that the survival probability from Georgiana Slough to Chipps Island cannot exceed that from Ryde to Chipps Island). A third alternative was a multivariate normal (MVN) distribution for the joint distribution of $\theta_{3,t}$, $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$, and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$, which allowed for correlation among these parameters within each release pair. In particular, $\theta_{3,t}$ was $\log_e$ transformed and, largely to facilitate fitting, an extension of a logistic model was used to transform $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and

$r_{\text{Ry}\to\text{Oc+IL},t}$, that is (dropping the subscript t to reduce notation),

$$\begin{bmatrix} \theta^1 \\ \theta^2 \\ \theta^3 \end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix} \beta_0 + \beta_1 \text{Exp}^* \\ \mu_{\text{Ry}\to\text{CI}} \\ \mu_{\text{Ry}\to\text{Oc}} \end{bmatrix}, \right.$$

$$\left. \boldsymbol{\Sigma} = \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 \end{bmatrix} \right)$$

where

$$\theta^1 = \log_e(\theta_3)$$

$$\theta^2 = \log_e\left(\frac{r_{\text{Ry}\to\text{CI}}}{1 - r_{\text{Ry}\to\text{CI}} - r_{\text{Ry}\to\text{Oc+IL}}}\right)$$

and

$$\theta^3 = \log_e\left(\frac{r_{\text{Ry}\to\text{Oc+IL}}}{1 - r_{\text{Ry}\to\text{CI}} - r_{\text{Ry}\to\text{Oc+IL}}}\right).$$

A fourth alternative was to use the ratio of exports to total river flow instead of the absolute level of exports. A fifth alternative was to remove the random effects, that is, to make the level 2 models deterministic.

For level 3, various prior distributions were tried for the fixed parameters in level 2. We used the inverse gamma distributions instead of uniform distributions (equation 11) for the variances of the random effects, that is, σ_θ^2, $\sigma^2_{r_{\text{Ry}\to\text{CI}}}$, and $\sigma^2_{r_{\text{Ry}\to\text{Oc+IL}}}$. For the multivariate normal model, an inverse Wishart distribution was used as the prior for the variance–covariance matrix, $\boldsymbol{\Sigma}$.

Not all possible combinations of the models for each level were fit. During the fitting process it became clear that certain options at one level led to clearly poorly fitting models (e.g., removing the random effects at level 2 led to a drastic drop in model fit no matter what options were selected at the other levels).

Model fitting, assessment, and comparison.—To fit the BHMs we used the program WinBUGS (Lunn et al. 2000), which generated samples from the joint posterior distribution for the parameters, random effects, and expected numbers of recoveries. WinBUGS is based on a technique known as Markov chain–Monte Carlo (MCMC; Gilks et al. 1996), which is a computer simulation method in which samples are generated from a Markov chain that has a limiting distribution equal to the distribution of interest (in this case the joint posterior distribution).

By a limiting distribution it is meant that the samples do not initially come from the desired distribution but that when "enough" samples have been generated (the so-called burn-in period), all additional samples do come from the desired distribution. WinBUGS includes measures (e.g., the Brooks–Gelman–Rubin statistic; Brooks and Gelman 1998), based on the results of simulating from multiple Markov chains with differing initial values, for determining an adequate burn-in period. Informally stated, given widely different starting values, the point at which the chains begin to overlap (i.e., to begin mixing) is the necessary burn-in period; at that point, presumably, the samples are coming from the limiting distribution and are not stuck at some local mode of the posterior distribution. Values of the Brooks–Gelman–Rubin statistic that are near 1.0 are evidence for convergence, values below 1.1 often being adequate (Gelman et al. 2004:297). Three different chains with differing initial values were run in parallel and the summary statistics are based on the pooled output after burn-in.

For a given model, the goodness of fit was assessed by calculating Bayesian P-values (Gelman et al. 2004) for each of the observations. The P-value is the proportion of time a predicted value exceeds the observed value, that is,

$$\text{Bayesian } P\text{-value} = \frac{1}{L}\sum_{l=1}^{L} I(y_l^{\text{pred}} \geq y),$$

where $I(\bullet)$ is an indicator function that equals 1 when the condition inside $(\bullet)$ is met. The predicted value, y_l^{pred}, is found by simulating y from its probability distribution evaluated at the lth parameter value in the MCMC sample. Ideally, the observed values will lie in the central portion of the simulated posterior predictive distribution, equally distributed around the median predicted values. A Bayesian P-value near 0 or 1 is indicative of a poor fit for the particular observation.

The models were compared using the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC can be viewed as a measure of overall model fit while penalizing model complexity. When two models are compared, the one with the lower DIC value is judged to have better predictive capabilities. Reversible jump MCMC (RJMCMC; Green 1995) was used to compare two models, one model with exports as a covariate (equation 7) and one without exports. Given the data, a set of models, and a corresponding set of prior probabilities that a given model is the correct model (the prior model probability), RJMCMC calculates posterior model probabilities.

Results

The recovery fractions for the Georgiana Slough releases were consistently less than those for the Ryde releases, with the exception of the fraction recovered at

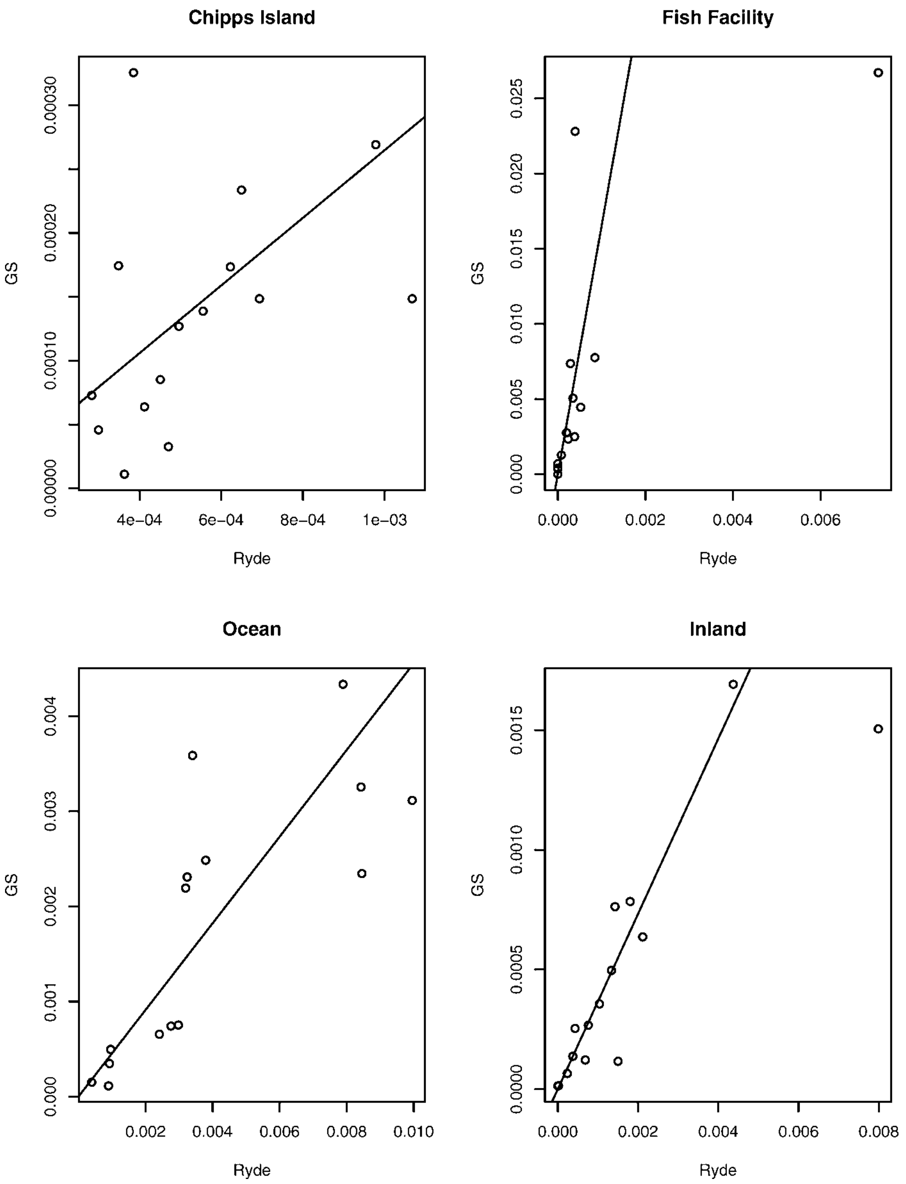
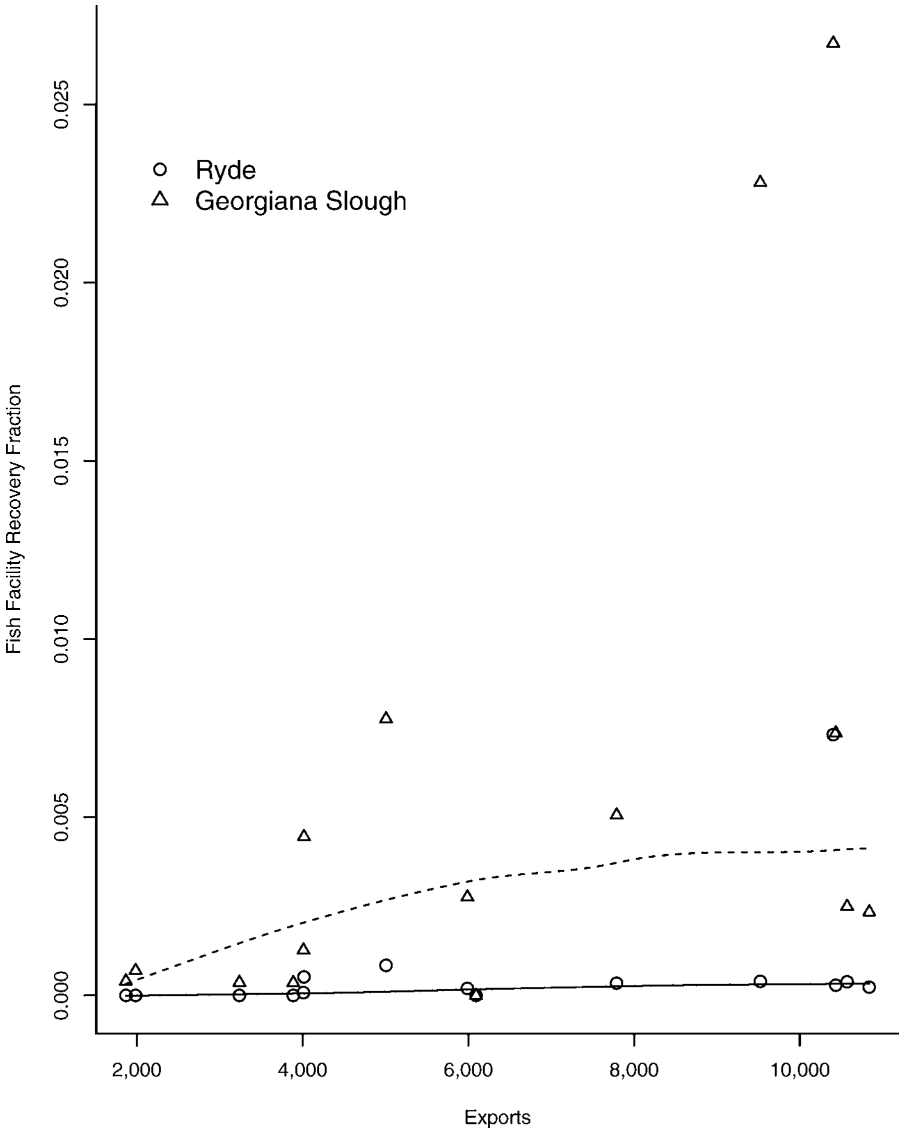


FIGURE 2.—Comparison of the recovery fractions at Chipps Island, in the ocean fisheries, at the fish salvage facilities, and among inland recoveries for Georgiana Slough and Ryde releases, by release pair. The straight lines have slopes equal to the means of the ratios of the recovery fractions.

the fish facilities (Figure 2). The means of the ratios of the recovery fractions equaled 0.26, 0.46, and 0.37 for the Chipps Island, ocean fisheries, and inland recoveries, respectively. Conversely, at the fish facilities, Georgiana Slough releases were about 16 times more likely to be recovered. Also, the fraction of fish facility recoveries from the Georgiana Slough releases tended to increase (from about 0.001 to 0.025) as exports increased from 2,000 cfs to 10,000 cfs (1 cfs = 0.028 m^3/s), although there was considerable variability at any given level of exports (Figure 3). This suggested a higher probability of ending up at the pumps with greater exports. In contrast, the fraction of the Ryde releases ending up at the fish facilities was less than 0.001 (group 3—a case with high exports—being an exception); these results are generally supportive of the assumption that Ryde releases were unaffected by exports.



?9 FIGURE 3.—Expanded recovery fractions at the SWP and CVP fish facilities versus export level. The lines are loess smooths for the Georgiana Slough (dashed) and Ryde releases (solid).

Nonhierarchical Analyses

The release-pair-specific point estimates, $\hat{\theta}_1$ and $\hat{\theta}_2$, and corresponding standard errors are shown in Table 2. As expected, given the additional information provided by the ocean and inland recoveries, the standard errors for $\hat{\theta}_2$ tended to be smaller than those for $\hat{\theta}_1$. The difference in standard errors was smaller for the most recent releases (groups 14 and 15), for which there is probably incomplete inland recovery information for the older-age returns. The variation in the estimates of θ_t was quite large between release groups, with values ranging from 0.13 to 0.80 (based on $\hat{\theta}_2$).

The fitted models of θ_t as a function of exports (equations 2 and 4) are

$$\hat{\theta}_{1,t} \approx \text{Normal}(0.265 - 0.086\text{Exp}_t^*, 0.18^2)$$

and

$$\log_e(\hat{\theta}_{2,t}) \approx \text{Normal}(-0.935 - 0.214\text{Exp}_t^*, 3.88^2).$$

The P-values for a one-sided test of the significance

TABLE 2.—Comparison of release-pair-specific fitted values of the ratio of the survival probability of Georgiana Slough releases to that of Ryde releases (θ). The non-Bayesian, nonhierarchical results are maximum likelihood estimates and standard errors based on Chipps Island recoveries alone ($\hat{\theta}_1$) and combined Chipps Island, ocean, and inland recoveries ($\hat{\theta}_2$). The Bayesian hierarchical values are the posterior distribution means and standard deviations from the model with a multivariate normal distribution at level 2 and θ modeled as a function of exports. See text for more details.

	Non-Bayesian, nonhierarchical				Bayesian hierarchical	
Group	$\hat{\theta}_1$	SE	$\hat{\theta}_2$	SE	$E(\theta_{3,t} \mid \text{data})$	SD
1	0.14	0.07	0.27	0.031	0.28	0.031
2	0.26	0.14	0.39	0.097	0.38	0.084
3	0.15	0.12	0.38	0.035	0.38	0.035
4	0.21	0.11	0.51	0.050	0.50	0.049
5	0.07	0.05	0.13	0.040	0.16	0.041
6	0.28	0.08	0.80	0.065	0.79	0.064
7	0.28	0.10	0.50	0.044	0.51	0.043
8	0.50	0.19	0.59	0.054	0.58	0.052
9	0.15	0.10	0.27	0.042	0.28	0.041
10	0.85	0.27	0.63	0.060	0.62	0.057
11	0.36	0.10	0.26	0.016	0.26	0.016
12	0.03	0.03	0.22	0.029	0.23	0.029
13	0.26	0.14	0.20	0.029	0.22	0.029
14	0.25	0.09	0.32	0.082	0.32	0.076
15	0.19	0.09	0.42	0.081	0.38	0.070

of the slope coefficient for exports with the alternative hypothesis that $\beta_1 < 0$ are 0.05 for the $\hat{\theta}_1$ model and 0.04 for the $\log_e(\hat{\theta}_2)$ model. Neither model fit particularly well, however; the R^2 values were 0.19 and 0.21 for the two models, respectively.

Bayesian Hierarchical Model

For each model the burn-in time was 50,000 iterations per chain; a further 150,000 iterations per chain were carried out, and every tenth realization was used for the posterior samples. The negative binomial model was an exception; owing to the somewhat slow computational speed for that model, the burn-in time was 50,000 iterations, and this was followed by 50,000 sample iterations. There were three types of evidence for convergence to the posterior distribution: Brooks–Gelman–Rubin statistics between 1.0 and 1.03 for all parameters; plots of the parameters for the three chains against the simulation number (trace plots) showing considerable overlap and movement in chain values (which would be consistent with good mixing); and DIC values that were stable between runs.

All of the BHMs with a multinomial distribution for the observations (level 1) and random effects (level 2) had nearly equal DIC values (models 1–6 in Table 3). Spiegelhalter et al. (2002) support the rule of thumb that models within 1–2 of the minimal DIC value deserve consideration (as used by Burnham and Anderson [1998] for the Akaike information criterion). Notably, this set included a model without exports. The results were robust to the choice of the prior for the standard deviation of the random effects (σ), either the uniform or inverse gamma distribution. Either covariate, exports or exports/flow, led to equivalent DIC values. The posterior means for $\theta_{3,t}$ were much the same for these models.

The Bayesian P-values were essentially identical for these multinomial, random-effect models. Fifty-three of the 60 observations (88%) had Bayesian P-values that fell within the middle 90% of the posterior predictive distributions. There were too few observed recoveries ($P = 0.02$–0.04) for two cases ($y_{\text{Ry}\to\text{CI},1}$ and $y_{\text{Ry}\to\text{CI},6}$) and too many observed recoveries ($P = 0.95$–1.00) for five others ($y_{\text{GS}\to\text{CI},5}$, $y_{\text{GS}\to\text{CI},9}$, $y_{\text{GS}\to\text{CI},12}$, $\hat{y}_{\text{Ry}\to\text{Oc+IL},14}$, and $\hat{y}_{\text{GS}\to\text{Oc+IL},14}$).

Replacing the multinomial distribution with the negative binomial distribution (model 7) and excluding random effects (model 8) led to sizeable increases in the DIC values (Table 3), especially for the latter

TABLE 3.—Summary of Bayesian hierarchical models. The level 1 column specifies the distributions (Mn = multinomial, NB = negative binomial). The level 2 column shows models for $\theta_{3,t}$, N denoting the normal distribution and MVN the multivariate normal distribution; the models for the recovery probabilities ($r_{\text{Ry}\to\text{CI},t}$ and $r_{\text{Ry}}\to\text{IL},t$) are those shown in equations (8) and (9) in the text except for the MVN model (1) and the model without random effects (8). The level 3 column specifies the prior distribution for the random effects variance; U = uniform, IG = inverse gamma, and IW(I, 4) = inverse Wishart, I being the identity matrix.

Model	Level 1	Level 2	Level 3	$E(\beta_1)$	$\Pr(\beta_1 < 0)$	$E(\sigma_\theta)$	DIC
1	Mn	$\log_e(\theta_{3,t}), \ldots \sim .\text{MVN}(\beta_0 + \beta_1 \text{Exp}_t^*, \ldots, \Sigma)$	$\Sigma \sim \text{IW}[I, 4]$	−0.194	0.92	0.53	460.0
2	Mn	$\log_e(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \text{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \text{U}(0, 20)$	−0.170	0.89	0.50	460.0
3	Mn	$\log_e(\theta_{3,t}) \sim .\text{N}\left(\beta_0 + \beta_1 \frac{\text{Exp}}{\text{Flow}_t}, \sigma_\theta^2\right)$	$\sigma \sim \text{U}(0, 20)$	−0.706	0.86	0.51	460.0
4	Mn	$\log_e(\theta_{3,t}) \sim .\text{N}(\beta_0 + \beta_1 \text{Exp}_t^*, \sigma_\theta^2)$	$\sigma^2 \sim \text{IG}(0.001, 0.001)$	−0.166	0.90	0.48	459.9
5	Mn	$\text{logit}(\theta_{3,t}) \sim .\text{N}(\beta_0 + \beta_1 \text{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \text{U}(0, 20)$	−0.297	0.88	0.89	460.0
6	Mn	$\log_e(\theta_{3,t}) \sim .\text{N}(\beta_0, \sigma_\theta^2)$	$\sigma \sim \text{U}(0, 20)$			0.51	460.1
7	NB	$\log_e(\theta_{3,t}) \sim .\text{N}(\beta_0 + \beta_1 \text{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \text{U}(0, 20)$	−0.168	0.89	0.46	487.0
8	Mn	$\log_e(\theta_{3,t}) = \beta_0 + \beta_1 \text{Exp}_t^*$		−0.079	0.99		4,281.8

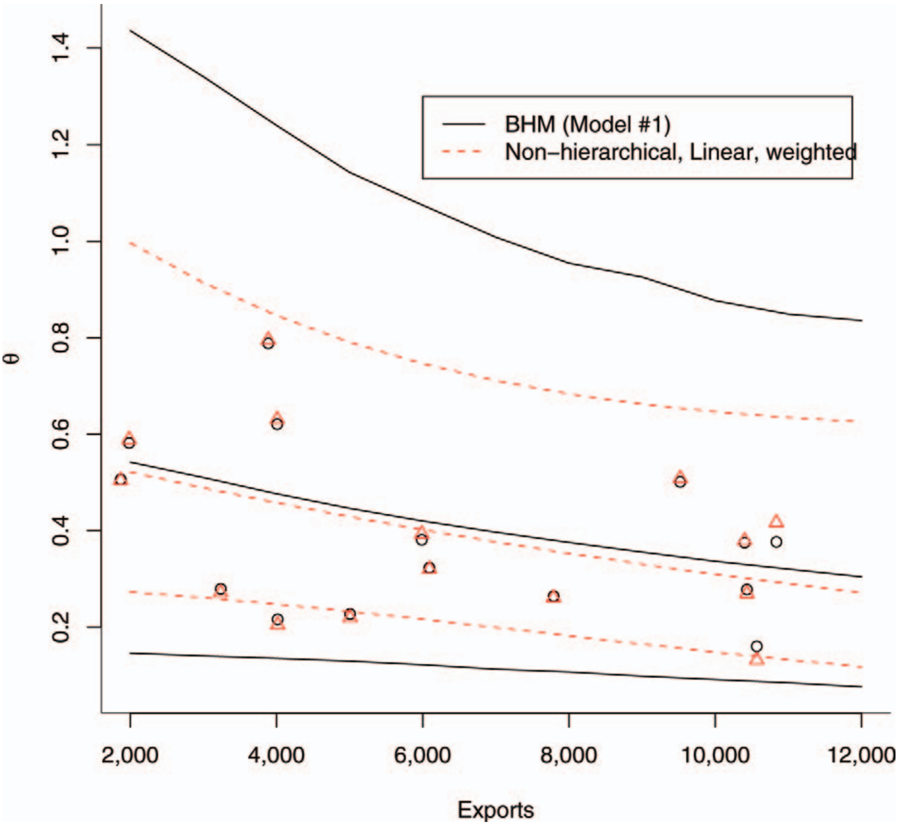


FIGURE 4.—Expected values and 2.5–97.5% prediction intervals for θ at different levels of exports produced by Bayesian hierarchical model (BHM) 1 (solid lines) and the nonhierarchical model (dashed lines) using Chipps Island and combined ocean and inland recoveries (equation 4). The circles denote posterior mean fitted values for θ from the BHM, the triangles maximum likelihood estimates.

model. Many of the Bayesian *P*-values for the nonrandom-effects model were close to 0 or 1. The negative binomial model's parameters, k_{CI} and k_{Oc}, were quite large (with posterior means of 214 and 279, respectively), providing little evidence for overdispersion.

Referring now to model 1 (the results for which are nearly identical to those for models 2–6), the recovery probabilities for Ryde releases at Chipps Island were an order of magnitude lower than those for the ocean fisheries and inland recoveries; the median for $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ was 0.0004, versus 0.0038 for $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}$. Given that recovery probabilities are the product of survival and capture probabilities, an $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ of that value seems reasonable for the Chipps Island trawl based on independent estimates of Chipps Island trawl capture probabilities on the order of 0.001–0.002 (Newman 2003). The correlations between θ, $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$, and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ (on the transformed scales) were weakly positive: between θ and $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ the posterior mean for $\sigma_{1,2}$ was 0.21; between θ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ $E[\sigma_{1,3}]$ was 0.18; and between $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ $E[\sigma_{2,3}]$ was 0.25. Thus, within release pairs, when survival was higher for one segment it tended to be higher for the other segments.

