Migration and Survival of Juvenile Chinook Salmon through the Sacramento–San Joaquin River Delta during the Winter of 2006-2007

Prepared by:

Russell W. Perry and John R. Skalski

School of Aquatic and Fishery Sciences
University of Washington
Box 355020
Seattle, WA 98195-5020

Abstract

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating from natal tributaries of the Sacramento River must negotiate the Sacramento–San Joaquin River Delta (hereafter, "the 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 fraction of the population using different migration routes and survival within those routes. We developed a mark-recapture model for application to acoustic telemetry data to explicitly estimate the route-specific components of population-level survival in the Delta. The point estimate of survival through the Delta for a release made in December, 2006 ($\hat{S}_{Delta} = 0.351$, $\widehat{SE} = 0.101$) was lower than for a release made in January, 2007 ($\hat{S}_{Delta} = 0.543$, $\widehat{SE} = 0.070$). The observed difference in $\hat{S}_{Delta}$ between releases can be attributed to 1) changes in the proportion of fish migrating through each route, and 2) differences in survival for given migration routes. Survival estimates for routes through the interior Delta were lower than for the Sacramento River during both releases, but only 9% of fish migrated through the interior Delta for the January release compared to 35% for the December release. 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, survival through two routes was higher for the January release relative to December, also contributing to the higher $\hat{S}_{Delta}$ observed for the January release. The lower proportion of fish migrating through the interior Delta during the January release was driven by closure of the Delta Cross Channel, a man-made channel that diverts water from the Sacramento River to the interior Delta. Our study shows how concurrent estimation of both population distribution and survival among different migration routes is critical to understand the effect of water management actions on population-level survival of juvenile salmon.

Table of Contents

Table of Figures

Table of Tables

Acknowledgements

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 (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 B 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 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 D_1 in Route D, Figure 1). In addition to these human influences on water flow through the Delta, natural
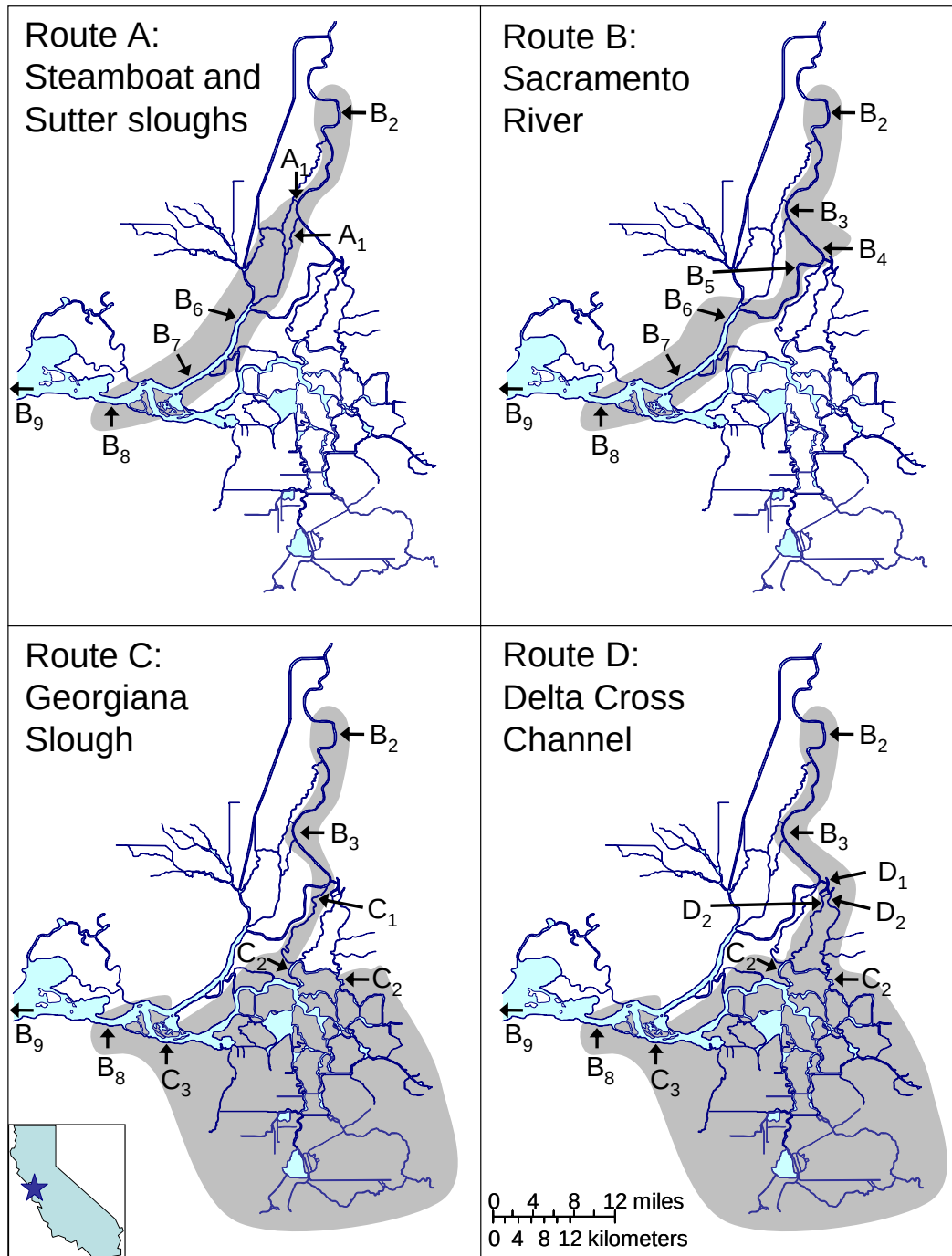
Figure 1.—Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. Arrows show the location of telemetry stations specific to each route. The first river junction occurs where Steamboat and Sutter sloughs (A1) diverge from the Sacramento River at station B3. The second junction occurs where the Delta Cross Channel (D1) and Georgiana Slough (C1) diverge from the Sacramento River at station B4. For routes C and D, the interior Delta is the shaded region to the south of station C2. Telemetry stations with the same label (A1, C2, and D2) were pooled as one station in the mark-recapture model. Station B9 pools all telemetry stations in San Francisco Bay downstream of B8. The release site (not shown) was 22 km upriver of station B2.