For all models with exports the posterior mean value for β_1 was negative, indicating a negative association between θ and exports. For models 1–5, $\Pr(\beta_1 < 0)$ ranged from 0.86 to 0.92. The variation in the relationship with exports, however, was quite large, as both the size of $E(\sigma_\theta)$ and the plot of the predicted θ values against exports (Figure 4) indicate. While the plot shows a decline in the mean value of θ as exports increase (e.g., when exports are 2,000 cfs, the mean value of θ is 0.54, whereas when exports are 10,000 cfs, it is 0.34), the range of individual values is very wide. The upper bounds on θ for export levels less than 7,200 cfs exceed 1.0, allowing for the possibility that Georgiana Slough releases occasionally have higher survival than Ryde releases.

Given the similarity in DIC values among models 1–

6 and the fact that our primary interest was the effect of exports, we applied reversible jump MCMC to just two models that differed only with respect to the inclusion (model 2) or exclusion of exports (model 6). The posterior probability for the model including exports was only 1%, compared with 99% for the model without exports; thus, there is scant evidence for a relationship between θ and exports. However, such results could be due to the low signal-to-noise ratio, as measured by the ratio of the posterior mean for β_1 to the posterior means for σ_θ, $\sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}$, and $\sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{OC+CI}}}$. Repeated simulations of 15 sets of recoveries with the actual release numbers and export levels were made with model 2 (equations 5–11) using the posterior mean values for the parameters (e.g., $E[\beta_1] = -0.17$). Despite the fact that the true model did have θ as a function of exports, RJMCMC typically yielded posterior probabilities for this model in the range of 1–3%. Even doubling the number of release pairs and extending the range of export levels to ±2 SDs of the observed values did not change these results. However, if the environmental variation were artificially decreased (e.g., by an order of magnitude), RJMCMC gave posterior probabilities for the correct model (the model with exports) ranging from 90% to 99%.

Nonhierarchical versus Hierarchical Models

The posterior means and standard deviations of θ_t from the BHMs (1–6) were quite similar to the (approximate) maximum likelihood estimates ($\hat{\theta}_{2,t}$) and the standard errors (Table 2). This indicates that the influence of the prior distributions on the Bayesian results was slight. The posterior standard deviations of θ_t were generally slightly less than the standard errors, presumably a result of the "borrowing of strength" from other release–recovery data that informs the estimates.

Model-based predictions of θ_t as a function of exports were quite similar for the BHM (equations 5–11) and the nonhierarchical model (equation 4), but the prediction intervals for the BHM were considerably wider (Figure 4). The observed variation in the estimates of θ_t (shown in Figure 4) seems more consistent with the wider BHM prediction intervals than the nonhierarchical model intervals.

Discussion

We conclude that, for a paired release the survival to Chipps Island of Georgiana Slough releases is considerably less than that of Ryde releases. The ratios of the recovery fractions of the two releases at Chipps Island, in the ocean fisheries, and at the inland sites were consistently much less than 1.0 (Figure 2), and the posterior means and maximum likelihood estimates of θ_t were at most 0.8 (Table 2). The posterior median of θ_t was 0.35 from a model without exports (BHM 6).

Factors other than exports that could cause lower relative survival for Georgiana Slough releases include water temperature, predation, and pollution (Moyle 1994). Higher water temperatures have been associated with higher mortality through the delta (Baker et al. 1995). For the paired releases we analyzed, however, the temperatures at release were very similar at Ryde and Georgiana Slough. Regarding predation, Stevens (1966) found more salmon in the stomachs of striped bass *Morone saxatilis* located in the so-called flooded-islands portion of the delta (south of the Georgiana Slough release point) than in the stomachs of striped bass in the Sacramento River.

Regarding the relationship between relative survival and export level, the point estimates of the effects of exports were consistently negative and for the BHMs the probability that the effects are negative was 86–92%. However, as a result of the low signal-to-noise ratio, the DIC values and posterior model probabilities indicate that the predictive ability of models without exports is equivalent to that of models with exports. The environmental variation is large enough that our failure to find a stronger association could be a function of inadequate sample size. Previous analyses (Newman 2008:72) of the relationship between the number of paired releases and the precision of the estimated slope parameter for exports showed that 100 paired releases were needed (based on $\beta_1 = -0.57$ for a logistic transformation of θ) to yield a coefficient of variation of 20%. The RJMCMC analysis of simulated data was consistent with those findings.

Exports do affect Georgiana Slough releases more than Ryde releases, as the fraction of Georgiana Slough releases recovered at the CVP and SWP fish salvage facilities increases with increasing exports (Figure 2). The intent of the salvage operations is to increase survival by relocating those fish away from the pumping facilities, and perhaps there is some mitigating effect. However, at the SWP facility there is an enclosed area, Clifton Court Forebay, where fish suffer mortality due to predators (Gingras 1997) before entering the salvage facilities. Experiments with marked salmon in the vicinity of the SWP fish facility have yielded estimates of "presalvage" mortality in the range of 63–99%, with an average of 85% (Gingras 1997), although the quality of these estimates has been called into question (Kimmerer 2008).

A tangential question is whether or not the fish facility recovery fractions are related to exports or the export–flow ratio (i.e., the absolute or relative level of exports). Over the range of values observed in these studies, exports and the export–flow ratio are linearly associated (Pearson correlation coefficient = 0.83), so that it is difficult to disentangle the effects of the two factors. Deliberate fixing of export levels at varying levels of flow would be one possible way of determining whether it is the absolute or the relative level of exports that affects the fraction of Georgiana Slough releases recovered at the fish salvage facilities. However, current water management policies and operational standards make such manipulations difficult to conduct. Export levels are largely determined by state and federal water project agencies based on water demand, conditions in the delta, water quality, and operational standards as well as endangered species biological opinions. Owing to the lack of randomization of export levels and the relatively low numbers of releases, the effects of exports may be confounded by other conditions that cause survival to increase or decrease. The pairing aspect of the design may control for such confounding factors, however.

Given the low signal-to-noise ratio, instead of repeating coded wire tag release–recovery experiments for many more years, we recommend releasing fish with acoustic tags and relocating them with strategically placed receivers. Such a system could provide more precise information about when and where mortality is occurring, yielding estimates of reach-specific survival (Muthukumarana et al. 2008). How much of an effect the interior delta mortality has on the total population of Sacramento River juvenile Chinook salmon (whatever the causes) depends on the fraction of the out-migrating population that moves into the interior delta. Using coded wire tag release–recovery data, Kimmerer (2008) estimated that the overall mortality is 10% at the highest export levels, assuming a presalvage mortality of 80% at the fish facilities. Pilot studies using acoustic tags have recently been carried out to estimate the proportion of out-migrants entering the delta (Perry et al. 2009, this issue), and once this proportion is identified, the benefits of preventing fish from entering the interior delta can be estimated more accurately.

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REFERENCE EXHIBIT H

Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta during the Winter of 2007-2008

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Abstract

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating from natal tributaries of the Sacramento River may use a number of possible migration routes to negotiate the Sacramento–San Joaquin River Delta (hereafter, "the Delta"), each of which may influence their probability of surviving. In a previous report, we developed and applied a mark-recapture model to data from acoustically tagged juvenile late-fall Chinook salmon that migrated through the Delta during the winter of 2007. This study was repeated during the winter of 2008, and this report presents findings from our second year of research. First, population-level survival through the Delta (S_{Delta}) during 2008 was substantially lower than in 2007, and we found little difference in S_{Delta} between releases. For releases in December 2007, $\hat{S}_{\text{Delta}}$ was 0.174 ($\widehat{\text{SE}}$ =0.031) and for January 2008, $\hat{S}_{\text{Delta}}$ was 0.195 ($\widehat{\text{SE}}$ = 0.034), compared to 0.351 and 0.543 for the same release groups in 2007. In contrast to our previous study, we found that the fraction of the population entering the interior Delta was similar between releases (26.7% for December, 31.1% for January), despite the Delta Cross Channel being open during December and closed during January. However, similar to previous findings, survival of fish migrating through the interior Delta was significantly less than survival probabilities for fish remaining in the Sacramento River. The ratio of survival for fish migrating through the interior Delta relative to the Sacramento River was ≤35.2% ($\widehat{\text{SE}}$ ≤0.11) during both releases. Thus, migration routes through the interior Delta reduced population-level survival by a similar magnitude during both releases because differences in survival between routes remained constant, as did the fraction of fish entering the interior Delta. Reach-specific survival rates in the Sacramento River (expressed as a function of reach length) were higher than reaches within other migration routes. These findings indicated that variation in route-specific survival was driven by consistent differences among migration routes, rather than by specific reaches within a route. Our studies during 2006 and 2007 highlight the variation in survival and migration route probabilities that can be expected in future research, but nonetheless, consistent patterns in route-specific survival and migration are beginning to emerge.

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Introduction

Many stocks of Chinook salmon (*Oncorhynchus tshawytscha*) in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998). In the Central Valley of California, the winter, spring, and fall/late fall runs of Chinook salmon are federally listed as endangered, threatened, and a "species of concern," respectively (NMFS 1997). Recently, due to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a Federal Disaster and closed the 2008 salmon fishery along the West Coast (NOAA 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Brandes and McLain 2001; Baker and Morhardt 2001; Williams 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento-San Joaquin River Delta (hereafter, "the Delta"), a complex network of natural and man-made river channels linking the Sacramento River with San Francisco Bay (Nichols et al. 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the mainstem Sacramento River leading directly into San Francisco Bay (see Route A in Figure 1). However, they may also migrate through longer secondary routes such as the interior Delta, the network of channels to the south of the mainstem Sacramento River (see Routes C and D in Figure 1).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the Delta. Inflow into the Delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the Delta, water distribution is affected by two water pumping projects in the Southern Delta (the State Water Project and Central Valley Project). These projects pump water from the Delta for agricultural and municipal uses and can export up to 65% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior. In addition to these human influences on water flow through the Delta, natural processes include seasonal rainfall

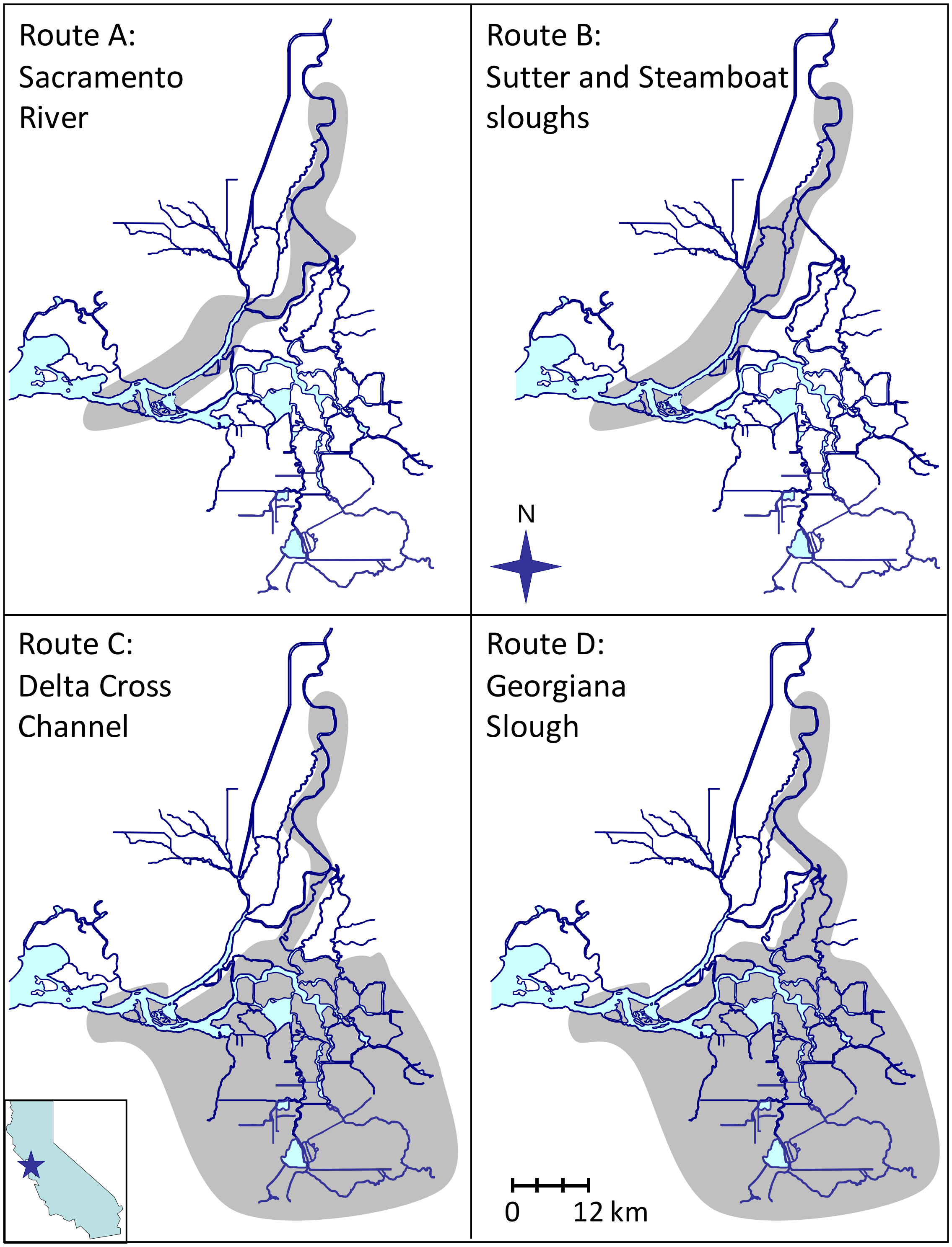

Figure 1.—Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. For routes C and D, the interior Delta is the large shaded region at in southern-most section of the migration route.

and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and bi-weekly time scales.

As juvenile salmon disperse among the complex channel network of the Delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. For example, juvenile salmon entering the interior Delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, which may decrease survival of fish using this migratory pathway (Kjelson et al.1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003; Kimmerer 2008; Newman 2008, Newman and Brandes in press). However, whether low survival through a particular route has a large effect on survival of the population will depend on the fraction of the population migrating through that route (Newman and Brandes, in press; Perry et al. 2008, in press). Thus, population-level survival rates of juvenile salmon migrating through the Delta will be driven by 1) the survival rates arising from biotic and abiotic processes unique to each migration route, and 2) the proportion of the population using each migration route.

Currently, there is limited understanding of how water management actions in the Delta affect population distribution and route-specific survival of juvenile salmon. In a previous study, we developed a mark-recapture model to estimate the route-specific components of population-level survival for acoustically tagged late-fall Chinook salmonsmolts migrating through the Delta during the winter of 2006/2007 (hereafter “2007”, Perry et al. 2008, in press). Our study provided the first comprehensive estimates of route-specific survival through the Delta and the fraction of the population using each major migration route. Furthermore, we explicitly quantified the relative contribution of each migration route to population-level survival. As with other authors (Newman and Brandes in press), we found that survival through the interior Delta was lower than survival of fish using the Sacramento River. We also found that the proportion of the population entering the interior Delta differed between releases, which influenced population-level survival by shifting a fraction of the population from a low-survival migration route (the interior Delta) to a high-survival route (the Sacramento River). However, we also found that differences between releases in population-level survival were caused by changes in survival for given migration routes. Thus, variation in population-level survival was driven both by variation in movement among routes as well as survival within routes.

In this report, we estimate survival and migration route probabilities for acoustically tagged late-fall Chinook salmon migrating through the Delta during the winter of 2007/2008 (hereafter, “2008”). While design aspects of our previous study were maintained, we also incorporated a number of changes in study design based on insights from the first year of study. The most important limitation in our previous study was small total sample size, as well as small sample size for specific migration routes. For example, we found that up to 40% of fish migrated through Sutter and Steamboat Slough (Route B in Figure 1), which diverts fish around the two routes leading into the interior Delta (Routes C and D in Figure 1). This led to low sample size and poor precision of parameter estimates for routes through the interior Delta, which in turn led to low power to detect differences in survival among migration routes. Thus, we took two approaches to improve precision. First, the total sample size was tripled from 140 tagged fish in 2007 to 419 tagged fish in 2008. Second, because the interior Delta is an important migration route with many management concerns, we also released a subsample of fish directly into the interior Delta via Georgiana Slough (Route D in Figure 1).

We also added new telemetry stations which allowed us to better partition survival among specific reaches and to quantify movement among channels within major migration routes. For example, in our previous study we observed a substantial difference between releases in survival for Sutter and Steamboat sloughs. However, because this migration route encompassed numerous unmonitored river channels it was impossible to determine whether changes in route-specific survival were due to shifts in mortality within a particular reach, or occurred due to changes in survival over all reaches with this route. Therefore, we incorporated additional telemetry stations with this migration route (and others) to better partition within-route survival among specific reaches and channels.

We first report results for population-level survival through the Delta, route-specific survival through the Delta, and dispersal among migration routes, contrasting estimates from this study to those from 2007. Given more detailed information within migration routes, we then examined patterns in reach-specific survival to understand whether variation in route-specific survival through the Delta was driven by particular reaches within a route. Last, in addition to dispersal among the major migration routes shown in Figure 1, we explicitly accounted for movement among other channels within routes, and discuss the influence of these movements on population-level migration and survival dynamics.

Methods

Telemetry System

Telemetry stations were deployed to monitor movement of tagged fish among four major migration routes through the Delta (Figure 1): the mainstem Sacramento River (Route A), Steamboat and Sutter Slough (Route B), the interior Delta via the Delta Cross Channel (Route C), and the interior Delta via Georgiana Slough (Route D; Figure 1). Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 2). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco Ltd., Model VR2) that identified individual fish based on the unique pattern of acoustic pulses emitted from a transmitter. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route is denoted as A_i from the release site to the last telemetry station in the Delta at Chipps Island (A_9). Sutter and Steamboat sloughs (labeled B_i) diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_7. We deployed numerous telemetry stations within Sutter and Steamboat sloughs to better quantify survival and movement within this region, relative to our previous study in 2007 (Perry et al. 2008, in press). Specifically, Sutter Slough and Miner Slough form a northern route and stations along this route are labeled B_{11} (entrance to Sutter Slough), B_{12}, and B_{13} (Miner Slough; Figure 2). A southern route is formed by Steamboat Slough and these stations are labeled as B_{21}, B_{22}, and B_{23}. The entrance to the interior Delta via the Delta Cross Channel was labeled as C_1 where it diverges from the Sacramento River at the second river junction. Telemetry stations within Georgiana Slough and the interior Delta were labeled as D_i beginning where Georgiana Slough diverges from the mainstem Sacramento River at the second river junction (D_1) until the convergence of the interior Delta with the Sacramento River at D_7. Following this hierarchy, routes A, B, C, and D contained 8, 6, 1, and 7 telemetry stations, whereas in 2007, the same routes contained 7, 1, 2, and 3 telemetry stations. In addition, to quantify movement between the lower Sacramento River and the lower San Joaquin River, we included a telemetry station within Three Mile Slough (E_1) for a total of 23 telemetry stations within the Delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see **Model Development** section below).

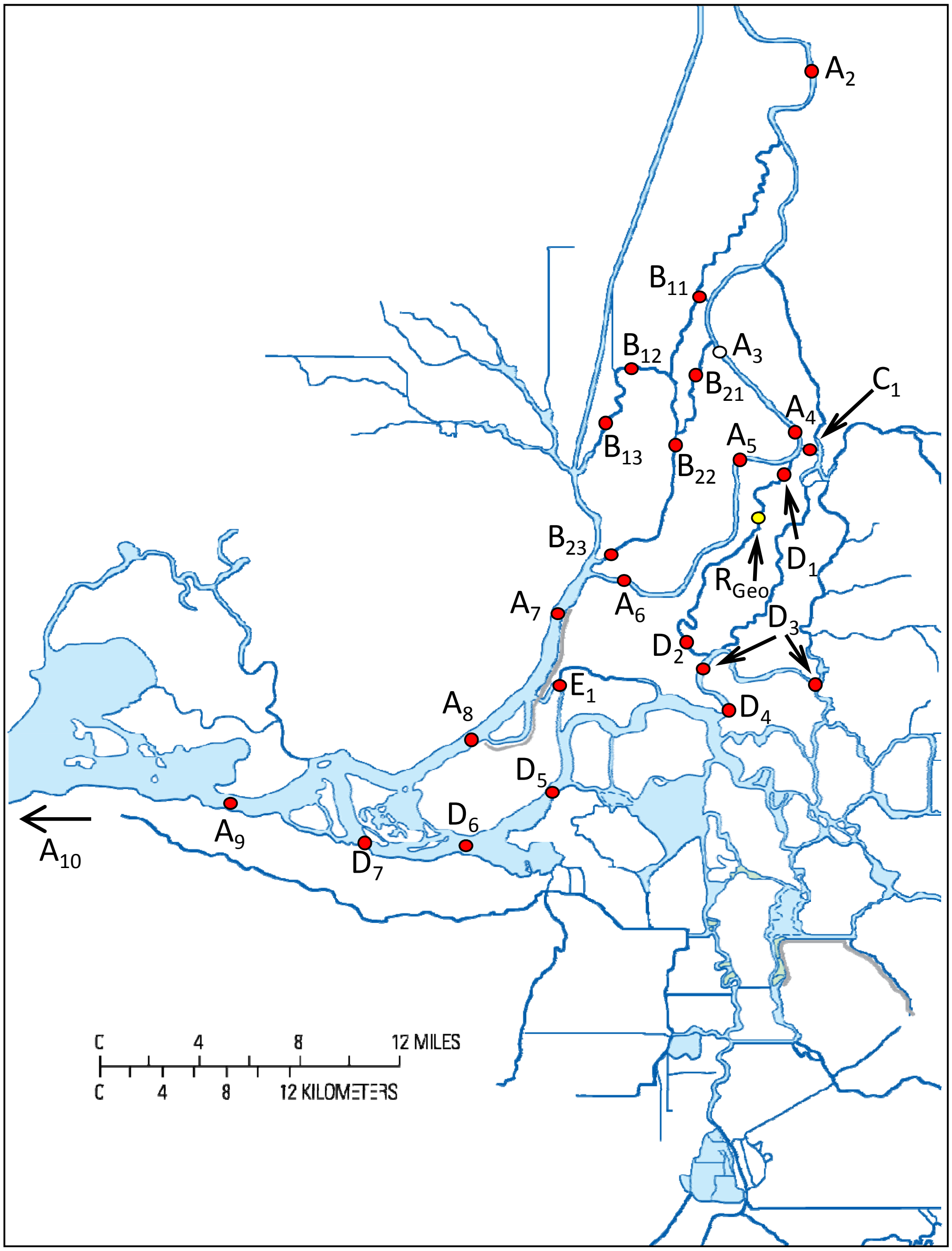

Figure 2.—Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2007/2008. Red-filled circles labeled as h_i show the location of telemetry station i with route h. The Delta extends from station A_2 at Freeport to station A_9 at Chipps Island. The first river junction occurs where Sutter Slough (B_{11}) and Steamboat Slough (B_{12}) diverge from the Sacramento River at location A_3. Location A_3 is denoted by an unfilled circle to indicate that a telemetry station was not implemented at this location during the winter of 2007/2008. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The two site labeled D_3 were treated as a single station in the mark-recapture model. The Sacramento release site was 19 river kilometers

upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

With this configuration of telemetry stations, survival in the final reach (downstream of A_8 and D_7) is confounded with detection probability at the last telemetry station (Skalski et al. 2001). Therefore, to estimate survival to the terminus of the Delta and detection probability at the last station in the Delta (A_9), we formed one additional telemetry station by pooling detections from numerous stations downstream of A_9 in San Francisco Bay (Figure 2). Most of these detections occurred at telemetry stations mounted to bridges that provided nearly complete cross-sectional coverage of San Francisco Bay, but single-monitor stations at other locations were also included.

Fish Tagging and Release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (approximately 340 river kilometers upstream of the release sites near Sacramento, CA). We used a 1.6-g tag with a 70-d expected battery life (Vemco Ltd., Model V7-2L-R64K). Except for a minimum size criteria of 140-mm fork length, fish were randomly selected for tagging resulting in a mean fork length of 155.0 mm (SD = 10.2) and mean weight of 42.0 g (SD = 9.6). The tag weight represented 3.8% of the mean fish weight (range = 1.9%–5.4%). Fish were fasted for 24 h prior to surgery to ensure they were in a post-absorptive state. To surgically implant transmitters, fish were anaesthetized and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4-0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for seven days prior to release.

To release fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (20 km upstream of A_2) or Georgiana slough (about 5 km downstream from D_1; Figure 2). Fish were then transferred to perforated 19-L buckets (2 fish per bucket) and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Releases at Sacramento were conducted at roughly hourly intervals, whereas release at Georgiana Slough were conducted every other hour over a 24-h period. Each release was carried out over a 24-h period to distribute release times over the tidal and diel cycle. The total sample size for the study was 419 acoustically tagged fish, with 208 fish released in December when the Delta Cross Channel was open and 211 fish released in January when the Delta Cross Channel was closed (Table 1). For the first release, 28% of the fish were released into Georgiana Slough, but this fraction was increased to 38% for the second release in anticipation that a lower proportion of the Sacramento release group would enter the interior Delta with the Delta Cross Channel closed (Table 1). Fish were released into Georgiana Slough two days later than the Sacramento release group to match release times in Georgiana Slough with the travel time of fish from Sacramento to Georgiana Slough (R. Perry, unpublished data).

Table 1.—Summary of release dates, locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2007/2008.

Release date	Release number	Release location	Sample size
4 December 2007	1	Sacramento	149
6 December 2007	1	Georgiana Slough	59
15 January 2008	2	Sacramento	130
17 January 2008	2	Georgiana Slough	81

Model Development

We expanded upon the model developed by Perry et al. (2008, in press) to explicitly quantify more detail in reach-specific survival of juvenile salmon through regions such as Sutter Slough, Steamboat Slough, and the interior Delta. As in our previous model, we estimate detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (ψ_{hl}). However, to capture complexity in movement of fish among different channels we also estimated joint survival-entrainment probabilities ($\phi_{hi,jk}$). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h = A, B, C, D; Figure 2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to i+1 within route h (i.e., to the next downstream telemetry station), conditional on surviving to station i (Figure 2 and 3). Route entrainment probabilities (ψ_{hl}) estimate the probability of a fish entering route h at junction l (l = 1, 2), conditional on fish migrating through junction l (Figures 2 and 3). Joint survival-entrainment probabilities ($\phi_{hi,jk}$) estimate the joint probability of surviving from site h_i to j_k and moving into route j. The $\phi_{hi,jk}$ parameters are estimated in reaches with river junctions that split into two channels, but where telemetry stations within each river channel are located some distance downstream the river junction. For example, fish passing station A_7 in the Sacramento River may enter Three Mile

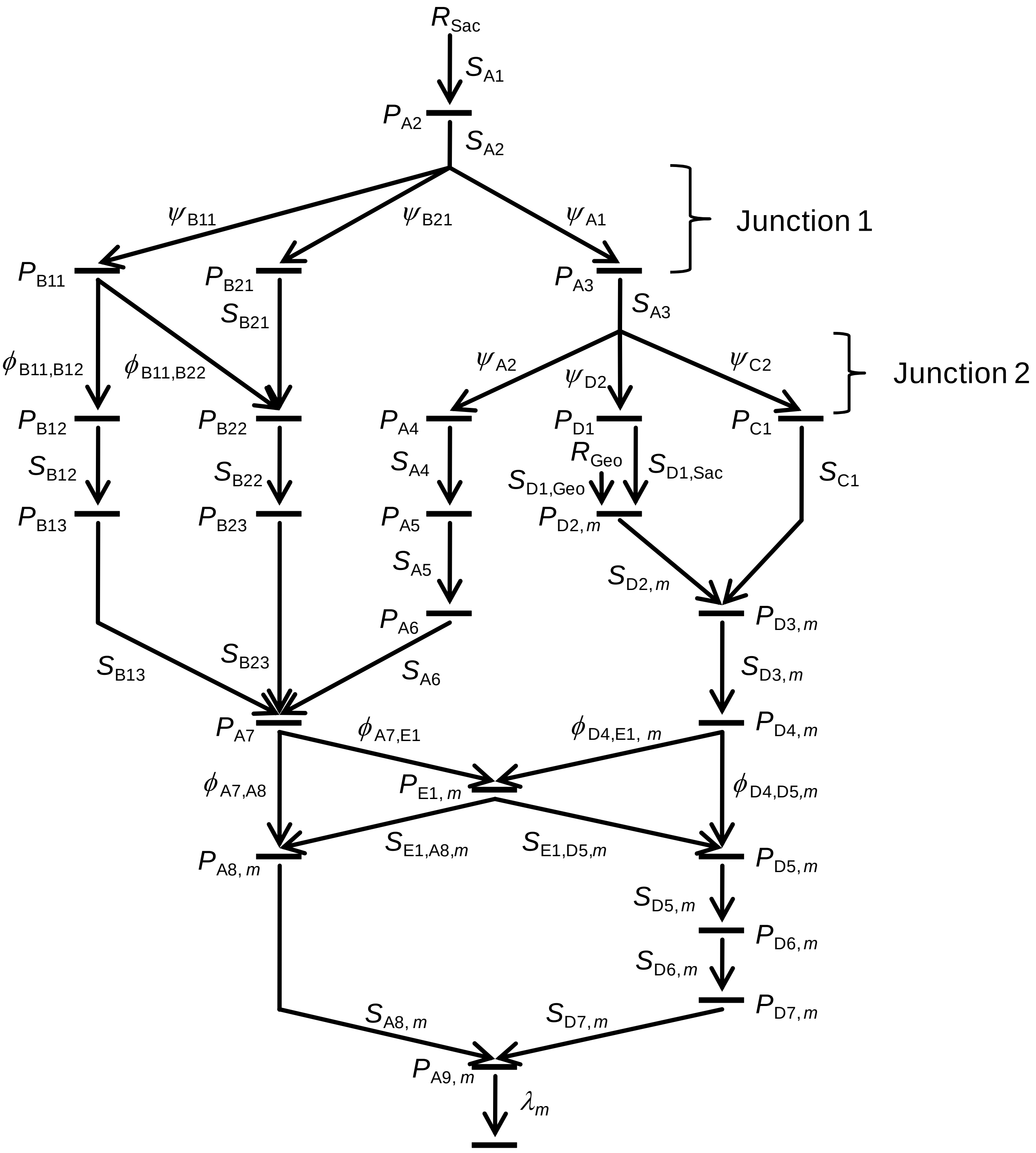

Figure 3.—Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (ψ_{hl}), and joint survival-entrainment ($\phi_{hi,\,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made December 2007 and January 2008. Release sites are denoted by R_m (m = Sac (Sacramento)

and Geo (Georgiana Slough)), and parameters subscripted by *m* denote parameters which can be estimated separately for each release site.

Slough (E_1) or remain the Sacramento River for another 5.5 km below this junction to pass station A_8 (Figure 2). Thus $\phi_{\mathrm{A7,A8}}$ is the joint probability of surviving from A_7 to its junction with Three Mile Slough, remaining in the Sacramento River at this junction, and then surviving from the junction to A_8.

In our 2007 study, telemetry arrays at the entrance to Sutter and Steamboat sloughs were pooled in the model to estimate a single route entrainment probability for both sloughs. For this study, however, telemetry stations within Sutter and Steamboat slough downstream of each entrance allowed us to estimate route entrainment probabilities separately for each slough (Figures 2 and 3). Thus, the parameter ψ_{B11} estimates the probability of being entrained into Sutter Slough at station B_{11} and ψ_{B21} estimates the probability of being entrained into Steamboat Slough at station B_{21}. Since route entrainment probabilities must sum to one at a given river junction, $1-\psi_{\mathrm{B11}}-\psi_{\mathrm{B21}}=\psi_{\mathrm{A1}}$ is the probability of remaining in the Sacramento River at the first junction (Figures 2 and 3). As in 2007, the second junction was modeled as a three-branch junction where ψ_{A2}, ψ_{C2}, and $1-\psi_{\mathrm{A2}}-\psi_{\mathrm{C2}}=\psi_{\mathrm{D2}}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2 (Figures 2 and 3).

Joint survival-entrainment probabilities were estimated for three reaches where 1) fish entering Sutter Slough (B_{11}) may subsequently continue down either Miner Slough (B_{12}) or Steamboat Slough (B_{22}), 2) fish entering the San Joaquin River at D_4 may subsequently exit this reach through either Three Mile Slough at E_1 or the San Joaquin River at B_5, and 3) fish passing A_7 in the Sacramento River may exit this reach at either E_1 or A_8 (Figures 2 and 3). Each of these reaches consist a single river channel, a junction where the channel splits, and then two separate channels through which fish migrate before being detected at telemetry stations in each channel. In these locations, interest may lie in estimating the proportion of fish entering each channel (i.e., the route entrainment probabilities, ψ_{hl}). However, when telemetry stations are located kilometers downstream of the river junction where fish enter one route or another, then estimates of ψ_{hl} may be biased if survival probabilities downstream of the junction differ between the two channels. However, the joint probability of surviving and migrating through a given channel (i.e., $\phi_{hi,jk}$) will remain unbiased in these circumstances. Although the $\phi_{hi,jk}$ parameters are difficult to interpret biologically, being the joint probability of entrainment and survival, their sum yields the total reach survival. Thus, in the three reaches where $\phi_{hi,jk}$ parameters are estimated, $S_{\mathrm{B11}} = \phi_{\mathrm{B11,B12}} + \phi_{\mathrm{B11,B22}}$, $S_{A7} = \phi_{\mathrm{A7,E1}} + \phi_{\mathrm{A7,A8}}$, and $S_{D4} = \phi_{\mathrm{D4,E1}} + \phi_{\mathrm{D4,D5}}$ are the probabilities of surviving from each upstream telemetry station to either of the next downstream stations.

Other than the differences noted above, our model structure for this study differed in two other aspects relative to our study conducted in 2007. First, in our previous study, about 14% of fish from one release passed the Delta Cross Channel when it was both open and closed, requiring us to incorporate a parameter to estimate the probability of fish passing the Delta Cross Channel under each condition (ω_{open}, see Perry et al. 2008, in press). However, for this study, only 3 fish (4%) released when the Delta Cross Channel was open passed the Delta Cross Channel after it had closed. Therefore, we did not include ω_{open} in the model. Second, having two release sites leads to two estimates of the same parameter for reaches within the interior Delta (e.g., $S_{\mathrm{D3},m} = S_{\mathrm{D3,Sac}}$ or $S_{\mathrm{D3,Geo}}$, Figure 3). With this model structure, the full model contains 75 unique parameters; 55 parameters from the Sacramento release and 20 for the Georgiana Slough release (Figure 3);

Parameter Estimation

Prior to parameter estimation, the records of tag-detections were processed to eliminate false positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given telemetry stations, and simultaneous tag transmissions "collide" to produce a valid tag code that is not actually present at the monitor (Pincock 2008). Our first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimized the probability of accepting a false positive detection, Pincock (2008) showed that a pair of false positive detections with a time interval <30 min occurred on average once every 30 d when simulating ten tags simultaneously present at a monitor. Thus, our second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002). The detection records of about 10% of tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento and San Joaquin rivers (sites A_7–A_8 and D_5–D_7), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, a fish with the history AA0AAAAEDDDAA indicates it was released at Sacramento ("A"), detected in the Sacramento River at A_2 ("A"), and not detected in the Sacramento River at A_3 ("0"). This fish was subsequently detected at every other telemetry station as it emigrated from the Sacramento River ("AAAA") through Three Mile Slough ("E"), down the San Joaquin River ("DDD"), and finally past Chipps Island into San Francisco Bay ("AA"). Each detection history represents one cell of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, route entrainment, and joint survival-entrainment probabilities (See Perry et al. 2008 for an example). Given these cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters:

$$L_{km}\left(\underset{\sim}{\beta}\middle| R_{km}, n_{jkm}\right) \propto \prod_{j=1}^{J} \pi_{jkm}^{n_{jkm}}$$

where L_{km} is the likelihood for the kth release group (k = 1, 2) at the mth release site (m = Sacramento (Sac), Georgiana Slough (Geo)), R_{km} is the number of fish released for each release group and release site, n_{jkm} is the number of fish with the jth detection history in the kth release group at the mth release site, and π_{jkm} is the probability of the jth detection history in the kth release group at the mth release site expressed as a function of the parameters ($\underset{\sim}{\beta}$). The likelihood was numerically maximized with respect to the parameters using algorithms provided in the software programs R (R Development Core Team 2008) and USER (Lady et al. 2008). Parameters were estimated separately for each release (k) but simultaneously for both release sites by expressing the joint likelihood as the product of $L_{k,\text{Sac}}$ and $L_{k,\text{Geo}}$. The variance-covariance matrix was estimated as the inverse of the Hessian matrix. We used the delta method (Seber 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\psi_{C2} = 1 - \psi_{B2} - \psi_{D2}$). Uncertainty in parameter estimates is presented both as standard errors and 95% profile likelihood confidence intervals.

Although we planned to have a telemetry station in the Sacramento River at junction 1 (A_3), this station was not implemented in 2008, so we set P_{A3} to zero. Absence of this telemetry station makes it impossible to uniquely estimate the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B12}. However, these parameters can be estimated by assuming that $S_{A2} = S_{A3}$. This assumption was supported by estimates of S_{A2} and S_{A3} in 2007 (Perry et al. 2008, in press). Nonetheless, given that three of four releases thus far (in 2007 and 2008) have occurred without a telemetry station at A_3, we undertook a sensitivity analysis to examine the magnitude of bias introduced into route entrainment probabilities due to deviation from the assumption that $S_{A2} = S_{A3}$ (see Appendix 2). Since it is impossible to apportion mortality between the reach above and below A_3, we examined bias under the extreme scenarios where all mortality occurs either upstream of the first river junction (i.e., $S_{A3} = 1$) or downstream of the first river junction (i.e., $S_{A2} = 1$).

For each release, the full model was considered as the model with the fewest parameter constraints which still allowed all parameters to be uniquely estimated. When parameter estimates occur at the boundaries of one (or zero) they cannot be estimated through iterative maximum likelihood techniques and must be set to one (or zero). In our study, many detection probabilities were set to one because all fish passing a given location were known to have been detected at that location. In some cases, survival probabilities were fixed to one because all fish detected at a given telemetry station were also detected at the next downstream location. In addition, parameters for Route C (the Delta Cross Channel) were set to zero for the second release when the Delta Cross Channel was closed. A full detailing of parameter constraints applied under the full model can be found in Appendix Table 1.2.

The purpose of including a separate release into Georgiana Slough was to improve precision within the interior Delta by boosting the sample size of fish migrating through this region. Pooling data across release sites can improve precision but assumes that the fish released into the Sacramento River and Georgiana Slough experience similar survival and detection probabilities in reaches through which both release groups migrate. Therefore, we used likelihood ratio tests (Casella and Berger, 2002) to evaluate hypotheses about equality in detection and survival parameters between release sites. Lack of significance at $\alpha = 0.05$ indicates that the full model fits the data no better than the reduced model where parameters are set equal among releases, in which case the reduced model is selected over the full model. For each release, we first compared the full model to a reduced model where all parameters were set equal between releases. We then used parameter estimates from the selected model for estimating population-level and route-specific survival through the Delta.

Survival through the Delta

Survival through the Delta is defined as the probability of survival from the entrance to the Delta at station A_2 (Freeport) to the exit of the Delta at station A_9 (Chipps Island). Population-level survival through the Delta was estimated from the individual components as:

$$S_{\text{Delta}} = \sum_{h=\text{A}}^{\text{D}} \psi_h S_h \qquad (1)$$

where S_h is the probability of surviving the Delta given the specific migration route taken through the Delta, and ψ_h is the probability of migrating through the Delta via one of four migration routes (A = Steamboat Slough, B = Sacramento River, C = Georgiana Slough, D = Delta Cross Channel). Thus, population survival through the Delta is a weighted average of the route-specific survival probabilities with weights proportional to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\psi_{\text{A}} = \psi_{\text{A1}}\psi_{\text{A2}} \qquad (2)$$

$$\psi_{\text{B}} = \psi_{\text{B11}} + \psi_{\text{B21}} \qquad (3)$$

$$\psi_{\text{C}} = \psi_{\text{A1}}\psi_{\text{C2}} \qquad (4)$$

$$\psi_{\text{D}} = \psi_{\text{A1}}\psi_{\text{D2}} \qquad (5)$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (ψ_{C}) is the product of these route entrainment probabilities, $\psi_{\mathrm{A1}}\psi_{\mathrm{C2}}$. Since route entrainment probabilities can be estimated separately for Sutter Slough and Steamboat Slough, the probability of migrating through either Sutter or Steamboat Slough (ψ_{B}) is the sum of the route-entrainment probabilities for each slough (ψ_{B11} and ψ_{B21})

When population level survival can be broken down into components of route-entrainment probabilities and reach specific survival, then survival through the Delta for a given migration route (S_h) is simply the product of the reach-specific survival probabilities that trace each migration path through the Delta between the points A_2 and A_9 (see Perry et al. 2008, in press). However, when joint survival-entrainment probabilities are included in the model, survival through a given route must take into account all possible within-route pathways that involve the $\phi_{hi,jk}$ parameters. For example, survival through the Delta for fish that remain in the Sacramento River through the first and second river junctions is expressed as:

$$S_{\mathrm{A}} = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{\mathrm{A4}}S_{\mathrm{A5}}S_{\mathrm{A6}}\left(\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}\right)$$

The bracketed term is the weighted average survival between A_7 (Rio Vista) and A_9 (Chipps Island) with the $\phi_{hi,jk}$ parameters weighting survival of fish that remain in the Sacramento River ($\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}}$) and survival of fish that finish their migration in the lower San Joaquin after passing through Three Mile Slough ($\phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}$). Thus, Delta survival for Route A (the Sacramento River) includes some mortality of fish that enter the interior Delta, and it is impossible to factor out this mortality without explicitly estimating route entrainment probabilities at the junction of the Sacramento River with Three Mile Slough. Nonetheless, the $\phi_{hi,jk}$ parameters provide information about the relative contribution of the interior Delta to survival through Route A. For example, $\phi_{\mathrm{A7,E1}} \ll \phi_{\mathrm{A7,A8}}$ would suggest that movement through Three Mile Slough is a small component of the total survival for fish that migrated in the Sacramento River up to that point. Survival through the Delta for fish taking the Delta Cross

Channel (Route C) and Georgiana Slough (route D) is expressed similarly, and explicitly accounts for fish that pass through Three Mile Slough and finish their migration in the lower Sacramento River:

$$S_C = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{C1} S_{D3} \left(\phi_{D4,D5} S_{D5} S_{D6} S_{D7} + \phi_{\mathrm{D4,E1}} S_{\mathrm{E1,A8}} S_{\mathrm{D8}} \right),$$

and $$S_D = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{D1} S_{D2} S_{D3} \left(\phi_{D4,D5} S_{D5} S_{D6} S_{D7} + \phi_{\mathrm{D4,E1}} S_{\mathrm{E1,A8}} S_{\mathrm{A8}} \right).$$

To facilitate comparison with findings from our first year in 2007, we pooled Sutter and Steamboat Slough into a single migration route, but survival through the Delta can be estimated separately for fish that enter Sutter Slough and fish that enter Steamboat Slough:

$$S_B = \psi_{B11} S_{B1} + \psi_{B21} S_{B2}$$

where S_{B} is survival through the Delta for fish that enter either Sutter or Steamboat Slough, S_{B1} and S_{B2} are survival through the Delta for fish that enter Sutter Slough and Steamboat Slough, respectively, and where S_{B1} and S_{B2} are estimated as:

$$S_{B1} = S_{A2} \left(\phi_{B11,B12} S_{B12} S_{B13} + \phi_{B11,B22} S_{B22} S_{B23} \right) \left(\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}} S_{\mathrm{E1,D5}} S_{\mathrm{D5}} S_{\mathrm{D6}} S_{\mathrm{D7}} \right),$$

and $$S_{B2} = S_{A2} S_{B21} S_{B22} S_{B23} \left(\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}} S_{\mathrm{E1,D5}} S_{\mathrm{D5}} S_{\mathrm{D6}} S_{\mathrm{D7}} \right).$$

For fish entering Sutter Slough, note that the first bracketed term in S_{B1} accounts for survival of fish taking either Miner Slough ($S_{\mathrm{B12}}S_{\mathrm{B13}}$) or Steamboat Slough ($S_{\mathrm{B22}}S_{\mathrm{B23}}$) weighted by the joint probability of surviving and taking each of these routes ($\phi_{B11,B12}$ and $\phi_{B11,B22}$).

We used an approach similar to Newman and Brandes (in press) to quantify survival through each migration route relative to survival of fish that migrate within the Sacramento River:

$$\theta_h = \frac{S_h}{S_{\mathrm{A}}} \qquad h \neq \mathrm{A}$$

We measured each route relative to route A because the Sacramento River is considered the primary migration route. For Georgiana Slough, θ_{D} is nearly analogous to θ estimated by Newman and Brandes (in press), who estimated the ratio of recovery rates of coded wire tagged fish released into Georgiana Slough and the Sacramento River near A_4. Survival through the Delta for route h is equal to Route A when $\theta_h = 1$, and survival through route h is less (greater) than Route A when θ_h is less (greater) than one. We interpreted survival through route h as significantly different than Route A at $\alpha = 0.05$ when $\theta_h = 1$ fell outside the 95% profile likelihood confidence interval of $\hat{\theta}_h$.

To aid in interpreting differences in survival through the Delta among routes and between releases, we examined variation in reach-specific survival rates. Survival probabilities estimate the proportion of fish that survive through a given reach, but direct comparison of survival probabilities among reaches can be hampered by variation in the length of each reach. In our study, reach length varied from just a few kilometers to over 20 km. Therefore, we scaled survival probabilities relative to reach length by calculating survival rates per unit distance:

$$s_{hi} = \sqrt[x_{hi}]{S_{hi}}$$

where s_{hi} is the per-kilometer probability of surviving from telemetry station h_i to the next downstream station, x_{hi} is the distance (km) from telemetry station h_i to the next downstream telemetry station, and S_{hi} is the probability of surviving over x_{hi} kilometers. For reaches where more than one exit location is possible (reaches beginning at B_{11}, A_7, and D_4), we used the average distance to each of the exit points. The length of some reaches is ill-defined because fish may take multiple, unmonitored routes (e.g., the interior Delta between D_4 and D_5). For these reaches, reach length was calculated as the shortest distance between upstream and downstream telemetry stations (usually the main channel). If fish took longer routes which led to higher mortality, then survival probabilities (S_{hi}) scaled to the shortest possible migration route (s_{hi}) would appear low relative to other routes. Thus, this approach is of utility in identifying reaches of high mortality relative to the shortest possible pathway through a reach.

Results

River conditions and migration timing

River conditions differed for the two release groups and influenced their travel times through the Delta (Figure 4). For first release, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport was between 10,000 ft^3/s and 14,000 ft^3/s. The central 80% of this release group passed junction 2 (Stations A_4, C_1, and D_1; Figure 1) over a 5-day period between 7 December and 11 December. The Delta Cross Channel closed at 1138 hours on 14 December 2007 and remained closed for the balance of the study (Figure 4). In contrast, the second release group passed the two river junctions on the descending limb of a freshet, during which flows declined from about 19,000 ft^3/s to 14,000 ft^3/s. Under these flow conditions, the second release group passed junction 2 over a two-day period between 17 January and 19 January. Travel times from release to junction 2 were also shorter for the second release group, with a median travel time of 2.7 d for the first release compared to 1.5 d for the second release.

During their migration through the lower regions of the Delta, most of first release group experienced relatively low and stable discharge accompanied by declining water exports, whereas migration of the second release group coincided with a second freshet during which discharge increased to about 40,000 ft^3/s and exports remained stable (Figure 4). As a consequence, 80% of the first release group passed Chipps Island over a 29-d period (12 December to 10 January), but the central 80% of the second release group passed Chipps Island over only a 16-d period (24 January to 9 February). Although the median travel time from release to Chipps Island for the first release (9.7 d) was less than for the second release (12.9 d), the 90th percentile for the first release (35.9 d) was substantially longer than for the second release (23.9 d). These findings suggest that the main effect of the freshet during the second release was to compress the tail of the travel time distribution rather than shift its central tendency. For both releases, it was difficult to compare travel time among migration routes because ≤4 fish per route were detected at Chipps Island for all routes but the Sacramento River.

Route-specific survival through the Delta

Comparison of parameters between release sites (Sacramento and Georgiana Slough) suggested no difference in survival or detection probabilities, allowing us to set parameters equal between release sites to improve precision of survival estimates. For both releases, likelihood ratio tests were not significant (for December, $\chi^2_9 = 12.4$, $P = 0.192$; for January, $\chi^2_9 = 14.8$, $P = 0.097$), so the reduced model was used to estimate route-specific survival and S_{Delta}. We found little difference between releases in survival through the Delta. The probability of surviving through the Delta was 0.174 for the December release and 0.195 for the January release (Table 2). For the December release, fish remaining in the Sacramento River exhibited higher survival than all other routes ($S_A = 0.283$), whereas fish migrating through the interior Delta via the Delta Cross Channel and Georgiana Slough exhibited the lowest survival ($S_C = 0.041$, $S_D = 0.087$,

Table 2 and Figure 5). In contrast, for the January release, fish migrating through Sutter and Steamboat sloughs (S_B = 0.245) exhibited similar survival as fish migrating within the Sacramento River (S_A = 0.244), whereas survival through the interior Delta via Georgiana Slough remained lower than the other migration routes (S_D = 0.086). For both releases, separate estimates of route-specific survival for Sutter Slough and Steamboat Slough revealed fish entering Steamboat Slough exhibited survival that was about 9 percentage points higher than for fish that entering Sutter Slough (Table 2).

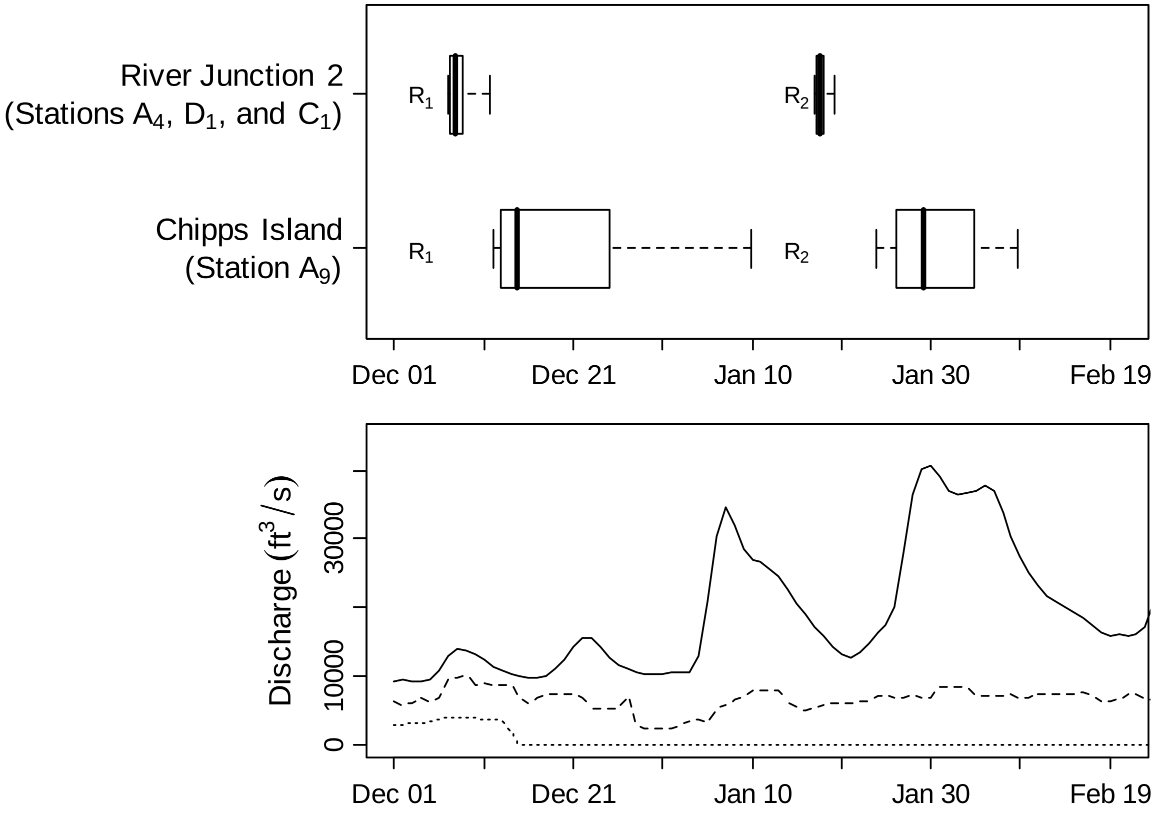

Figure 4.—River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2007/2008. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A4, C1, and D1) and at Chipps Island, the terminus of the Delta (telemetry station A9). The two release dates are shown as R_1 = 4 December 2006 for a release size of 149 tagged fish and R_2 = 15 January 2007 for a release size of 130 fish. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. River discharge (solid

line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

Table 2.—Route-specific survival through the Sacramento–San Joaquin River Delta (S_h) and the probability of migrating through each route (ψ_h) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 (R_1) and January 2008 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval	$\hat{\psi}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval
R_1: December 2007				
A) Sacramento R.	0.283 (0.054)	0.187, 0.397	0.387 (0.044)	0.304, 0.475
B) Sutter & Steamboat S.	0.136 (0.039)	0.073, 0.225	0.345 (0.042)	0.267, 0.430
B_1) Sutter S.	0.107 (0.037)	0.050, 0.196	0.230 (0.037)	0.163, 0.308
B_2) Steamboat S.	0.193 (0.060)	0.095, 0.327	0.115 (0.028)	0.068, 0.178
C) Delta Cross Channel	0.041 (0.021)	0.013, 0.096	0.117 (0.029)	0.068, 0.182
D) Georgiana S.	0.087 (0.028)	0.043, 0.153	0.150 (0.033)	0.094, 0.221
S_{Delta} (All routes)	0.174 (0.031)	0.119, 0.242		
R_2: January 2008				
A) Sacramento R.	0.244 (0.048)	0.160, 0.346	0.490 (0.048)	0.397, 0.584
B) Sutter & Steamboat S.	0.245 (0.059)	0.143, 0.372	0.198 (0.037)	0.133, 0.278
B_1) Sutter S.	0.192 (0.070)	0.078, 0.343	0.086 (0.026)	0.044, 0.147
B_2) Steamboat S.	0.286 (0.070)	0.162, 0.430	0.112 (0.029)	0.033, 0.253
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.086 (0.023)	0.048, 0.140	0.311 (0.045)	0.229, 0.403
S_{Delta} (All routes)	0.195 (0.034)	0.135, 0.268		

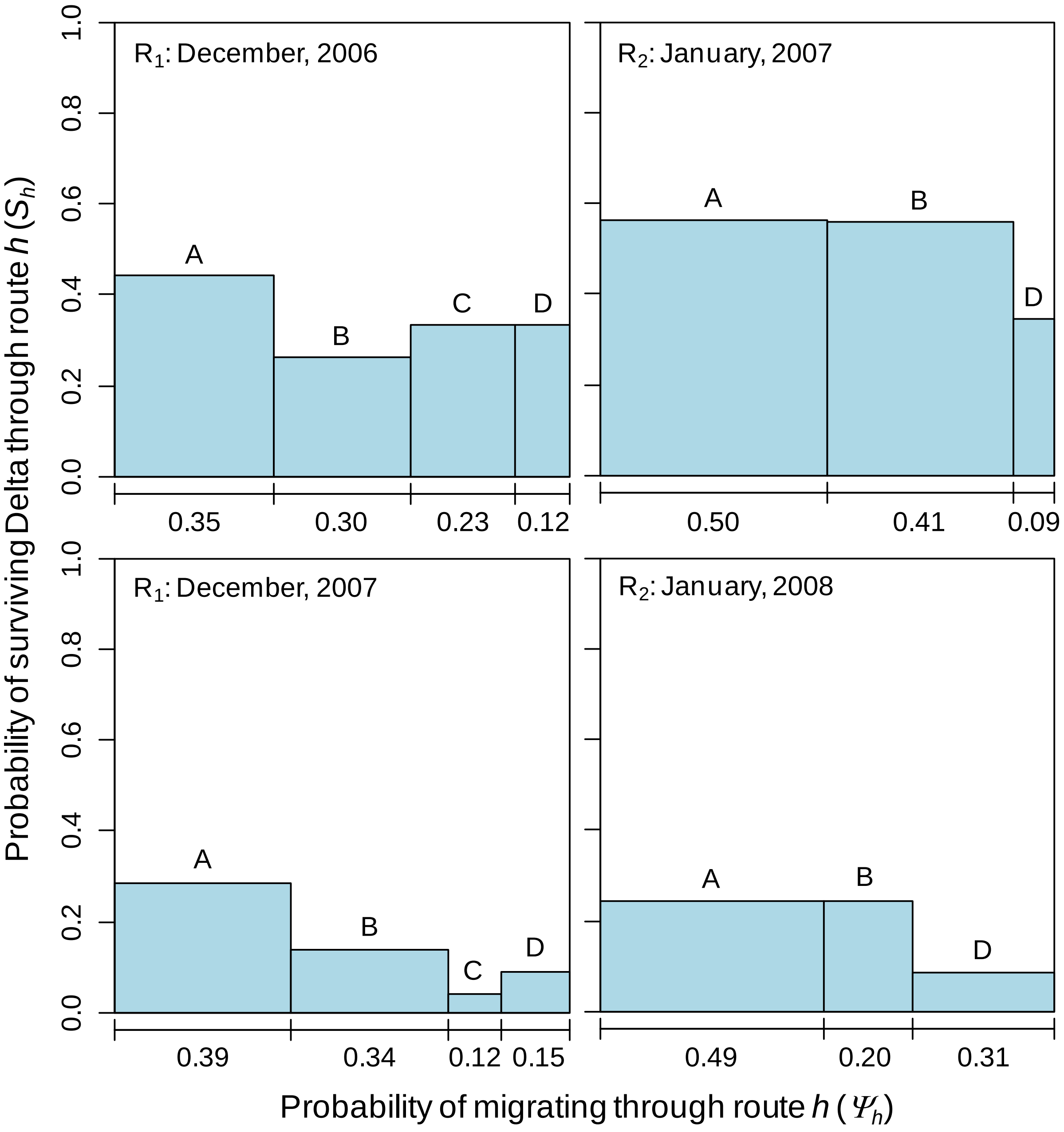

Figure 5.—Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon emigrating from the Sacramento River. The width of each bar shows the fraction of fish migrating through each route (ψ_h), and the total area under the bars yields S_{Delta}. The top panels show estimates from the winter of 2006/2007 (Perry et al. 2008, in press), and the bottom panels show estimates from this study during the winter of 2007/2008. Labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively.

We detected significant differences between survival for the Sacramento River and survival for other migration routes. For the December release, the ratio of survival for each major migration route relative to the Sacramento River (i.e., θ_h) ranged from 0.14 for the Delta Cross Channel to 0.48 for Sutter and Steamboat Slough, showing that survival through other routes was less than half that of the Sacramento River. Since $\theta_h = 1$ fell outside the 95% confidence intervals of $\hat{\theta}_h$ for all major routes, these findings support the hypothesis that all routes had significantly lower survival than the Sacramento River (Table 3). Considering Sutter Slough and Steamboat Slough separately, only the estimate of θ_{B2} for Steamboat Slough was not significantly different from one, likely due to small sample size and low precision for this secondary route. In contrast, in January, $\hat{\theta}_B = 1.005$ whereas $\hat{\theta}_D = 0.352$, showing that survival through the interior Delta (Route D) was only about one third that of other available routes. Survival for the interior Delta was significantly lower than for the Sacramento River for the January release, but survival for Sutter and Steamboat Slough (and each slough separately) was not significantly different than the Sacramento River (Table 3).

Table 3.—The ratio (θ_h) of survival through route *h* (S_h) to survival through the Sacramento River (S_A) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 and January 2008.

	R_1: December 2007		R_2: January 2008	
Migration route	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval
B) Sutter & Sutter S.	0.481 (0.132)	0.265, 0.794	1.005 (0.215)	0.621, 1.480
B_1) Sutter S.	0.380 (0.127)	0.182, 0.689	0.787 (0.273)	0.330, 1.365
B_2) Steamboat S.	0.683 (0.205)	0.346, 1.153	1.172 (0.255)	0.698, 1.714
C) Delta Cross Channel	0.146 (0.077)	0.044, 0.363	NA	
D) Georgiana S.	0.307 (0.109)	0.145, 0.596	0.352 (0.110)	0.186, 0.642

Migration Routing

For some migration routes, we found that the proportion of the population migrating through a given route deviated from the fraction of mean discharge in a route. As juvenile salmon migrated past the first river junction, 34.5% of fish left the Sacramento River to migrate through Steamboat and Sutter Slough (ψ_B, Figure 5 and Table 2), about 10 percentage points higher than the fraction of total discharge entering this route (Figure 6). In contrast, for the

January release, only 19.8% of fish entered Sutter and Steamboat Slough ($\hat{\psi}_{\mathrm{B}}$, Figure 5 and Table 2) despite 37% of river discharge entering this route (Figure 6). Route entrainment probabilities for each slough showed that the difference in $\hat{\psi}_{\mathrm{B}}$ between releases occurred at the entrance to Sutter Slough (Table 2). In December, twice the fraction of fish entered Sutter Slough ($\hat{\psi}_{\mathrm{B11}} = 0.230$) as compared to Steamboat Slough ($\hat{\psi}_{\mathrm{B21}} = 0.115$), whereas in January, the proportion entering Sutter Slough declined to 0.086 while the fraction entering Steamboat Slough remained unchanged at 0.112 (Table 2). As a consequence, 65% of fish remained in Sacramento River at the first river junction during the December release, whereas 80% remained in the Sacramento River for the January release (see ψ_{A1} in Appendix Table 1.3). Thus, for the January release, a larger fraction of the population remained in the Sacramento River at the first junction, which increased exposure of the population to the second river junction where they could enter into the interior Delta.

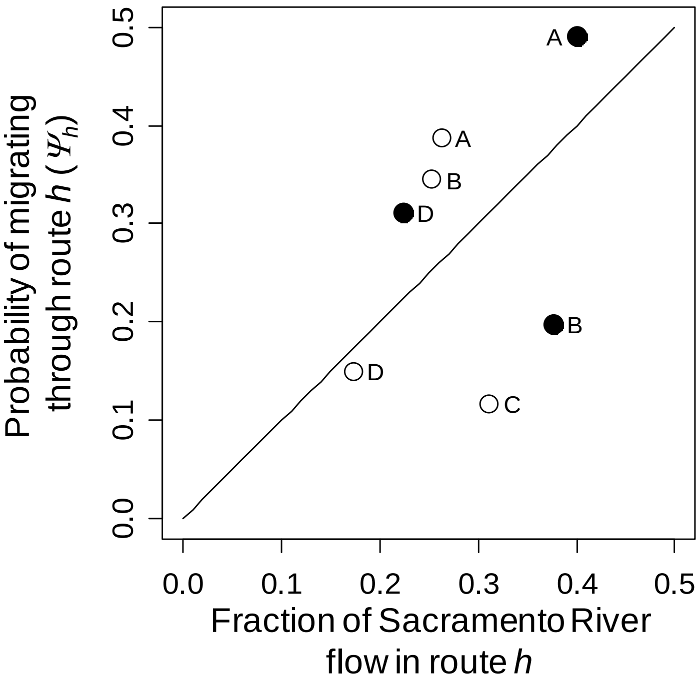

Figure 6.—The probability of migrating through route *h* (ψ_h) as a function of the proportion of total river flow in route *h* for tagged late-fall juvenile Chinook salmon released in December 2007 (open circles) and January 2008 (filled circles). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The fraction of river flow in each route was calculated as the proportion of tidally filtered daily discharge of each route relative to the total discharge of the Sacramento River at Freeport. The reference line shows where the fraction of fish migrating through each route is equal to the proportion of flow in each route (i.e., a 1:1 ratio).

For the December release, of fish that arrived at the second river junction where the Delta Cross Channel is located, 18% entered the Delta Cross Channel, 23% entered Georgiana Slough, and 59.2% remained in the Sacramento River (see ψ_{C2}, ψ_{D2}, and ψ_{A2} in Appendix Table 1.3). In contrast, for the January release when the Delta Cross Channel was closed, 38.8% of fish arriving at the second river junction entered Georgiana Slough, with the remaining 61.2% migrating through the Sacramento River. Accounting for both river junctions, migration route probabilities for the December release indicated that 38.7% of the population migrated within the Sacramento River and 26.7% of the population entered the interior Delta. However, only 11.7% entered the interior Delta through the Delta Cross Channel even though 31% of the flow entered the Delta Cross Channel (Figures 5 and 6, Table 2). During January, nearly one third of the population was entrained into the interior Delta through Georgiana Slough (Figure 5, Table 2) despite the Delta Cross Channel being closed. Consequently, the fraction of the population entering the interior Delta was similar between release dates.

Relative Contributions to S_{Delta}

Estimates of S_{Delta} were driven by 1) variation among routes in survival through the Delta ($\hat{S}_h$) and 2) the relative contribution of each route-specific survival to $\hat{S}_{Delta}$ as measured by migration route probabilities ($\hat{\psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_B$) relative to all other routes, but only 38.7% of the population migrated through this route ($\hat{\psi}_B$), representing a relatively small contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{Delta}$ and comprised 61.3% of the population ($\hat{\psi}_A + \hat{\psi}_C + \hat{\psi}_D$), thereby contributing substantially to $\hat{S}_{Delta}$ for the December release (Figure 5, Table 2). For the January release, 68.8% of the population ($\hat{\psi}_A + \hat{\psi}_B$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{Delta}$ for the January release (Figure 5, Table 2). In comparison, survival for the interior Delta via Georgiana Slough ($\hat{S}_C$) was lower than the other routes for the January release and accounted for 31.2% ($\hat{\psi}_C$) of the contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). Because the fraction of the population entering the interior Delta was similar for both releases, lower survival through the interior Delta reduced population-level survival by a similar magnitude for both releases.

Comparisons between 2007 and 2008

Some patterns in survival and migration route probabilities during 2008 differed considerably from 2007, whereas other patterns remained consistent. First, $\hat{S}_{\text{Delta}}$ for both releases in 2008 (Table 2) was lower than in 2007; $\hat{S}_{\text{Delta}}$ in 2007 was estimated at 0.351 and 0.543 for the December and January release groups (Perry et al. 2008, in press). Although $\hat{S}_{\text{Delta}}$ was lower in 2008 relative to 2007, the pattern of survival probabilities among routes was similar between releases and years (Figure 5). In both years, all routes exhibited lower survival than the Sacramento River during the December release, but only fish entering the interior Delta exhibited lower survival than the Sacramento River for the January release (Figure 5). Larger sample size and the additional release site in Georgiana Slough during 2008 improved precision of route-specific survival compared to our 2007 study, allowing us to detect differences in survival among routes. We also found notable differences between years in route entrainment probabilities at the two primary river junctions. In 2007, migration route probabilities were similar to the fraction of flow in each route, but migration route probabilities deviated from this pattern in 2008. Consequently, in 2008 we found little difference between releases in the fraction of fish entering the interior Delta, whereas in 2007, the fraction of fish was lower during the January release when the Delta Cross Channel was closed (Perry et al. 2008, in press).

Reach-specific patterns of survival and movement

We found high variation in survival rates among reaches, ranging from as low as 0.867 km^{-1} to 1.0 km^{-1} for a few reaches where all fish survived. To put the magnitude of these survival rates in perspective, only 24% of fish will survive a 10-km reach at a survival rate 0.867 km^{-1} (i.e., $= 0.867^{10} = 0.247$) and only 6% will remain after 20 km. In contrast, at a survival rate of 0.99 km^{-1}, 90% of fish will survive 10 km and 82% will still be alive after 20 km. Reaches with the lowest survival rates occurred downstream of telemetry stations B_{13}, B_{23}, and A_6 (i.e., the Cache Slough to Rio Vista region, Figure 7). Two out of three of these reaches were among the four lowest survival rates observed in each release, highlighting a region of high local mortality relative to the length of these reaches. In contrast, other than survival probabilities that were fixed to one (Appendix Table 1.3), the highest survival rates in both releases occurred in the first two reaches of the Sacramento River (downstream of A_2 and the Sacramento release site, A_1). These reaches were relatively long (~20 km each) and survival probabilities were >0.91 (see S_{A1} and S_{A2} in Appendix Table 1.3), leading to high survival rates relative to reach length. Reach-specific survival rates were consistent with differences among routes in survival through the Delta. For the December release, 8 of the 11 reaches with the highest survival rates were comprised of all 8 reaches in the Sacramento River (Route A, Figure 7). These reaches exhibited survival rates ≥ 0.96 km^{-1}. The remaining 11 reaches with the lowest survival rates were comprised solely of the other three routes, with no particular route exhibiting consistently lower reach-specific survival rates. All of these reaches exhibited survival rates <0.96 km^{-1}. For the January release, the highest-ranking survival rates were still dominated by reaches within the Sacramento River (6 of the 11 lowest mortality rates), but two reaches of the Sacramento River ranked in highest 50 percent of mortality rates (reaches beginning at A_6 and A_8).

Between releases, most reach-specific survival rates within the Sacramento River (Route A) and interior Delta (Route D) changed by less than 0.03 km^{-1} (Figure 8), and this finding agrees with the similarity in route-specific survival between releases (Figure 5). Furthermore, variation in survival rates between releases was low relative to the large variation in survival rates among reaches, especially for the Sacramento River (Figure 8). However, survival rates for all but one reach within Sutter and Steamboat sloughs increased substantially from December to January (Figure 8), which is consistent with the observed increase in survival through the Delta for this route. Thus, the observed difference in route-specific survival for Sutter and Steamboat sloughs was driven by coincident changes in survival rates for most reaches within this route and not by changes in survival within a particular reach.

One reach of particular management interest occurs downstream of D_4 in the interior Delta (see Figure 2). Although only about 17 km long by way of the San Joaquin River, this reach encompasses a large network of channels and includes the pumping stations and fish salvage facilities in the southern Delta. This reach exhibited the lowest probability of survival of

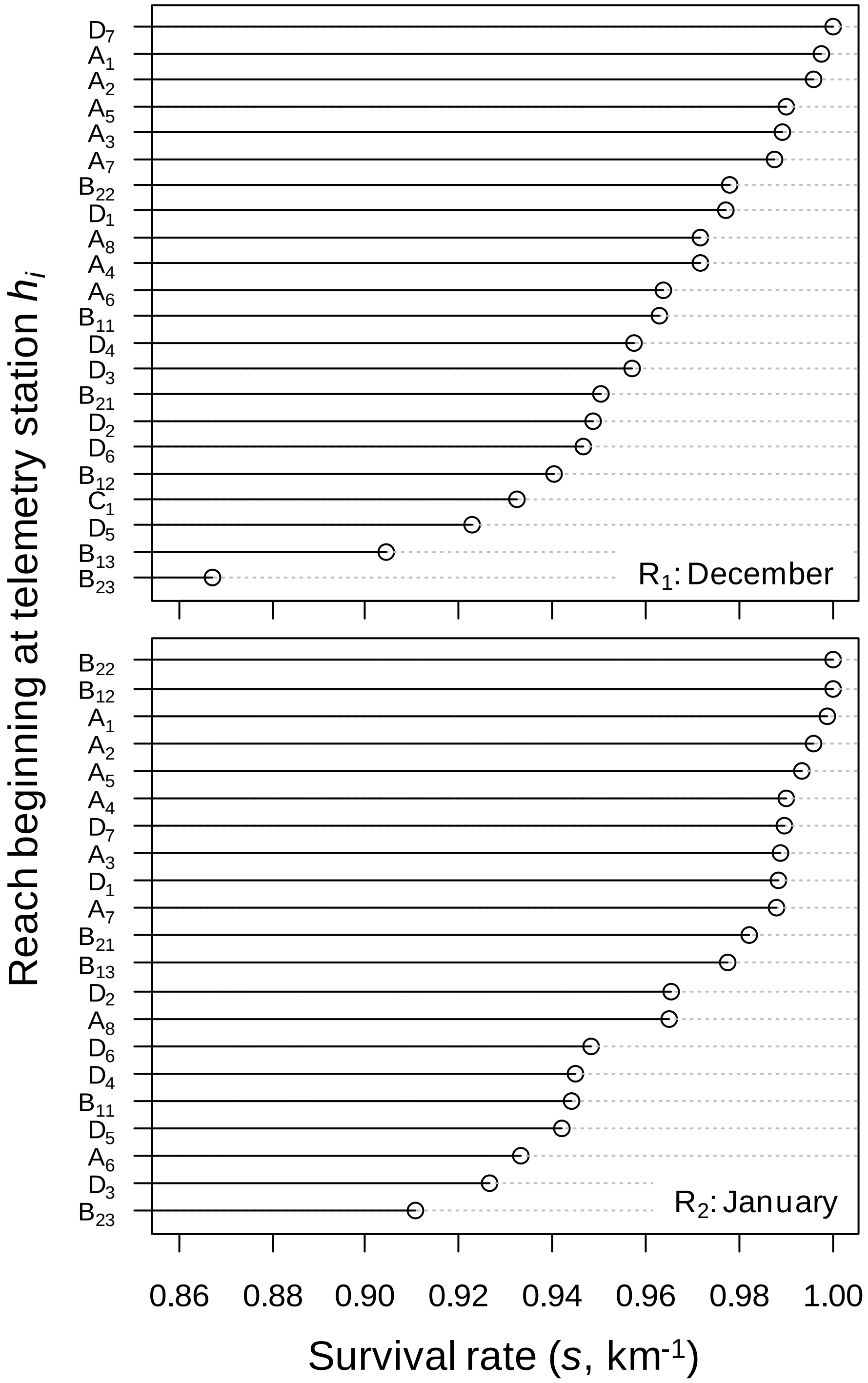

Figure 7.—Reach-specific survival rates plotted in ascending order for tagged late fall Chinook salmon released in December 2007 (top) and January 2008 (bottom). Survival rates scale survival probabilities (S_{hi}, Appendix Table 1.3) to the length of each reach from telemetry station h_i to the next downstream telemetry station.

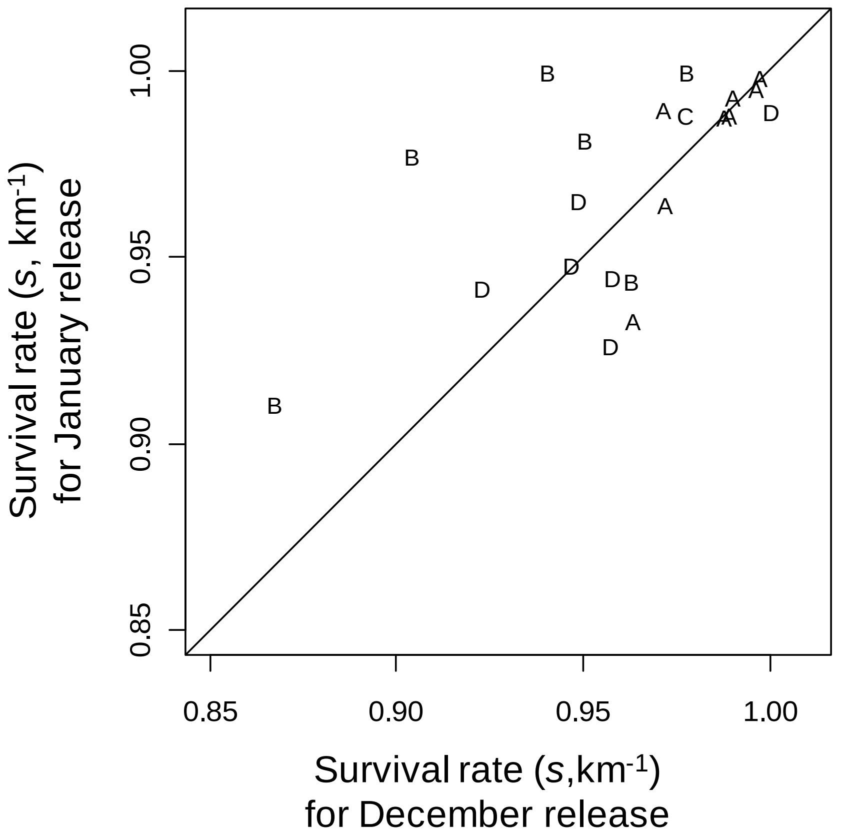

Figure 8.—Reach-specific survival rates for the December 2007 release compared to the January 2008 release for acoustically tagged late fall Chinook salmon migrating through the Sacramento-San Joaquin River Delta. The reference line shows where survival rates are equal between releases. Letters correspond to reaches within A = Sacramento River, B = Sutter and Steamboat sloughs, and D = the interior Delta via Georgiana Slough.

all reaches within the interior Delta, having observed survival probabilities of less than 50% (for R_1: $\hat{S}_{D4} = 0.484$, $\widehat{SE} = 0.071$; for R_2: $\hat{S}_{D4} = 0.395$, $\widehat{SE} = 0.080$; Appendix Table 1.3). However, when expressed as a function of reach length, other reaches within the interior Delta (Routes C and D) exhibited similar or lower survival rates than the reach downstream of D_4 (Figure 7). Direct mortality at the pumping stations appeared to contribute little to the estimate of S_{D4}. Both the State Water Project and Clifton Court Forebay were monitored by telemetry stations, but these stations could not be incorporated into the survival model because too few fish were detected at these locations to warrant parameter estimation. However, of the 76 fish passing D_4 that were never detected at or downstream of D_5 or E_1 (indicating probable mortality in this reach), only one fish was detected at the salvage facilities. Overall, six tagged fish were detected at the salvage facilities, and five of these were next detected at or downstream of D_5 or E_1 suggesting they had been salvaged at the fish facilities and transported to the lower Delta. Thus, mortality rates appear high in many reaches of the interior Delta relative the Sacramento River, not just the reach that includes a primary point source of known mortality (i.e., pumping stations and salvage facilities).

Although we could not estimate route entrainment probabilities at other junctions in the Delta, we explicitly accounted for observed movement among routes by estimating joint survival-entrainment probabilities. At the junction of Sutter Slough with Miner and Steamboat Slough (the reach downstream of B_{11}; Figure 2), $\hat{\phi}_{B11,B22}$ was about twice that of $\hat{\phi}_{B11,B12}$ during both releases (Appendix Table 1.3). If survival was similar for the two reaches downstream of the junction, then these findings suggest that about two-thirds of fish entering Sutter Slough migrated down Steamboat Slough and one-third traveled through Miner Slough.

For both releases we observed fish passing in both directions through Three Mile Slough (E_1 in Figure 2). However, Three Mile slough appears to play a relatively minor role in movement dynamics through the Delta relative to contribution of the major migration routes. In the Sacramento River, fish moving from A_7 to A_8 contributed a substantially larger fraction of the total survival through this reach (for R_1: $\hat{\phi}_{A7,A8} = 0.837$, $\widehat{SE} = 0.074$; for R_2: $\hat{\phi}_{A7,A8} = 0.781$, $\widehat{SE} = 0.070$) compared to fish moving from A_7 to E_1 (for R_1: $\hat{\phi}_{A7,E1} = 0.049$, $\widehat{SE} = 0.034$; for R_2: $\hat{\phi}_{A7,E1} = 0.109$, $\widehat{SE} = 0.046$). In the San Joaquin River, fish moving from D_4 to E_1 contributed more to the total reach survival for the first release compared to the second release. For the first release, $\hat{\phi}_{D4,E1} = 0.140$ ($\widehat{SE} = 0.049$) and $\hat{\phi}_{D4,D5} = 0.351$ ($\widehat{SE} = 0.070$), whereas for the second release $\hat{\phi}_{D4,E1} = 0.041$ ($\widehat{SE} = 0.023$) and $\hat{\phi}_{D4,D5} = 0.354$ ($\widehat{SE} = 0.079$). Whether a higher fraction of fish in the San Joaquin River passed through Three Mile Slough (E_1) during the first release is difficult to ascertain because lower survival in the San Joaquin River downstream of its junction with Three-Mile Slough may also account for the observed difference.

Discussion

In our previous study, $\hat{S}_{\text{Delta}}$ differed by nearly 20 percentage points between releases, and we attributed this observed difference to both a change in the proportion of fish entering the interior Delta and a change in survival within given migration routes (Perry et al. 2008, in press). In contrast, for this study, we attribute lack of an observed difference in $\hat{S}_{\text{Delta}}$ between releases to 1) less variation between releases in survival for given migration routes, relative to 2007, 2) lower-than-expected entrainment into the Delta Cross Channel, 3) a decline in the proportion of fish entering Sutter and Steamboat sloughs in January, and 4) little difference in the proportion of fish entering the interior Delta between releases. In 2007, survival through the Delta for both the Sacramento River and Sutter and Steamboat Slough increased substantially between December and January, partly driving the large observed difference in $\hat{S}_{\text{Delta}}$ between releases (Perry et al. 2008, in press). However, during 2008 only Sutter and Steamboat sloughs exhibited a sizeable increase in survival from December to January. However, although survival increased, the proportion of fish entering Sutter and Steamboat sloughs declined from 0.34 to 0.20 from December to January. Had the proportion of fish entering Sutter and Steamboat sloughs remained unchanged, population-level survival would have received a larger boost from the increase in survival observed for this route. Given that survival for routes through the interior Delta were significantly lower than the Sacramento River during both releases, the fraction of fish entering the interior Delta dictated the magnitude of decrease in population-level survival due to fish using this migration route. Thus, the magnitude of decrease in population-level survival attributed to the interior Delta remained unchanged between releases because similar fractions of the population entered the interior Delta during both releases. However, because maximum survival for any given route during both releases was <0.30, population-level survival would remain low regardless of the fraction of fish entrained in the interior Delta.

That estimates of population-level survival were ≤0.20 for an 80-km section of river begs the question of whether the untagged population also experienced such low survival. To put the magnitude of these estimates in perspective, survival of hatchery-reared juvenile Chinook salmon over 600 km and through eight dams of the Snake and Columbia rivers ranged from

31%-59% (Williams et al. 2001). Thus, the absolute magnitude of survival relative to the distance traveled is clearly low compared to a similarly developed river system. However, factors such as source of the study fish and the effects of the transmitter could have reduced survival probabilities relative to untagged fish. Fish in this study were obtained directly from Coleman National Fish Hatchery, tagged, and then released about 40 km upstream of the first channel junction in the Delta. Initial "culling" of unfit hatchery fish obtained directly from a hatchery, a process suggested by Muir et al. (2001) and Newman (2003), could have lead to lower absolute survival compared to a population that had migrated in-river from natal tributaries or hatcheries to the Delta. If this process were pronounced in our study, we might have expected 1) low survival in the first reach following release, and 2) fish released at Sacramento to have higher survival probabilities through the interior Delta relative to fish that were released directly into the interior Delta at Georgiana Slough. In contrast, survival probabilities for the first reach of the Sacramento River were higher than all other reaches within this route (see S_{A1}, Appendix Table 1.3). Furthermore, the model with equal survival probabilities between release sites was selected over the full model with different survival probabilities for each release, providing little evidence of a "culling" effect. As for the effect of the transmitter, Hockersmith et al. (2003) found no difference in survival between radio tagged and PIT-tagged juvenile Chinook salmon over a similar distance as that studied here. Thus, we found little evidence to suggest that the low population-level survival through the Delta was a function of the source of fish or tagging methodology used for the study.

The strength of inferences from our data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Although we found no evidence that survival probabilities were lower than expected due to fish source or tagging method, we also have little basis with which to compare survival estimates from our study population to actively migrating populations of wild or hatchery origin in the Delta. However, regardless of the absolute magnitude of survival, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, while it is uncertain whether untagged fish migrating concurrently with tagged fish also exhibited population-level survival of less than 20%, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival through the Delta relative to fish migrating within the Sacramento River. Therefore, the relative difference in survival among routes from our data should provide stronger inference to untagged populations than will inferences about the absolute magnitude of survival probabilities. From this perspective, although survival was low for all migration routes during 2008, survival for routes through the interior Delta was at most 35% that of survival for fish remaining in the Sacramento River (see θ_C and θ_D inTable 3). Future studies that include fish obtained from Coleman National Fish Hatchery paired with releases of in-river, actively migrating hatchery or wild fish would help to interpret the absolute magnitude of survival probabilities from this study in the context of other populations of interest.

The primary working hypothesis of management actions related to the operation of the Delta Cross Channel is that closing the Delta Cross Channel will increase population-level survival by reducing the fraction of the population entering the interior Delta where survival is lower than alternative migration routes. Implicit in this hypothesis is that the fraction of fish entering the interior Delta is proportional to the fraction of flow entering the interior Delta. However, in contrast to our previous findings, we found that the proportion of fish entering each migration route did not necessarily agree with the proportion of mean discharge entering a route. Furthermore, deviations from this “expected” relationship acted to decrease the proportion of fish entering the interior Delta during the December release, but increase it during the January release. Based on distribution of mean discharge, closing the Delta Cross Channel reduced the total fraction of flow entering the interior Delta from 48.4% during the December release to 22.5% during the January release. However, for the December release, the proportion of fish entering the Delta Cross Channel was only about one-third the proportion of flow entering this route, whereas the proportion of fish entering Georgiana Slough was similar to the proportion of flow (Figure 6). Thus, the proportion of fish entering the interior Delta was less than might otherwise be expected based only on the distribution of river flow during the December release. During the January release, only about 20% of fish entered Sutter and Steamboat Slough even though 37% of Sacramento River flow entered this route (Figure 6). Therefore, a higher fraction of fish remained in the Sacramento River relative to that expected based on the proportion of flow in this route, which in turn exposed a higher fraction of the population to entrainment into the interior Delta via Georgiana Slough. These findings show how variation in route entrainment probabilities at both major river junctions interacted to produce little observed difference between releases in the fraction of the population entering the Interior Delta, despite the Delta Cross Channel being open for the first release and closed for the second.

While dispersal of the population throughout the channel network of the Delta is likely driven in part by the distribution in mean river discharge among channels, our findings provide the first evidence that the distribution of fish entering each channel can deviate considerably from the distribution of flow entering each channel. Such deviation was expected by Burau et al. (2007), who identified a number of mechanisms likely to contribute to variation in route entrainment probabilities. First, flow distribution among the river channels at each junction varies with the tides on hourly time scales (Blake and Horn 2003). Thus, diel patterns in migration behavior (Wilder and Ingram 2006; Burau et al. 2007; Chapman et al. 2007) interacting with tidal fluctuations could produce route entrainment probabilities that deviate from that expected based on mean discharge. In addition, secondary circulation at river bends (Dinehart and Burau 2005) combined with swimming behavior of juvenile salmon could concentrate the lateral distribution of migrating fish along the outside of river bends where they become more (or less) likely to be entrained into a given channel at a river junction (Burau et al. 2007). These fine-scale processes are an active area of research in the Delta (Burau et al. 2007) and should provide new insights into the mechanisms driving variability in route entrainment probabilities at river junctions.

While some aspects of migration and survival dynamics differed greatly between years, other patterns remained consistent. Although population-level survival in 2008 was lower than in 2007, the pattern of survival among routes was similar. During both releases, survival of fish migrating through the interior Delta was significantly less than for fish that remained in Sacramento River, which is consistent our findings in 2007 (Perry et al. 2008, in press) and with the findings of previous studies (Brandes and McLain 2001; Newman and Rice 2002; Newman 2008, Brandes and Newman in press). This weight of evidence suggests that management actions that shift the distribution of the population from the interior Delta to the Sacramento River will improve population-level survival through the Delta. Similar to 2007, we also found that survival through the Delta for fish migrating in Sutter and Steamboat Sloughs was significantly lower than the Sacramento River during the December release, but was comparable to the Sacramento River during the January release. Higher total river discharge (Figure 4) in January combined with a higher fraction of that discharge entering Sutter and Steamboat sloughs

(Figure 6) could have improved migration conditions and reduced predation rates during the January release. Reach-specific survival rates increased for nearly all reaches of Sutter and Steamboat Slough (Figure 8), which is consistent with an increase in discharge through these reaches.

Quantifying survival rates per unit distance allowed us to identify patterns in reach-specific survival that generally followed the pattern of route-specific survival probabilities. Most reaches within the Sacramento River exhibited the highest survival rates during both releases, while most reaches within the interior Delta exhibited survival rates lower than the Sacramento River (Figure 7). These findings suggest that particular reaches within a route did not drive the observed differences in survival among migration routes. For instance, the lowest survival probabilities for the interior Delta were observed for the longest reach and included the most complex channel network with the pumping stations (see S_{D4} in Appendix Table 1.3). Yet survival rates for this reach were comparable to other reaches within this route when expressed as a function of reach length. In addition, we observed locally high mortality in the Cache Slough region downstream of stations B_{13}, B_{23}, and A_6 for both releases. Last, survival rates in Sutter and Steamboat sloughs increased in January for nearly all reaches within this route. These patterns of variation among reaches suggest that factors influencing survival are operating at a spatial scale larger than an individual reach.

Reach-specific survival rates expressed with respect to distance traveled changed little between releases relative to the variability observed among reaches, especially for the Sacramento River (Figure 9). These findings suggest that factors other than migration distance (e.g., travel time) may also influence mortality rates. In contrast, in the Columbia River, survival rates of juvenile Chinook salmon have been significantly related to migration distance, but only weakly correlated to travel time (Muir et al. 2001, Anderson et al. 2005). Anderson et al. (2005) offered a hypothesis explaining this apparently contradictory finding. When prey migrate through a “gauntlet” of predators, predator-prey encounter rates will be such that each prey encounters a predator at most once. Under these circumstances, predator-prey theory predicts that survival will be driven by distance traveled, but not by travel time. In contrast, when prey migration speeds are slow relative to predator swimming speeds such that multiple encounters are possible, then the situation reverses: the probability of survival becomes dependent on travel time. This hypothesis could partially explain the wide range in mortality rates among reaches within the Sacramento River, but low variability between releases (Figure 8). Within our study area the Sacramento River transitions from river-driven discharge in the uppermost reaches to tidally driven discharge in the lower reaches. Coincident with this transition, fish movement patterns shift from downstream-only movements to both upstream and downstream movements in the lower reaches of the Delta. Thus, in lower reaches of the Delta fish may pass through a given reach more than once, which could increase predator encounter rates relative to the length of each reach.

This research continues to provide critical information to understand factors influencing migration and survival dynamics of juvenile Chinook salmon migration through the Delta. Improved precision of parameter estimates allowed us detect statistically significant differences in survival among migration routes. While some findings were similar to our previous study, such as low survival through the Interior Delta relative to the Sacramento River, other findings deviated considerably between years. Survival through the Delta was less than 20% during 2008 (compared to 35%-54% in 2007), route-entrainment probabilities deviated from the fraction of mean river discharge entering each channel, and the proportion of the population entering the interior Delta was similar between releases despite closure of the Delta Cross Channel. Given the substantial variation in survival, route entrainment, and migration route probabilities observed among four releases and two years, we suspect that we are just beginning to unmask the temporal and spatial variability in migration and survival dynamics in the Delta. Nonetheless, even with such variability, patterns in survival and movement dynamics are beginning to emerge. With the addition of migration data collected during the winter of 2008/2009, we plan to formally model hypotheses about reach- and route-specific factors that influence survival and migration route probabilities. Such information should provide insights into management actions that will improve survival of juvenile salmon populations migrating through the Sacramento-San Joaquin River Delta.

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Appendix 1

Appendix Table 1.1.—Counts of detection histories for the model shown in Figure 3 for a release of R_1 = 208 fish on 4 December 2007 and R_2 = 211 fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A "0" indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with "0 0 0 D" indicate fish released in Georgiana Slough whereas those beginning with "A" are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0 0 0 0	11	0 0 0 D 0 0 0 0 0 0 0 0 0 0	5
0 0 0 D D 0 0 0 0 0 0 0 0	5	0 0 0 D D 0 0 0 0 0 0 0 0	4
0 0 0 D D D 0 0 0 0 0 0 0	7	0 0 0 D D D 0 0 0 0 0 0 0	21
0 0 0 D D D D 0 0 0 0 0 0	20	0 0 0 D D D D 0 0 0 0 0 0	32
0 0 0 D D D D D 0 0 0 0 0	6	0 0 0 D D D D D 0 0 0 0 0	4
0 0 0 D D D D E 0 0 0 0 0	3	0 0 0 D D D D E 0 0 0 0 0	1
0 0 0 D D D D D 0 D 0 0 0	2	0 0 0 D D D D 0 0 D 0 0 0	1
0 0 0 D D D D D 0 D D A 0	1	0 0 0 D D D D D 0 D 0 0 0	2
0 0 0 D D D D E A 0 0 A A	2	0 0 0 D D D D 0 0 D D 0 0	1
0 0 0 D D D D D 0 0 D A A	1	0 0 0 D D D D 0 0 0 0 A 0	1
0 0 0 D D D D D 0 D D A A	1	0 0 0 D D D D E A 0 0 0 A	1
A 0 0 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D D 0 D D 0 A	1
A A 0 0 0 0 0 0 0 0 0 0 0	18	0 0 0 D D D D 0 0 0 0 A A	1
A 0 B1 0 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D D 0 0 0 A A	1
A A B1 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D E A 0 0 A A	1
A A B2 0 0 0 0 0 0 0 0 0 0	3	0 0 0 D D D D D 0 D 0 A A	2
A A 0 A 0 0 0 0 0 0 0 0 0	7	0 0 0 D D D 0 D 0 0 D A A	1
A A B1 B1 0 0 0 0 0 0 0 0 0	4	0 0 0 D D D D D 0 0 D A A	1
A A B1 B2 0 0 0 0 0 0 0 0 0	1	A 0 0 0 0 0 0 0 0 0 0 0 0	6
A 0 B2 B2 0 0 0 0 0 0 0 0 0	1	A A 0 0 0 0 0 0 0 0 0 0 0	16
A A B2 B2 0 0 0 0 0 0 0 0 0	2	A A B1 0 0 0 0 0 0 0 0 0 0	4
A 0 0 C 0 0 0 0 0 0 0 0 0	1	A A B2 0 0 0 0 0 0 0 0 0 0	1
A A 0 C 0 0 0 0 0 0 0 0 0	9	A A 0 A 0 0 0 0 0 0 0 0 0	3
A A 0 D 0 0 0 0 0 0 0 0 0	6	A 0 0 D 0 0 0 0 0 0 0 0 0	2
A 0 0 A A 0 0 0 0 0 0 0 0	1	A A 0 D 0 0 0 0 0 0 0 0 0	4
A A 0 A A 0 0 0 0 0 0 0 0	5	A 0 0 A A 0 0 0 0 0 0 0 0	1
A A B1 B1 B1 0 0 0 0 0 0 0 0	7	A A 0 A A 0 0 0 0 0 0 0 0	6
A A B1 B2 B2 0 0 0 0 0 0 0 0	4	A 0 B1 B1 B1 0 0 0 0 0 0 0 0	1
A A B2 B2 B2 0 0 0 0 0 0 0 0	2	A 0 B2 B2 B2 0 0 0 0 0 0 0 0	1
A A 0 D D 0 0 0 0 0 0 0 0	1	A A B2 B2 B2 0 0 0 0 0 0 0 0	3
A A 0 0 A A 0 0 0 0 0 0 0	1	A A 0 D D 0 0 0 0 0 0 0 0	3
A A 0 A A A 0 0 0 0 0 0 0	4	A A 0 A A A 0 0 0 0 0 0 0	10
A A 0 D D D 0 0 0 0 0 0 0	1	A 0 0 D D D 0 0 0 0 0 0 0	1

Appendix Table 1.1.—Continued.

A A 0 A A 0 A 0 0 0 0 0 0	1	A A 0 D D D 0 0 0 0 0 0 0	2
A A B1 B2 B2 0 A 0 0 0 0 0 0	1	A A B1 B2 B2 0 A 0 0 0 0 0 0	1
A A B2 B2 B2 0 A 0 0 0 0 0 0	1	A A B2 B2 B2 0 A 0 0 0 0 0 0	1
A A 0 A A A A 0 0 0 0 0 0	2	A 0 0 A A A A 0 0 0 0 0 0	1
A A 0 C 0 D D 0 0 0 0 0 0	3	A A 0 A A A A 0 0 0 0 0 0	2
A A 0 D D D D 0 0 0 0 0 0	3	A 0 0 D D D D 0 0 0 0 0 0	4
A A B2 B2 B2 0 0 A 0 0 0 0 0	1	A A 0 D D D D 0 0 0 0 0 0	12
A A 0 A A 0 A A 0 0 0 0 0	1	A A B1 B1 B1 0 0 A 0 0 0 0 0	1
A A B1 B1 B1 0 A A 0 0 0 0 0	1	A 0 B1 B2 B2 0 0 A 0 0 0 0 0	1
A A B2 B2 B2 0 A A 0 0 0 0 0	1	A A B2 B2 B2 0 0 A 0 0 0 0 0	1
A 0 0 A A A A A 0 0 0 0 0	1	A A 0 A A A 0 A 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 0 0	9	A A 0 A A 0 A A 0 0 0 0 0	1
A A 0 D D D D D 0 0 0 0 0	1	A A B1 B1 B1 0 A A 0 0 0 0 0	2
A A 0 D D D D E 0 0 0 0 0	1	A A B2 B2 B2 0 A A 0 0 0 0 0	3
A A 0 D D D D 0 0 D 0 0 0	1	A 0 0 A A A A A 0 0 0 0 0	1
A A 0 A A 0 0 A 0 0 0 A 0	1	A A 0 A A A A A 0 0 0 0 0	5
A A B1 B2 B2 0 A A 0 0 0 A 0	1	A A 0 D D D D D 0 0 0 0 0	2
A A B2 B2 B2 0 A A 0 0 0 A 0	1	A A 0 A A A A E 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 A 0	2	A A 0 A A 0 A E 0 D 0 0 0	1
A A B1 0 B1 0 0 E D D D A 0	1	A A 0 A A A A 0 0 0 0 A 0	1
A A 0 0 A 0 A 0 0 0 0 0 A	1	A A 0 A A A A A 0 0 0 A 0	3
A A 0 D D D D D 0 D D 0 A	2	A A 0 A A A A E 0 D 0 A 0	1
A A 0 A A A A E D D D 0 A	1	A A 0 D D D D D 0 D D A 0	1
A A 0 A A A A 0 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 0 A	1
A A B2 B2 B2 0 0 A 0 0 0 A A	1	A 0 0 A A 0 A E 0 D 0 0 A	1
A A 0 A A A 0 A 0 0 0 A A	2	A A 0 D D D D 0 0 0 0 A A	1
A A 0 A A 0 A A 0 0 0 A A	1	A A 0 A A A 0 A 0 0 0 A A	1
A A B1 B1 B1 0 A A 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 A A	3
A A B2 B2 B2 0 A A 0 0 0 A A	2	A 0 B2 B2 B2 0 A A 0 0 0 A A	1
A A 0 A A A A A 0 0 0 A A	5	A A B2 B2 B2 0 A A 0 0 0 A A	2
A A 0 C 0 D D E A 0 0 A A	1	A 0 0 A A A A A 0 0 0 A A	1
A A 0 D D D D D 0 0 D A A	1	A A 0 A A A A A 0 0 0 A A	5
A A 0 D D D D D 0 D D A A	1	A A 0 D D D D 0 0 0 D A A	1
Total released (R_k)	208		211

Appendix Table 1.2.—Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
S_{A3}	$= S_{A2}$	ψ_{C2}	$= 0$
$S_{D7,\ Sac}$	$= 1$	$\phi_{D4,E1,Sac}$	$= 0$
$S_{E1,D5}$	$= 1$	S_{A3}	$= S_{A2}$
P_{A3}	$= 0$	S_{B12}	$= 1$
P_{A5}	$= 1$	S_{B22}	$= 1$
$P_{E1,Sac}$	$= 1$	S_{C1}	$= 0$
P_{B11}	$= 1$	$S_{D7,Sac}$	$= 1$
P_{B21}	$= 1$	$S_{E1,D5}$	$= \phi_{D4,D5,Geo}$
P_{B22}	$= 1$	$S_{E1,A8,Sac}$	$= 0$
P_{B13}	$= 1$	P_{A3}	$= 0$
P_{B23}	$= 1$	P_{A4}	$= 1$
P_{C1}	$= 1$	P_{A5}	$= 1$
P_{D1}	$= 1$	P_{B11}	$= 1$
$P_{D2,Sac}$	$= 1$	P_{B12}	$= 1$
$P_{D3,Sac}$	$= 1$	P_{B13}	$= 1$
$P_{D4,Sac}$	$= 1$	P_{B21}	$= 1$
$P_{D7,Sac}$	$= 1$	P_{B22}	$= 1$
$S_{D7,Geo}$	$= 1$	P_{B23}	$= 1$
$P_{D2,Geo}$	$= 1$	P_{C1}	$= 0$
$P_{D3,Geo}$	$= 1$	P_{D1}	$= 1$
$P_{D4,Geo}$	$= 1$	$P_{D2,Sac}$	$= 1$
$P_{D5,Geo}$	$= 1$	$P_{D3,Sac}$	$= 1$
$P_{D7,Geo}$	$= 1$	$P_{D4,Sac}$	$= 1$
$P_{A8,Geo}$	$= 1$	$P_{E1,Sac}$	$= 1$
$P_{A9,Geo}$	$= 1$	$P_{D2,Geo}$	$= 1$
$P_{E1,Geo}$	$= 1$	$P_{D3,Geo}$	$= 1$
$S_{A8,Geo}$	$= 1$	$P_{A8,Geo}$	$= 1$
		$P_{E1,Geo}$	$= 1$
		$S_{A8,Geo}$	$= 1$

Appendix Table 1.3.—Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2007 (R_1) and January, 2008 (R_2). Parameters not estimated are indicated by an "NA" in the estimate column, and parameters fixed at a constant value are noted by an "NA" in the profile likelihood column.

	R_1: December 2007		R_2: January 2008	
Parameter	Estimate ($\widehat{SE}$)	95% Profile likelihood interval	Estimate ($\widehat{SE}$)	95% Profile likelihood interval
S_{A1}	0.951 (0.019)	0.907, 0.981	0.975 (0.020)	0.927, 1.000
S_{A2}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A3}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A4}	0.841 (0.055)	0.715, 0.928	0.942 (0.032)	0.857, 0.985
S_{A5}	0.874 (0.062)	0.734, 0.984	0.914 (0.061)	0.785, 1.000
S_{A6}	0.843 (0.075)	0.671, 0.963	0.728 (0.078)	0.563, 0.864
S_{A7}	0.886 (0.068)	0.733, 1.000	0.890 (0.058)	0.758, 1.000
S_{A8}	0.618 (0.090)	0.441, 0.789	0.548 (0.087)	0.380, 0.716
S_{B11}	0.715 (0.087)	0.534, 0.876	0.600 (0.155)	0.299, 0.855
S_{B12}	0.692 (0.128)	0.423, 0.893	1.000	NA
S_{B13}	0.308 (0.149)	0.087, 0.623	0.765 (0.221)	0.282, 1.000
S_{B21}	0.800 (0.103)	0.560, 0.946	0.923 (0.074)	0.702, 0.995
S_{B22}	0.790 (0.094)	0.576, 0.929	1.000	NA
S_{B23}	0.616 (0.130)	0.360, 0.841	0.728 (0.123)	0.464, 0.921
S_{C1}	0.286 (0.121)	0.099, 0.545	NA	
$S_{D1,Sac}$	0.667 (0.111)	0.437, 0.852	0.818 (0.067)	0.665, 0.923
$S_{D1,Geo}$	0.814 (0.051)	0.702, 0.898	0.938 (0.027)	0.872, 0.977
S_{D2}	0.900 (0.039)	0.808, 0.959	0.932 (0.025)	0.873, 0.970
S_{D3}	0.862 (0.045)	0.758, 0.934	0.772 (0.051)	0.672, 0.885
S_{D4}	0.491 (0.073)	0.352, 0.635	0.395 (0.080)	0.262, 0.604
S_{D5}	0.658 (0.129)	0.411, 0.946	0.733 (0.180)	0.415, 1.000
S_{D6}	0.700 (0.145)	0.393, 0.915	0.709 (0.181)	0.155, 1.000
S_{D7}	1.000	NA	0.866 (0.159)	0.463, 1.000
$S_{E1,D5}$	1.000	NA	0.750 (0.288)	0.245, 1.000
$S_{E1,A8}$	0.433 (0.189)	0.130, 0.780	0.683 (0.279)	0.165, 1.000
ψ_{A1}	0.655 (0.042)	0.570, 0.733	0.802 (0.037)	0.722, 0.868
ψ_{B11}	0.230 (0.037)	0.163, 0.308	0.086 (0.026)	0.044, 0.147
ψ_{B21}	0.115 (0.028)	0.068, 0.178	0.112 (0.029)	0.063, 0.178
ψ_{A2}	0.592 (0.056)	0.481, 0.696	0.612 (0.053)	0.506, 0.711
ψ_{C2}	0.179 (0.043)	0.105, 0.273	0.000	NA
ψ_{D2}	0.230 (0.048)	0.146, 0.331	0.388 (0.053)	0.289, 0.494

Appendix Table 1.3.—Continued.

$\phi_{\mathrm{B11,B12}}$	0.482 (0.096)	0.305, 0.674	0.400 (0.155)	0.146, 0.700
$\phi_{\mathrm{B11,B22}}$	0.233 (0.077)	0.108, 0.403	0.200 (0.127)	0.036, 0.499
$\phi_{\mathrm{A7,A8}}$	0.837 (0.074)	0.679, 0.978	0.781 (0.07)	0.634, 0.914
$\phi_{\mathrm{A7,E1}}$	0.049 (0.034)	0.008, 0.143	0.109 (0.046)	0.040, 0.220
$\phi_{\mathrm{D4,D5}}$	0.351 (0.070)	0.225, 0.497	0.354 (0.079)	0.225, 0.564
$\phi_{\mathrm{D4,E1}}$	0.140 (0.049)	0.063, 0.253	0.041 (0.023)	0.010, 0.102
P_{A2}	0.959 (0.018)	0.915, 0.985	0.852 (0.034)	0.777, 0.910
P_{A3}	0	NA	0.000	NA
P_{A4}	0.949 (0.035)	0.850, 0.991	1.000	NA
P_{A5}	1.000	NA	1.000	NA
P_{A6}	0.821 (0.072)	0.655, 0.932	0.781 (0.073)	0.620, 0.899
P_{A7}	0.829 (0.064)	0.683, 0.928	0.850 (0.057)	0.719, 0.937
$P_{\mathrm{A8,Sac}}$	0.905 (0.064)	0.734, 0.983	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A8,Geo}}$	1.000	NA	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A9,Sac}}$	0.812 (0.084)	0.618, 0.937	0.846 (0.071)	0.678, 0.949
$P_{\mathrm{A9,Geo}}$	1.000	NA	0.846 (0.071)	0.678, 0.949
P_{B11}	1.000	NA	1.000	NA
P_{B12}	0.900 (0.095)	0.628, 0.994	1.000	NA
P_{B21}	1.000	NA	1.000	NA
P_{B22}	1.000	NA	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	1.000	NA	1.000	NA
P_{C1}	1.000	NA	NA	
P_{D1}	1.000	NA	1.000	NA
P_{D2}	1.000	NA	1.000	NA
P_{D3}	1.000	NA	1.000	NA
P_{D4}	1.000	NA	0.958 (0.041)	0.829, 0.998
P_{D5}	0.922 (0.075)	0.699, 0.995	0.500 (0.118)	0.133, 0.872
P_{D6}	0.778 (0.139)	0.458, 0.959	0.500 (0.134)	0.255, 0.745
P_{D7}	1.000	NA	0.385 (0.135)	0.046, 0.848
P_{E1}	1.000	NA	1.000	NA
λ	0.748 (0.082)	0.570, 0.883	0.759 (0.080)	0.585, 0.888

Appendix 2

Evaluation of bias in survival and route entrainment probabilities

Since a telemetry station at location A_3 was not implemented during 2008, the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B21} could not be uniquely estimated without imposing constraints on the parameters. Therefore, we estimated these parameters under the constraint that $S_{A2} = S_{A3}$. Although estimates from one release in 2007 showed little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press), station A_3 has not been monitored for three of the four releases thus far. If S_{A2} is not equal to S_{A3}, then associated estimates of route entrainment and survival probabilities will be biased. Here we evaluate the magnitude of bias introduced by assuming $S_{A2} = S_{A3}$, when in fact S_{A2} differs from S_{A3}.

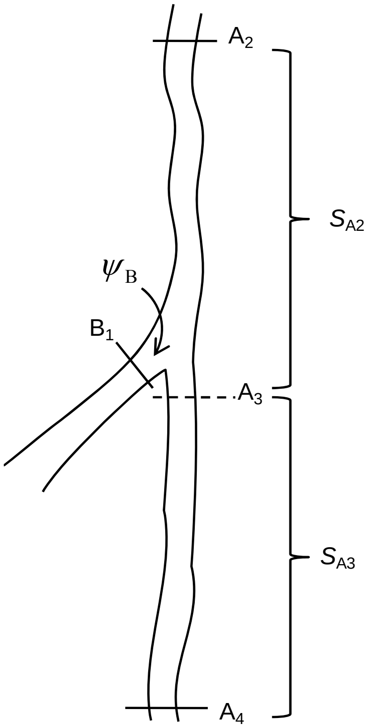
To illustrate the potential bias that might be incurred, we first simplified the problem by assuming a two-branch junction (Appendix Figure 2.1). We were interested not only in bias in ψ_B, but also in bias that might occur in the product $S_{A2}S_{A3}$. This product appears in equations for route specific survival through the Delta for Routes A, C, and D (i.e., S_h). Thus, bias in this product is more relevant than bias in each of the reach-specific survival probabilities. Appendix Figure 2.1 shows a schematic of the problem with the underlying survival and route entrainment parameters. Without a telemetry station at location A_3, only two parameters can be estimated from information provided by telemetry stations at B_1 and A_4. The two estimable parameters are the joint probabilities of the underlying parameters between stations A_2 and B_1, and between A_2 and A_4:

$$\phi_{A2,\,B1} = S_{A2}\psi_B \tag{A1}$$

$$\phi_{A2,\,A4} = S_{A2}S_{A3}\left(1-\psi_B\right) \tag{A2}$$

Where $\phi_{A2,\,B1}$ is the joint probability of surviving the first reach and entering channel B, and $\phi_{A2,\,A4}$ is the joint probability of surviving the first reach, remaining in channel A, and surviving the second reach. These two parameters can always be estimated without bias from the data, as can the total survival from A_2 to either of the downstream exit points:

$$S_{total} = \phi_{A2,\,B1} + \phi_{A2,\,A4} \tag{A3}$$



Appendix Figure 2.1.—Schematic of a two-branch river junction showing location of telemetry stations at A_2, B_2, and A_4. The dashed line notes lack of a telemetry station at A_3. Brackets show the probability of surviving between A_2 and A_3 and between A_3 and A_4. The probability of entering Channel B is Ψ_B, and the probability of remaining in Channel A is 1-Ψ_B.

To quantify bias, we substituted Eqns. A1 and A2 into Eqn. A3, set $S_{A3} = S_{A2}$, and then solved Eqn. A3 for S_{A2} and Eqn. A1 for ψ_B:

$$\tilde{S}_{\mathrm{A2}} = \frac{\psi_{\mathrm{B}} - \sqrt{\psi_{\mathrm{B}}{}^{2} - 4S_{\mathrm{total}}\left(\psi_{\mathrm{B}} - 1\right)}}{2\left(\psi_{\mathrm{B}} - 1\right)} \tag{A4}$$

and $$\tilde{\psi}_{\mathrm{B}} = \frac{\phi_{\mathrm{A2,\,B1}}}{\tilde{S}_{\mathrm{A2}}} \tag{A5}$$

Here, $\tilde{S}_{\mathrm{A2}}$ and $\tilde{\psi}_{\mathrm{B}}$ will be the biased estimates that result when assuming $S_{A2} = S_{A3}$ when in fact $S_{A2} \neq S_{A3}$; and S_{total} and $\phi_{\mathrm{A2,\,B1}}$ are calculated based on the true values of S_{A2}, S_{A3}, and ψ_B.

Estimates of S_{total} from our data will be unbiased regardless of bias that might be present in estimates of S_{A2}, S_{A3}, or ψ_B, and we used this fact to establish the maximum possible bias that could arise by assuming $S_{A2} = S_{A3}$. For example, for the first release in December 2008, we estimated $\hat{\psi}_B = 0.345$ and $\hat{S}_{A2} = \hat{S}_{A3} = 0.919$ (Appendix Table 1.3), resulting in $\hat{S}_{total} = 0.87$. Now suppose $\hat{\psi}_B = \tilde{\psi}_B = 0.345$ is the biased estimate of ψ_B: What true values of ψ_B, S_{A2}, and S_{A3} could have produced the observed estimate, $\tilde{\psi}_B$? First, the true parameter values ψ_B, S_{A2}, and S_{A3} are constrained such that $\hat{S}_{total} = 0.87$ (according to Eqn. A3) and $\tilde{\psi}_B = 0.345$ (according to Eqn. A5). Also, given that $\hat{S}_{total} = 0.87$, S_{A2} and S_{A3} are further constrained such that all of the observed mortality could have occurred in either the first reach (i.e., $S_{A3} = 1$) or the second reach (i.e., $S_{A2} = 1$). Clearly, mortality will occur in both reaches, but we used these two scenarios to bound the extremes of bias that could possibly occur given that $\hat{S}_{total} = 0.87$ and $\tilde{\psi}_B = 0.345$. Thus, maximum bias is calculated by setting $S_{A2} = 1$ (or $S_{A3} = 1$), and then finding the true values of S_{A3} (or S_{A2}) and ψ_B that satisfy $S_{total} = 0.87$ and $\tilde{\psi}_B = 0.345$. Should the maximum possible bias be low under these extreme scenarios, then we can infer that the realized bias would be even less.

Under these extreme scenarios, we found that maximum possible bias was quite low. For the December release, maximum absolute bias in ψ_B was less than 0.028, and bias in $S_{A2}S_{A3}$ was less than 0.035 (Appendix Table 2.1). Maximum possible bias for the January release was even less (Appendix Table 2.1). These findings suggest that the realized bias in these parameters will be much less than the maximum possible bias, given that we know mortality occurs in both reaches, and that past evidence suggests little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press). Our estimates are robust to deviations from $S_{A2} = S_{A3}$ partly due to the relatively high total survival (S_{total}) observed in this reach. Since S_{total} constrains the range of possible true values of S_{A2} and S_{A3}, as S_{total} decreases S_{A2} and S_{A3} may take on a wider range of values between 0 and 1. Thus, as S_{total} decreases, the possible maximum bias will increase under the extreme scenarios of all mortality occurring in either one reach or another.

Although this sensitivity analysis shows that bias was likely minimal, the appropriate course of action is to ensure a telemetry station is implemented at A_3 in future years. Given the influence of Sutter and Steamboat sloughs on migration dynamics through the entire Delta, this river junction is too important to rest future research on such assumptions.

Appendix Table 2.1.—Maximum possible bias induced by assuming $S_{A2} = S_{A3}$, when in fact, all mortality occurs in either the upstream reach or the downstream reach.

	True values				Estimates when assuming $S_{A2} = S_{A3}$		Bias	
Release	S_{A2}	S_{A3}	ψ_B	S_{total}	$\tilde{S}_{A2}$	$\tilde{\psi}_B$	$\psi_B - \tilde{\psi}_B$	$S_{A2}S_{A3} - \tilde{S}_{A2}^2$
R_1: December	0.870	1.000	0.364	0.870	0.918	0.345	-0.019	-0.025
	1.000	0.810	0.318	0.870	0.920	0.345	0.028	0.035
R_2: January	0.852	1.000	0.213	0.852	0.914	0.198	-0.014	-0.016
	1.000	0.819	0.182	0.852	0.915	0.198	0.017	0.017

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[Article]

Estimating Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta

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Abstract.—Juvenile Chinook salmon *Oncorhynchus tshawytscha* emigrating from natal tributaries of the Sacramento River must negotiate the Sacramento–San Joaquin River Delta, a complex network of natural and man-made channels linking the Sacramento River with San Francisco Bay. Natural processes and water management actions affect the fractions of the population using the different migration routes through the delta and survival within those routes. However, estimating these demographic parameters is difficult using traditional mark–recapture techniques, which depend on the physical recapture of fish (e.g., coded wire tags). Thus, our goals were to (1) develop a mark–recapture model to explicitly estimate the survival and migration route probabilities for each of four migration routes through the delta, (2) link these route-specific probabilities to population-level survival, and (3) apply this model to the first available acoustic telemetry data of smolt migration through the delta. The point estimate of survival through the delta for 64 tagged fish released in December 2006 ($\hat{S}_{\text{delta}} = 0.351$; SE = 0.101) was lower than that for 80 tagged fish released in January 2007 ($\hat{S}_{\text{delta}} = 0.543$; SE = 0.070). We attributed the observed difference in survival between releases to differences in survival for given migration routes and changes in the proportions of fish using the different routes. Our study shows how movements among, and survival within, migration routes interact to influence population-level survival through the delta. Thus, concurrent estimation of both route-specific migration and survival probabilities is critical to understanding the factors affecting population-level survival in a spatially complex environment such as the delta.

Many stocks of Chinook salmon *Oncorhynchus tshawytscha* in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998). In the Central Valley of California, the winter, spring, and fall–late fall runs of Chinook salmon are federally listed as endangered, threatened, and a "species of concern," respectively (NMFS 1997). Recently, owing to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a federal disaster and closed the 2008 salmon fishery along the West Coast (NOAA 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Baker and Morhardt 2001; Brandes and McLain 2001; Williams 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento–San Joaquin River Delta, a complex network of natural and man-made river channels (Nichols et al. 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the main-stem Sacramento River leading directly into San Francisco Bay (see route A in Figure 1). However, they may also migrate through longer secondary routes such as the interior delta, the network

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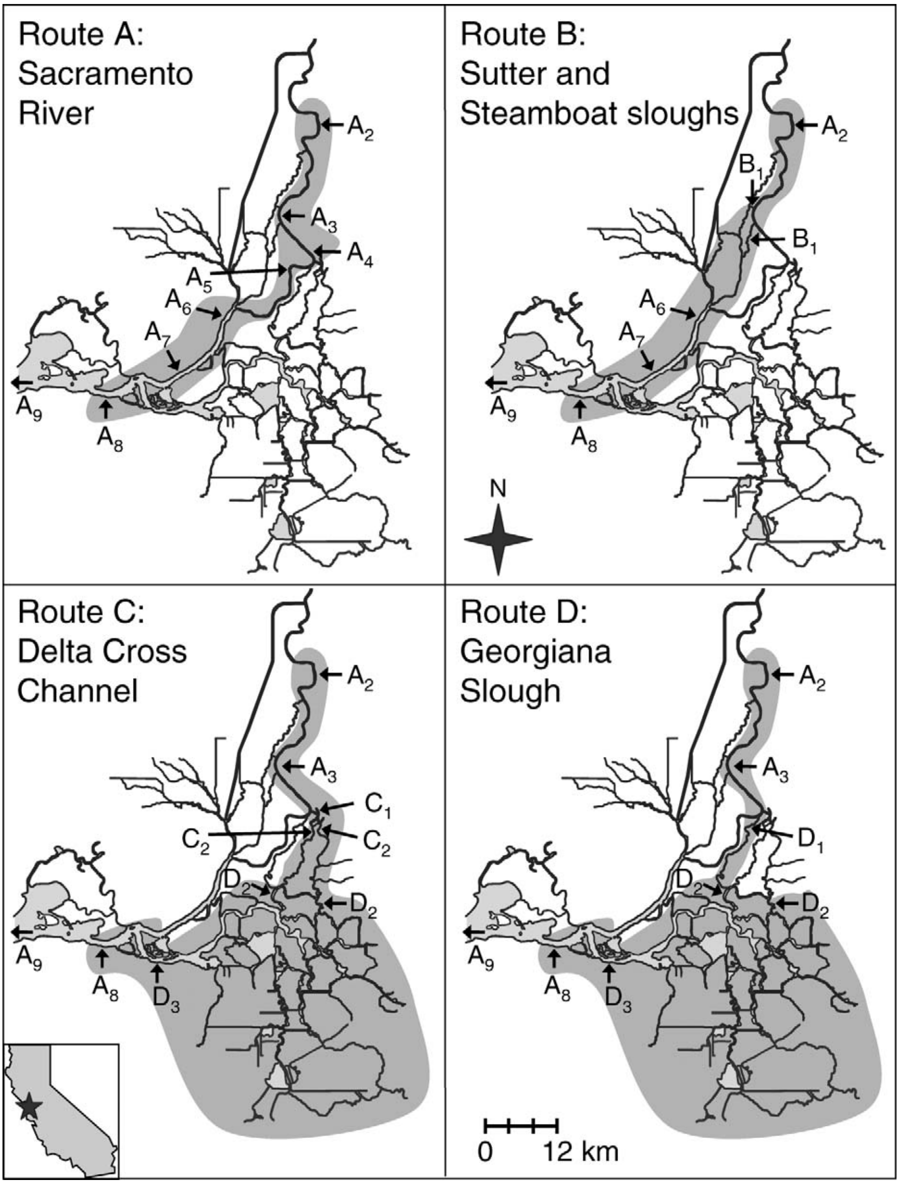

FIGURE 1.—Maps of the Sacramento–San Joaquin River Delta, with shaded regions showing the river reaches that comprise four different migration routes. Arrows show the locations of the telemetry stations specific to each route. The delta extends from station A_2 at Freeport to station A_8 at Chipps Island. The first river junction occurs where Sutter and Steamboat sloughs (B_1) diverge from the Sacramento River at station A_3. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. For routes C and D, the interior delta is the large shaded region to the south of station D_2. Telemetry stations with the same label (B_1, C_2, and D_2) were pooled as one station in the mark–recapture model. Station A_3 was not operational during the first release in December 2006. Station A_9 pools all of the telemetry stations in San Francisco Bay downstream of A_8. The release site (rkm 92) was 19 rkm upriver of station A_2 (rkm 73).

of channels to the south of the main-stem Sacramento River (see routes C and D in Figure 1).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the delta. Inflow into the delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the delta, water distribution is affected by two water pumping projects in the southern delta (the State Water Project and Central Valley Project). These projects pump water from the delta for agricultural and municipal uses, and can export up to 50% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior delta (see C_1 in route C, Figure 1). In addition to these human influences on water flow through the delta, natural processes include seasonal rainfall and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and biweekly time scales.

As juvenile salmon migrate among the complex channel network of the delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and, ultimately, survival. For example, growth of juvenile salmon in the Yolo Bypass, a seasonally inundated flood plain, was significantly greater than in the main-stem Sacramento River (Sommer et al. 2001). In contrast, juvenile salmon entering the interior delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, both of which may decrease survival of fish using this migratory pathway (Brandes and McLain 2001; Newman and Rice 2002; Newman 2003; Kimmerer 2008; Newman and Brandes 2009, this issue). These examples show that population-level survival rates of juvenile salmon migrating through the delta will be driven by (1) the survival rates arising from the biotic and abiotic processes unique to each migration route, and (2) the proportion of the population using each migration route. In turn, natural and human-imposed variation in discharge and water distribution will affect population dispersal and survival rates within each channel, driving population-level survival through the delta.

Currently, there is limited understanding of how water management actions in the delta affect population distribution and route-specific survival of juvenile salmon. Evidence suggests that survival of fish migrating through the interior delta decreases with increasing water exports (Brandes and McLain 2001; Newman 2003). Water exports could decrease survival by increasing migration times through the interior Delta, by increasing encounter rates with predators, and by direct entrainment of fish at pumping facilities located in the interior delta. Operation of the Delta Cross Channel likely affects the proportion of the population entering the interior Delta. To date, the proportion of fish migrating through the interior delta has not been estimated, yet such estimates are critical to understand the relative effect of water management actions on the population as a whole (Newman and Brandes 2009). Thus, currently lacking is a population-level approach that quantifies dispersal of the population among migration routes and that measures survival within these routes to better understand the influence of management actions on population-level survival.

In this study, we develop a mark–recapture model for the delta to explicitly estimate the probability of migrating through each of four migration routes and the probability of surviving through each route. Next, we quantify population-level survival through the delta as a function of the route-specific migration and survival probabilities. We then apply this model to the first available acoustic telemetry data of juvenile late-fall run Chinook salmon. Acoustic telemetry is a passive "capture" technique enabling individual fish to be detected repeatedly by multiple telemetry stations as they migrate through the delta. Given estimates of route-specific survival and movement through the delta from the acoustic telemetry data, we then examine how each of these components interacted to affect survival of the population migrating through the delta.

Methods

Telemetry system

Telemetry stations were deployed in the delta to monitor movement of tagged fish among four major migration routes through the delta (Figure 1): the main-stem Sacramento River (route A); Sutter and Steamboat sloughs (route B); the interior delta via the Delta Cross Channel (route C); and the interior delta via Georgiana Slough (route D). Although there are numerous possible migration pathways, we focused on these routes because management actions likely have the largest influence on movement and survival among these routes. For example, fish may enter the interior delta from the Sacramento River through either the Delta Cross Channel or Georgiana Slough, where they subsequently become vulnerable to migration delays and entrainment at the water pumping projects. Steamboat and Sutter sloughs may be an important migration route because fish using this route bypass the Delta Cross Channel and Georgiana Slough (Figure 1). Thus, fish migrating through Steamboat and Sutter sloughs are unable to enter the interior delta through the Delta Cross Channel or Georgiana Slough.

Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 1). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco, Ltd.; Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route was denoted as A_i from the release site (A_1 located at river kilometer [rkm] 92) to the last telemetry station in the delta at Chipps Island (A_8 at rkm −9; by convention, rkm 0 is defined at the southern tip of Sherman Island, which is 9 rkm upstream of station A_8). Migrating juvenile salmon first arrive at Sutter and Steamboat sloughs (B_1, rkm 43 and rkm 38), which diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_6 (rkm 19). Fish remaining in the Sacramento River then pass the Delta Cross Channel and Georgiana Slough at the second river junction. For the Delta Cross Channel, stations were labeled with C_i beginning where the Delta Cross Channel diverges from the Sacramento River at C_1 (rkm 60) and ending when these river channels converge with the interior delta at D_2 (rkm 40 and rkm 47). Telemetry stations within Georgiana Slough and the interior delta were labeled as D_i where Georgiana Slough branches off the main-stem Sacramento River (D_1, rkm 58) until convergence of the interior delta with the Sacramento River at D_3 (rkm 5). Following this hierarchy, routes A, B, C, and D contained eight, one, two, and three telemetry stations, respectively, for a total of 14 telemetry stations within the delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see the section on model development below). With this configuration of telemetry stations, survival in the final reach is confounded with detection probability at the last telemetry station (Skalski et al. 2001). Therefore, to estimate survival to the terminus of the delta and detection probability at the last station in the delta (A_8), we formed one additional telemetry station by pooling detections from numerous tag detecting monitors downstream of A_8 in San Francisco Bay. Most of these detections occurred at three primary stations that provided nearly complete cross-sectional coverage of San Francisco Bay at bridges located at rkm −37, rkm −64, and rkm −77, but single-monitor stations at other locations were also included.

Fish tagging and release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (rkm 431). For the first release in December, we used a 1.44-g tag (Vemco, Ltd.; Model V7–1 L-R64K, 40-d expected battery life), and for the second release in January we used a 1.58-g tag (Vemco, Ltd.; Model V7–2 L-R64K-2, 95-d expected battery life). Except for a minimum size criterion of 140-mm fork length (FL), fish were randomly selected for tagging, resulting in a mean FL of 164.6 mm (SD = 10.9) and mean weight of 53.5 g (SD = 12.6). The tag weight represented 2.7% of the mean fish weight (range = 1.3–3.8%) for the December release and 3.0% (range = 1.9–4.9%) for the January release. Although recommendations for maximum tag-to-body weight ratios have varied (Jepsen et al. 2004), we followed Adams et al. (1998) guidance for a maximum tag-to-body weight ratio of 5%. Fish were fasted for 24 h prior to surgery to ensure they were in a postabsorptive state. To surgically implant transmitters, fish were anesthetized in 90 mg/L tricaine methanesulfonate (MS-222) until they lost equilibrium. A fish was then placed in a light anesthetic bath (30 mg/L MS-222), ventral side up, and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4–0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for 7 d prior to release. All fish survived the recovery period. We observed no aberrant physiological or behavioral effects of tagging, based on laboratory studies examining growth, wound healing, and tag retention of late-fall Chinook salmon (A. Ammann, unpublished data).

Next, fish were transported to release sites in the Sacramento River near Sacramento, California (rkm 92). Fish were then transferred to net-pens (3-m square holding nets supported by pontoons) at the release site and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Fish were transported and held in four separate groups, and each group was released at roughly 6-h intervals over a 24-h period on 5 December 2006 (release 1) and again on 17 January 2007 (release 2). Each release was carried out over a 24-h period to distribute tagged fish over the tidal and diel cycle. The total sample size consisted of 64 acoustically tagged fish in December 2006 and 80 acoustically tagged fish in January 2007.

Model development

We developed a mark–recapture model that estimates three sets of parameters: detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (ψ_{hl}). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h = A, B, C, D; Figure 2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to $i + 1$ within route h, conditional on surviving to station i (Figure 2). Route entrainment probabilities (ψ_{hl}) estimate the probability of a fish entering route h at junction l (l = 1, 2), conditional on fish surviving to junction l (Figure 2). In addition, the parameter ω_{open} estimates the probability

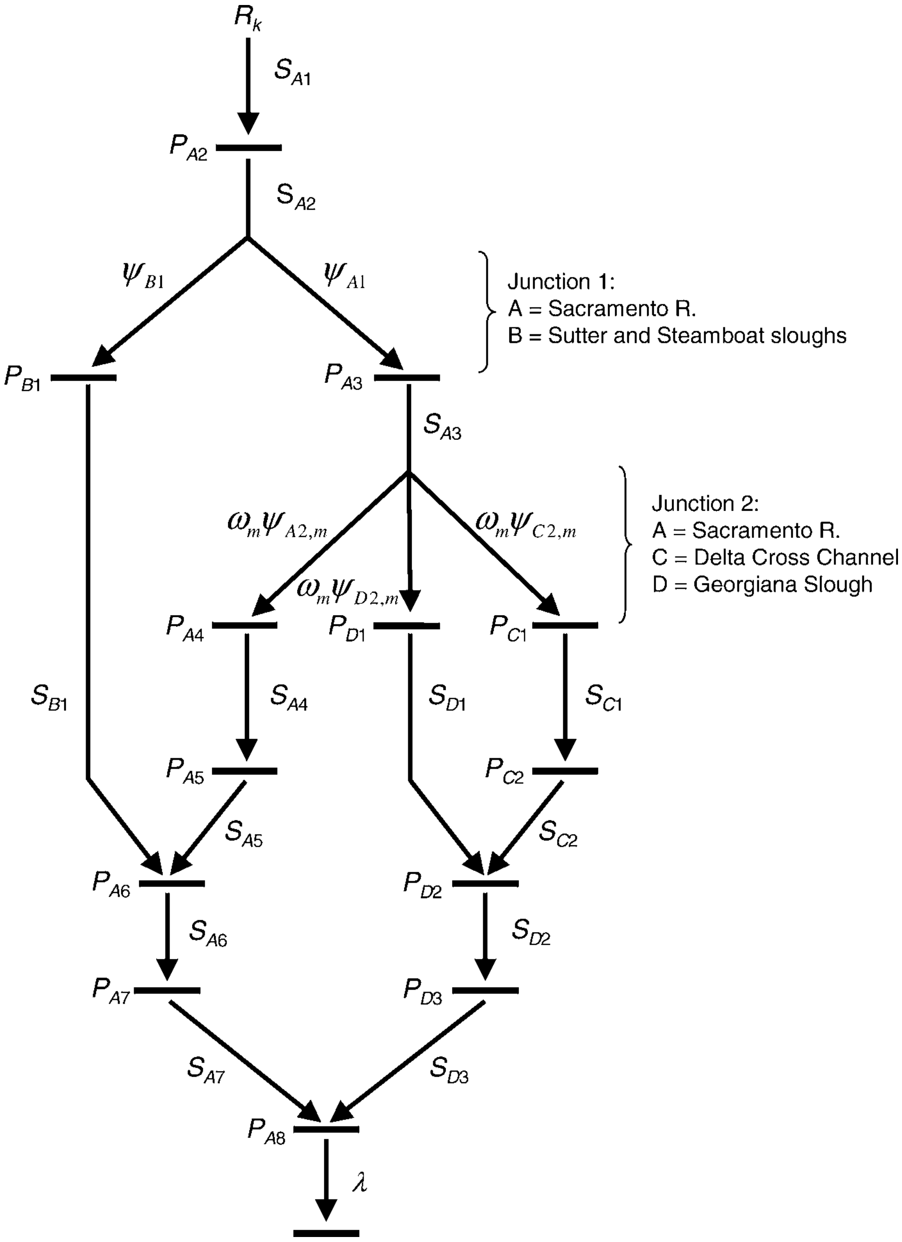

FIGURE 2.—Schematic of the mark–recapture model used to estimate survival (S_{hi}), detection (P_{hi}), and route entrainment (ψ_{hl}) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made on 5 December 2006 and 17 January 2007. See text and Figure 1 for additional information.

of fish passing junction 2 when the Delta Cross Channel was open. This model can be classified as a generalization of the standard Cormack–Jolly–Seber (CJS) mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) and a special case of a multistate mark–recapture model where the route entrainment probabilities represent a constrained matrix of state transition probabilities (Lebreton and Pradel 2002; Williams et al. 2002). Statistical assumptions associated with a model of this structure are detailed in Burnham et al. (1987) and Skalski et al. (2002).

The first river junction was modeled as a two-branch junction where detections at the entrance to either Sutter or Steamboat Slough (station B_1; Figure 1) were pooled to estimate a single route entrainment probability. Thus, the parameter ψ_{B1} estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Figure 2). Conversely,

$$1 - \psi_{B1} = \psi_{A1}$$

is the probability of remaining in the Sacramento River at the first junction (Figure 2). The second junction was modeled as a three-branch junction, where

$$\psi_{A2}, \psi_{C2}, \quad \text{and} \quad 1 - \psi_{A2} - \psi_{C2} = \psi_{D2}$$

estimate the probabilities of remaining in the Sacramento River (route A), being entrained into the Delta Cross Channel (route C), and entering Georgiana Slough (route D) at junction 2 (Figure 2). Because ψ_{C2} equals 0 when the Delta Cross Channel is closed, route entrainment probabilities at junction 2 depend on the position of the Delta Cross Channel gate when fish migrate past this location (Figure 2).

While some survival probabilities estimate survival within a given river channel from telemetry station i to $i + 1$ (e.g., S_{A2}), others represent survival of fish migrating through a number of possible migration pathways. For example, fish entering Sutter or Steamboat Slough at B_1 may migrate through a northern or a southern channel (Figure 1). The parameter S_{B1}, estimating survival between sites B_1 and A_6, therefore represents an average of survival in each channel weighted by the proportion of fish using each channel. Note, however, that to separately estimate the underlying components of S_{B1}, additional telemetry stations would need to be placed at key channel junctions within this route. Similar survival probabilities include S_{C2} and S_{D2}, the latter of which encompasses much of the interior delta (Figure 1).

With this model structure, the full model contains 33 parameters: 13 detection probabilities, 13 survival probabilities, five route entrainment probabilities, and ω_{open} (Figure 2). The final parameter, λ, estimates the joint probabilities of surviving downstream of A_8 and being detected at telemetry stations comprising A_9. Thus, λ has little biological meaning but must be included in the model in order to estimate survival to the terminus of the delta at A_8.

Parameter estimation

Prior to parameter estimation, the records of tag detections were processed to eliminate false-positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False-positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given monitor, and simultaneous tag transmissions "collide" to produce a valid tag code that is not actually present at the monitor (Pincock 2008). Our first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimizes the probability of accepting a false-positive detection, Pincock (2008) showed that a pair of false-positive detections with a time interval of less than 30 min occurred on average once every 30 d when simulating 10 tags simultaneously present at a monitor. Thus, our second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002). The detection records of five tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento River (sites A_6–A_8), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

We used maximum likelihood techniques to estimate parameters based on a multinomial probability model that categorized each fish into a mutually exclusive and exhaustive detection history. Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, the history 1A0AAAAAA indicates a fish was released ("1"), detected in the Sacramento River at A_2 ("A"), not detected in the Sacramento River at A_3 ("0"), and then subsequently detected at every other telemetry station in the Sacramento River ("AAAAAA"). This model has 912 possible detection histories, but with release sample sizes of $R_1 = 64$ and $R_2 = 80$ tagged fish, not all histories are observed.

Each detection history represents one of the 912 cells of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, and route entrainment probabilities. For example, the probability of history 1A0AAAAAA can be expressed as

$$S_{A1}P_{A2}S_{A2}\psi_{A1}(1 - P_{A3})S_{A3}\omega_{open}\psi_{A2,\,open}P_{A4}S_{A4}P_{A5} \\ \times S_{A5}P_{A6}S_{A6}P_{A7}S_{A7}P_{A8}\lambda.$$

In words, the probability of this detection history is the joint probability of surviving the first reach (S_{A1})

and being detected at A_2 (P_{A2}); surviving the second reach (S_{A2}), remaining in the Sacramento River at junction 1 (ψ_{A1}), and not being detected at A_3 ($1 - P_{A3}$); and surviving the third reach (S_{A3}), remaining in the Sacramento River at junction 2 ($\psi_{A2,\text{open}}$) when the Delta Cross Channel was open (ω_{open}), and surviving and being detected at all remaining stations in the Sacramento River (Figure 2).

Given the cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters, that is,

$$L(\underset{\sim}{\theta} \mid R_k, n_j) \propto \prod_{j=1}^{912} \pi_j^{n_j}$$

where R_k is the number of fish released in the kth release-group ($k = 1, 2$), n_j is the number of fish with the jth detection history, and π_j is the probability of the jth detection history expressed as a function of the parameters ($\underset{\sim}{\theta}$). The likelihood was numerically maximized with respect to the parameters by using algorithms provided in the software programs R (R Development Core Team 2008) and USER (Lady et al. 2008). The variance–covariance matrix was estimated as the inverse of the Hessian matrix. We used the delta method (Seber 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\psi_{D2} = 1 - \psi_{A2} - \psi_{C2}$). Uncertainty in parameter estimates is presented both as SEs and 95% profile likelihood confidence intervals.

Parameters were estimated separately for each release, but the model for each release was reduced from the full model because not all parameters could be estimated from the tag detection data. For the first release in December, P_{A3} equaled 0 because station A_3 was not operational, rendering limited ability to uniquely estimate the parameters S_{A2}, ψ_{B1}, and S_{A3}. However, S_{A2} and ψ_{B1} can be estimated under the assumption that S_{A2} equals S_{A3}, which was supported by the similarity of S_{A2} and S_{A3} measured during the second release (for R_2: $\hat{S}_{A2} = 0.959$, SE = 0.024; $\hat{S}_{A3} = 0.976$, SE = 0.025). The Delta Cross Channel gate was closed for the second release, so ω_{open} and ψ_{C2} were set to zero, which eliminated P_{C1}, S_{C1}, P_{C2}, and S_{C2} from the model. For both releases, a number of detection probabilities were set to 1 because of perfect detection data. Last, due to low detection frequencies in the interior delta, the parameters S_{D1} and S_{D2} could not be estimated for the first release, but the product $S_{D1}S_{D2}$ was estimable as a single parameter. Likewise, for the second release only the product $S_{D1}S_{D2}S_{D3}$ was estimable as a single parameter.

Survival through the delta.—Our model estimates the individual components that comprise survival of the population migrating through the delta, defined as survival of tagged fish from the entrance to the delta at station A_2 (Freeport, rkm 73) to the exit of the delta at station A_8 (Chipps Island, rkm −9). Population-level survival through the delta was estimated from the individual components as

$$S_{\text{delta}} = \sum_{h=\text{A}}^{\text{D}} \psi_h S_h \qquad (1)$$

where S_h is the probability of surviving the delta given the specific migration route taken through the delta, and ψ_h is the probability of migrating through the delta via one of four migration routes (A = Sacramento River, B = Sutter and Steamboat sloughs, C = Delta Cross Channel, D = Georgiana Slough). Thus, population survival through the delta is a weighted average of the route-specific survival probabilities with weights equal to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\psi_A = \psi_{A1}\psi_{A2} \qquad (2)$$

$$\psi_B = \psi_{B1} \qquad (3)$$

$$\psi_C = \psi_{A1}\psi_{C2} \qquad (4)$$

$$\psi_D = \psi_{A1}\psi_{D2} \qquad (5)$$

For instance, consider a fish that migrates through the delta via the Delta Cross Channel (route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{C2}. Thus, the probability of a fish migrating through the delta via the Delta Cross Channel (ψ_C) is the product of these route entrainment probabilities, $\psi_{A1}\psi_{C2}$. For release 1, when the Delta Cross Channel was both open and closed, $\psi_{h2} = \omega_{\text{open}}\psi_{h2,\text{open}} + (1 - \omega_{\text{open}})\psi_{h2,\text{closed}}$.

Survival through the delta for a given migration route (S_h) is the product of the reach-specific survival probabilities that trace each migration path through the delta between points A_2 and A_8 (Figures 1, 2):

$$S_A = S_{A2}S_{A3}S_{A4}S_{A5}S_{A6}S_{A7} \qquad (6)$$

$$S_B = S_{A2}S_{B1}S_{A6}S_{A7} \qquad (7)$$

$$S_C = S_{A2}S_{A3}S_{C1}S_{C2}S_{D2}S_{D3} \qquad (8)$$

and

$$S_D = S_{A2}S_{A3}S_{D1}S_{D2}S_{D3}. \tag{9}$$

We also compared our estimates of S_{delta} described above with estimates produced by a standard three-station CJS model. We included telemetry stations A_2, A_8, and A_9 in this model. Here, S_{delta} is estimated directly from the model as the probability of surviving from station A_2 to A_8. We compared the two approaches to ensure they produced similar estimates and to examine the SEs produced under each approach. Given that the CJS model contained many fewer parameters (four for R_1 and five for R_2), we suspected that the CJS model might yield more precise estimates of S_{delta}.

Results

River Conditions and Migration Timing

For the first release in December, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport (U.S. Geological Survey [USGS] gauge 11447650 near station A_2; Figure 1) increased from 365 to 682 m^3/s (Figure 3). The Delta Cross Channel was open when most of these fish passed the second river junction (Figure 3). However, the Delta Cross Channel closed at 1000 hours on 15 December 2006 and remained closed for the balance of the study (Figure 3). River discharge receded to about 500 m^3/s when fish from the December release were migrating through the lower reaches of the delta (Figure 3). In contrast to December, river discharge for the January release was low and stable during much of the migration period (Figure 3). Daily discharge of the Sacramento River remained near 500 m^3/s until 9 February, after which discharge increased to 1,100 m^3/s. However, this increase in flow occurred after most fish had passed through the lower reaches of the delta (Figure 3). Water exports at the delta pumping stations were stable within each migration period, averaging 305 m^3/s for the December migration period and 193 m^3/s for the January period (Figure 3).

Coincident with lower river discharge, fish released in January took substantially longer to migrate through the delta and exhibited higher variation in travel times relative to fish released in December (Figure 3). Among routes, travel times for the December release from the release point to the lower delta (stations A_7 and D_3) were quickest for fish migrating through Sutter and Steamboat sloughs (median = 7 d; interquartile range (25th to 75th percentile) = 6.1–11.7 d; $n = 5$), followed by the Sacramento River (median = 10.7 d; interquartile range = 9.3–12.5 d; $n = 9$) and the interior delta via the Delta Cross Channel and Georgiana Slough (median = 13.8 d; interquartile range = 13.4–19.1 d; $n = 5$). For the January release, travel times were similar for fish migrating through the Sacramento River (median = 18.1 d; interquartile range = 13.2–23.9 d; $n = 19$) and Sutter and Steamboat sloughs (median = 17.8 d; interquartile range = 12.7–27.3 d; $n = 17$). We obtained travel times through the interior delta for only one fish in the January release, which took 33.9 d to travel from release to the lower delta.

Migration Routing

As juvenile salmon migrated past the first river junction, a large proportion of both release-groups left the Sacramento River and migrated through Sutter and Steamboat sloughs (for R_1: $\hat{\psi}_{B1} = 0.296$; for R_2: $\hat{\psi}_{B1} = 0.414$). For the December release, most fish remaining in Sacramento River encountered the second river junction when the Delta Cross Channel was open ($\hat{\omega}_{open} = 0.861$; SE = 0.058), and 39% percent of these fish were entrained into the Delta Cross Channel ($\hat{\psi}_{C2,open} = 0.387$; SE = 0.087). Regardless of release-group or position of the Delta Cross Channel gate, similar fractions of fish passing junction 2 were entrained into Georgiana Slough (for R_1: $\hat{\psi}_{D2,open} = 0.161$, SE = 0.066; $\hat{\psi}_{D2,closed} = 0.200$, SE = 0.179; for R_2: $\hat{\psi}_{D2,closed} = 0.150$, SE = 0.056). The remaining 45% of fish passing junction 2 when the Delta Cross Channel was open stayed in the Sacramento River ($\hat{\psi}_{A2,open} = 0.452$; SE = 0.089), whereas nearly twice that fraction remained in Sacramento River when the Delta Cross Channel was closed (for R_1: $\hat{\psi}_{A2,closed} = 0.800$, SE = 0.179; for R_2: $\hat{\psi}_{A2,closed} = 0.850$, SE = 0.056).

A substantial proportion of fish migrating past junction 2 entered the interior delta through the Delta Cross Channel and Georgiana Slough. However, a lower proportion of the population entered the interior delta because some fish bypassed the second river junction by migrating through Sutter and Steamboat sloughs (Figure 1). Accounting for population distribution among all routes, 23.5% were entrained into the Delta Cross Channel ($\hat{\psi}_C$), 11.7% entered Georgiana Slough ($\hat{\psi}_D$), and 35.2% migrated within the Sacramento River ($\hat{\psi}_A$) for the December release when the Delta Cross Channel was open during much of the migration period (Table 1). In contrast, 8.8% migrated through Georgiana Slough and 49.8% remained in the Sacramento River in January when the Delta Cross Channel was closed (Table 1). Because Sutter and Steamboat sloughs rejoin the Sacramento River upstream of telemetry station A_6, much of this migration route through the delta (route B) consists of the main-stem Sacramento River (Figure 1). Thus for the December release, 64.8% of fish took migration routes largely consisting of the Sacramento River ($\hat{\psi}_A$

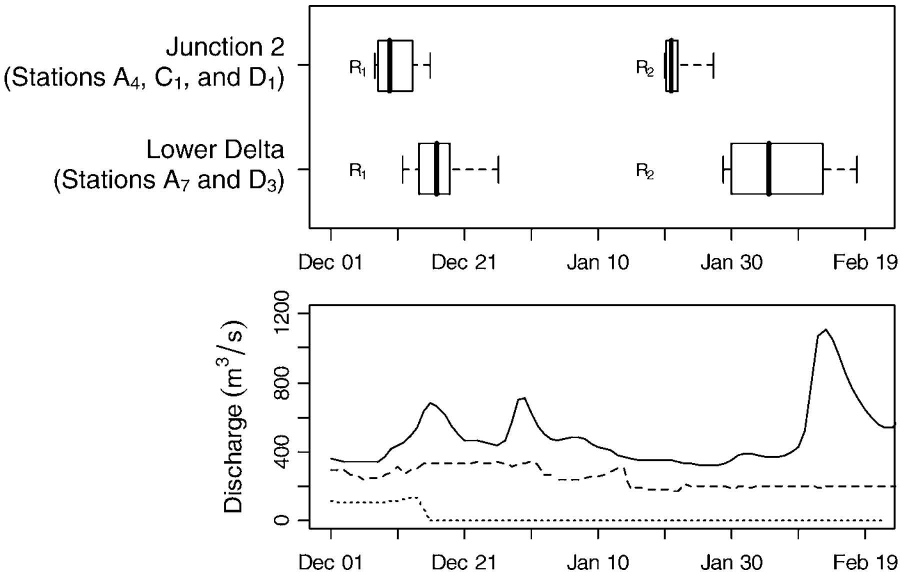

FIGURE 3.—In the upper panel are box plots showing the distribution of arrival dates at junction 2 on the Sacramento River and near the exit of the delta. The two release dates shown are 5 December 2006 (R_1; 64 tagged fish) and 17 January 2007 (R_2; 80 fish). The whiskers represent the 10th and 90th percentiles, the boxes encompass the 25th to 75th percentiles, and the lines within the boxes are the median arrival dates. The lower panel shows river discharge (solid line), which is the tidally filtered daily discharge of the Sacramento River at Freeport (near telemetry station A_2); the Delta Cross Channel discharge (dotted line), which is the tidally filtered daily discharge at that point; and water exports (dashed line), which are the total daily discharge of water from the delta at the pumping projects.

$+ \hat{\psi}_B$) and 35.2% were entrained into the interior delta via the Delta Cross Channel and Georgiana Slough ($\hat{\psi}_C + \hat{\psi}_D$; Table 1). In contrast, only 8.8% percent of fish were entrained into the interior delta through Georgiana Slough in January when the Delta Cross Channel was closed, the remaining 91.2% migrating mostly within the Sacramento River ($\hat{\psi}_A + \hat{\psi}_B$; Table 1).

We found that migration route probabilities (ψ_h) corresponded well with the fraction of total river discharge in each route (Figure 4). Distribution of river flow among the four migration routes was calculated as the fraction of mean discharge of each route relative to the mean discharge of the Sacramento River at Freeport (near station A_2), upstream of the two river junctions. Steamboat and Sutter sloughs diverted 33.4% and 37.6%, respectively, of the mean flow of the Sacramento River during the December and January migration period, accounting for the large proportion of

TABLE 1.—Route-specific survival through the Sacramento–San Joaquin River Delta ($\hat{S}_h$) and the probability of migrating through each route ($\hat{\psi}_h$) for acoustically tagged fall-run juvenile Chinook salmon released on 5 December 2006 and 17 January 2007. Also shown is population survival through the delta, which is the average of route-specific survival weighted by the probability of migrating through each route; NA = not applicable.

Migration route	$\hat{S}_h$ (SE)	95% profile likelihood interval	$\hat{\psi}_h$ (SE)	95% profile likelihood interval
		5 December 2006		
Sacramento River	0.443 (0.146)	0.222–0.910	0.352 (0.066)	0.231, 0.487
Steamboat and Sutter sloughs	0.263 (0.112)	0.102–0.607	0.296 (0.062)	0.186, 0.426
Delta Cross Channel	0.332 (0.152)	0.116–0.783	0.235 (0.059)	0.133, 0.361
Georgiana Slough	0.332 (0.179)	0.087–0.848	0.117 (0.045)	0.048, 0.223
All routes	0.351 (0.101)	0.200–0.692		
		17 January 2007		
Sacramento River	0.564 (0.086)	0.403–0.741	0.498 (0.060)	0.383, 0.614
Steamboat and Sutter sloughs	0.561 (0.092)	0.388–0.747	0.414 (0.059)	0.303, 0.531
Delta Cross Channel	NA		0.000	NA
Georgiana Slough	0.344 (0.200)	0.067–0.753	0.088 (0.034)	0.036, 0.170
All routes	0.543 (0.070)	0.416–0.691		

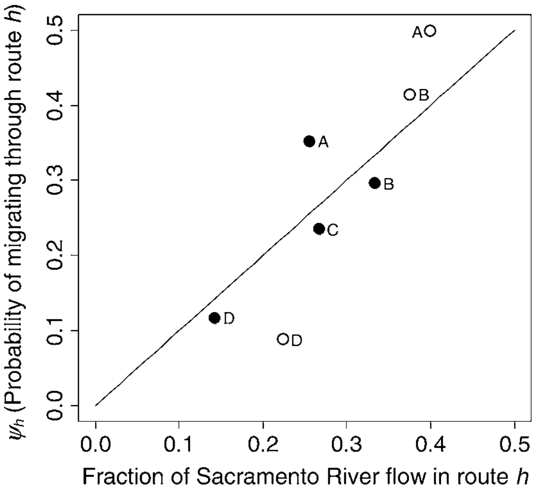

FIGURE 4.—The probability of migrating through route h as a function of the proportion of total river flow in route h for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (filled symbols) and 17 January 2007 (open symbols). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The 45° reference line shows where the fraction migrating through a particular route is equal to the proportion of flow in that route.

fish using this migration route (Figure 4). At the second river junction, operation of the Delta Cross Channel influenced the relative discharge of the Sacramento River as flow in the Sacramento River downstream of junction 2 represented 25.6% of its total discharge when the Delta Cross Channel was open (December release) compared with 40.0% when the Delta Cross Channel was closed (January release). The increase in relative flow of the Sacramento River due to closure of the Delta Cross Channel was accompanied by an increase in the fraction of fish migrating through this route (Figure 4). For both releases, the proportion of fish migrating within the Sacramento River was about 10% points higher than the fraction of flow remaining in the Sacramento River, and for the January release the fraction migrating through Georgiana Slough was about 10% lower than the fraction of flow (Figure 4).

Survival through the Delta

Overall, the estimate of survival through the Delta for the December release was lower than for January (for R_1: $\hat{S}_{\text{delta}} = 0.351$; for R_2: $\hat{S}_{\text{delta}} = 0.543$; Table 1) despite higher discharge and shorter travel times through the delta for the December release (Figure 2). The CJS model produced nearly the same point estimates and SEs (for R_1: $\hat{S}_{\text{delta}} = 0.351$, SE = 0.101; for R_2: $\hat{S}_{\text{delta}} = 0.536$, SE = 0.070). This finding supports the validity of our more complex model to reconstruct survival through the delta from the individual components of reach-specific survival and route entrainment probabilities, while also maintaining precision about $\hat{S}_{\text{delta}}$. Relative to the small sample size of this study, precision was favorable due to high detection probabilities at most telemetry stations (Table 2).

TABLE 2.—Maximum likelihood estimates of detection probabilities (P_{hi}) at the ith telemetry station within route h for acoustically tagged late-fall-run juvenile Chinook salmon released on 5 December 2006 and 17 January 2007. Detection probabilities not shown here were set to one because all fish known to pass a given telemetry station were detected at that station. For the first release, P_{A3} was set to zero because this station was not operational during the first release.

	5 December 2006		17 January 2007	
Parameter	Estimate	SE	Estimate	SE
P_{A2}			0.986	0.014
P_{A3}			0.975	0.025
P_{A4}			0.970	0.030
P_{A6}	0.857	0.094	0.641	0.077
P_{A7}			0.941	0.040
P_{A8}	0.500	0.158	0.645	0.088
P_{D2}	0.600	0.219		

Relative contributions to S_{delta}

Estimates of $\hat{S}_{\text{delta}}$ were driven by (1) variation among routes in survival through the delta ($\hat{S}_h$), and (2) the relative contribution of each route-specific survival to $\hat{S}_{\text{delta}}$ as measured by migration route probabilities ($\hat{\psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_{\text{A}}$) relative to all other routes, but only 35% of the population migrated through this route ($\hat{\psi}_{\text{A}}$), representing a relatively small contribution to $\hat{S}_{\text{delta}}$ (Table 1). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{\text{delta}}$ and comprised 65% of the population ($\hat{\psi}_{\text{B}} + \hat{\psi}_{\text{C}} + \hat{\psi}_{\text{D}}$), thereby contributing substantially to $\hat{S}_{\text{delta}}$ for the December release (Table 1). For the January release, 91% of the population ($\hat{\psi}_{\text{A}} + \hat{\psi}_{\text{B}}$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{\text{delta}}$ for the January release (Table 1). In comparison, survival for the interior delta via Georgiana Slough ($\hat{S}_{\text{D}}$) was lower than the other routes, but this route accounted for only 9% of the population ($\hat{\psi}_{\text{D}}$), having little influence on $\hat{S}_{\text{delta}}$ (Table 1).

The observed difference in $\hat{S}_{\text{delta}}$ between releases can be attributed to (1) a change in the relative contribution of each route-specific survival to $\hat{S}_{\text{delta}}$, and (2) differences in survival for given migration routes. Survival estimates for interior Delta routes ($\hat{S}_C$ and $\hat{S}_D$) were lower than for the Sacramento River ($\hat{S}_A$) during both releases but contributed only 9% for the January release when the Delta Cross Channel was closed, compared with 35% ($\hat{\psi}_C + \hat{\psi}_D$) for the December release when the Delta Cross Channel was open (Table 1). Thus, lower contribution of interior Delta routes to $\hat{S}_{delta}$ partly accounts for the higher $\hat{S}_{delta}$ observed for the January release. However, higher $\hat{S}_{delta}$ for January was also a consequence of changes in route-specific survival for the Sacramento River and Sutter and Steamboat sloughs, both of which were higher for the January release compared with December. These findings show how both survival through given routes and population distribution among routes interacted to affect $\hat{S}_{delta}$ during the two releases.

Discussion

Our study highlights the importance of quantifying both movement among migration routes and survival within routes to understand factors affecting population-level survival. Measuring survival through different migration routes (S_h) between the same beginning and end points (from telemetry station A_2 to A_8; Figure 1) provides direct insight into the effect of different migration routes on survival through the entire delta. Furthermore, the migration route probabilities (ψ_h) measure the contribution of each route-specific survival to the overall survival of the population migrating through the delta. Thus, our modeling approach provides a natural framework for understanding how these route-specific components interact to affect population-level survival through the delta. Operation of the Delta Cross Channel is an important water management action that may influence population-level survival by affecting the fraction of the population entering the interior delta where survival is typically lower than alternative migration routes (this study; Newman and Brandes 2009). Thus, without information about both population distribution among routes and survival within routes, it would be difficult to quantify how management actions affect these underlying components that give rise to population-level survival.

We show that route-specific survival and movement among migration routes interact to influence population-level survival, but the next challenge is to quantify the mechanisms causing variation in route-specific survival. Within each release, travel times for fish migrating through the interior delta were longer than alternative routes, possibly contributing to lower survival through the interior delta. Relative to the December release, however, survival for the January release was higher for two migration routes (Sacramento River and Sutter and Steamboat sloughs) despite lower discharge and longer travel times through these routes during January (Figure 3). Thus, instantaneous mortality rates (i.e., per time) in these two routes were lower in January than in December, suggesting that factors other than travel time also contribute to variation in survival within and among migration routes. Such factors may include variation in environmental conditions (e.g., water temperature, turbidity, tides) or temporal shifts in the spatial distribution of predators, both of which influence predator–prey interactions. Our study just begins to shed light on this variation, but with replication over a wide range of environmental conditions our framework will allow us to explicitly quantify mechanisms influencing the route-specific components of population survival.

Our findings are consistent with a series of studies that have estimated survival of juvenile salmon in the delta with coded wire tags (Brandes and McLain 2001; Newman and Rice 2002; Newman 2008; Newman and Brandes 2010). In general, similar to our study, these studies found that survival of fish released into the interior delta via Georgiana Slough was lower than survival of fish released into the Sacramento River downstream of Georgiana Slough (Newman 2008; Newman and Brandes 2009). Specifically, Newman and Brandes (2009) found that the ratio of survival for Georgiana Slough releases relative to Sacramento River releases was less than one for all release-groups, indicating significantly lower survival for fish migrating through the interior delta (see Table 2 *in* Newman and Brandes 2009). In our study, an analogous estimate is $S_{D1}S_{D2}S_{D3}/S_{A5}S_{A6}S_{A7}$ (i.e., survival from D_1 to A_8 relative to A_5 to A_8; Figure 1). The estimate of this ratio was 0.625 (SE = 0.352) for the December release and 0.591 (SE = 0.351) for the January release. Although the SEs indicate that these estimates do not differ from one (i.e., equal survival), the point estimates parallel the previous studies and fall well within their observed release-to-release variation. This evidence continues to support the hypothesis that survival for fish migrating through the interior delta is lower than for fish that remain in the Sacramento River. While past research has revealed differences in survival among migration routes, it was impossible to quantify how these survival differences influenced survival of the population. In contrast, our study builds on past research by explicitly estimating the relative contribution of route-specific survival to population-level survival, as quantified by migration route probabilities (ψ_h).

Given that 30–40% of the population migrated through Sutter and Steamboat sloughs (Table 1), this migration route plays a key role in population-level survival by reducing the probability of fish entering the interior Delta. Fish migrating through Sutter and Steamboat sloughs do not encounter the Delta Cross Channel or Georgiana Slough, which directly reduces the fraction of fish entering the interior Delta via these routes. This relation is couched explicitly in our model: the probability of migrating through the interior Delta can be expressed as

$$\psi_C + \psi_D = (1 - \psi_B)(\psi_{C2} + \psi_{D2}).$$

Note that the fraction entering the interior Delta ($\psi_C + \psi_D$) decreases as the fraction migrating through Sutter and Steamboat sloughs (ψ_B) increases. This relationship highlights a critical linkage among migration routes that drives the dispersal process of juvenile salmon migrating through the delta. Furthermore, closure of the Delta Cross Channel reduces channel capacity of the Sacramento River at the second river junction, which slightly increases the proportion of river flow diverted into Sutter and Steamboat sloughs at the first river junction (J. R. Burau, USGS, personal communication). Thus, in addition to eliminating a route through the interior delta, closure of the Delta Cross Channel may decrease the proportion of fish entrained into the interior delta by increasing the fraction of fish entering Sutter and Steamboat sloughs. However, whether population-level survival is increased by management actions that shift the population distribution among migration routes will depend on the relative difference in survival among alternative routes.

In general, migration route probabilities increased with the fraction of total river discharge in each migration route, but both the form of this relationship and the factors influencing migration route probabilities requires further study. Flow distribution among the river channels at each junction varies with the tides on hourly time scales. Thus, migration route probabilities in our model represent an average of time-specific route entrainment probabilities that depend on the flow distribution when each fish passes a river junction. Furthermore, the spatial distribution of migrating salmon across a river channel may deviate from the spatial distribution of flow, which could cause a disproportionate number of salmon to be entrained into a given river channel relative to the proportion of flow in that channel. For example, in the Columbia River, juvenile salmon pass through shallow spillways at dams in higher proportions than the fraction of flow passing through spillways (Plumb et al. 2003; Zabel et al. 2008) because of the surface-biased distribution of salmon. Similar behavioral processes at river junctions in the delta would manifest as consistently positive or negative deviations from the 1:1 line in Figure 4 (i.e., where the proportion of flow = proportion of fish in a given route). Given these processes and our initial findings, we hypothesize that (1) changes in the distribution of average river flow at river junctions will effect coincident changes in average migration route probabilities, (2) consistent deviations in migration route probabilities relative to flow distribution may arise from a mismatch in the spatial distribution of fish relative to flow, and (3) variability in release-specific migration route probabilities will be driven by the interaction between fish arrival timing at a river junction and hourly scale changes in flow distribution at river junctions. Thus, on average, we suspect that closure of the Delta Cross Channel will reduce the proportion of fish entrained into the interior delta by reducing the fraction of mean discharge entering the interior delta. However, hourly scale variation in flow distribution at river junctions will likely magnify release-to-release variation in migration route probabilities, requiring replication over a range of conditions to confirm whether migration route probabilities are indeed positively related to the proportion of average river flow entering a given migration route.

Strictly speaking, inferences from our study population apply directly to the population of hatchery-origin late fall Chinook salmon 140-mm FL or larger migrating through the delta between December and mid-February under the environmental conditions observed during our study. However, four distinct populations of juvenile Chinook salmon (fall, late fall, winter, and spring) of both hatchery and wild origin use the delta to varying degrees at different times of year during different life stages. Although our framework can be applied to any of these populations, inferences from our data should be considered in the context of the similarity of target populations to our study population. Between December and mid-February, most fish captured in midwater trawls in the lower delta at Chipps Island (near station A_8) range in size from about 110 to 200 mm (Brandes and McLain 2001) and likely represent actively migrating smolts from the late fall and winter run of Chinook salmon (Hedgecock et al. 2001). Fall-run fry (i.e., < 50-mm FL) begin appearing in the delta in January and overlap with the arrival of spring-run parr (>50-mm FL) in March, both of which rear and grow in the delta to sizes smaller than 120-mm FL until complete emigration by late June (as presumed by absence in catch data; Williams 2006 and references therein). Inferences from our data to fall-run fry and spring-run parr are not well supported due to differences in size, seasonal timing, and residence time in the delta. In addition, survival of hatchery-origin fish may differ from that of wild fish (Reisenbichler and McIntyre 1977; Kostow 2004), but factors influencing relative differences in survival among migration routes (e.g., interior delta relative to Sacramento River) are likely to act similarly on both wild and hatchery populations. Thus, inferences about such relative differences may provide critical information for better understanding mechanisms influencing population-level survival of both hatchery and wild populations.

Estimating both movement and survival rates among different habitats is difficult yet critically important because these demographic parameters can have important consequences on population dynamics and viability (Beissinger and McCullough 2002). In our study, strategically located telemetry stations yield information on the movement of individual fish, while the mark–recapture model allows unbiased estimation of demographic parameters by correcting for the imperfect detection probability of each telemetry station. Similar models have been applied extensively to estimate animal migration and survival rates among geographic areas over time (Hilborn 1990; Hestbeck et al. 1991; Williams et al. 2002), but relatively few studies have focused on survival through space among alternative migration pathways (but see Skalski et al. 2002). Our framework could be applied to any migrating fish population that uses a number of alternative migration routes and is particularly well suited to dendritic networks such as river systems and their estuaries. For example, by situating telemetry stations at appropriate tributary confluences in a main-stem river, our modeling framework could be used to estimate both reach-specific survival and dispersal of adult salmonids among spawning tributaries. Here, movement rates (ψ) estimate the proportion of the population using each tributary, providing important information about relative contribution of subpopulations in each tributary to the population as a whole. Our study shows how combining telemetry with mark–recapture models provides a powerful approach to estimate demographic parameters in spatially complex settings.

This study has provided the first quantitative glimpse into the migration dynamics of juvenile salmon smolts in the Sacramento River. Route-specific survival through the delta (S_h) measured the consequence of migrating through different routes on survival through the delta, while migration route probabilities (ψ_h) quantified the relative contribution of each route-specific survival to population-level survival. In years to come, increases in sample size and replication over variable environmental conditions will bolster inferences drawn from the acoustic tag data and increase understanding of the mechanisms influencing survival. Cumulative knowledge gained from this population-level approach will identify the key management actions in the delta that must be rectified if Sacramento River salmon populations are to recover.

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