processes include seasonal rainfall and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and bi-weekly 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 mainstem Sacramento River (Sommer et al. 2001). In contrast, juvenile salmon entering the interior Delta are exposed to entrainment at the water pumping projects (i.e., fish entering the pumping stations by moving with the flow of water), 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). 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 survival of fish migrating through the interior Delta, where water pumping projects are located, decreases with increasing water exports (Brandes and McLain 2001; Newman 2003; Newman 2008). 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. Thus, currently lacking is a population-level approach that quantifies dispersal of the population among migration routes and measures survival within these routes to better understand the influence of management actions on population-level survival.

In this study, we developed a mark-recapture model for use with acoustic telemetry data to estimate both distribution and survival of juvenile late-fall run Chinook salmon migrating through the Delta. In the Delta, traditional mark-recapture techniques that depend on the physical recapture of fish (e.g., coded wire tags) lack the high recapture rates needed to obtain

precise estimates of survival. Furthermore, these traditional techniques are not conducive to estimating the fraction of fish using alternative migration routes due to the effort required to capture fish within each route. In contrast, telemetry is a passive detection technique that enables individual fish to be detected repeatedly by multiple telemetry stations during their migration through the Delta. In addition, recent advances in telemetry technology have progressively reduced the size of transmitters, making it possible to study movements of juvenile salmonids without significantly altering their behavior or survival (Hockersmith et al. 2003). Given estimates of reach-specific survival and population distribution in the Delta, we examined how each of these components interacted to drive 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): Steamboat and Sutter Slough (Route A), the mainstem Sacramento River (Route B), the interior Delta via Georgiana Slough (Route C), and the interior Delta via the Delta Cross Channel (Route D). Although there are numerous possible migration routes, we focused on these routes because management actions likely have the largest influence on distribution and survival among these routes. Fish enter the interior Delta from the Sacramento River through either the Delta Cross Channel or Georgiana Slough where they subsequently become vulnerable to entrainment at the water pumping projects. Steamboat and Sutter sloughs, diverging from the Sacramento River upstream of Georgiana Slough and the Delta Cross Channel, 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 Slough are not subject to entering into the interior Delta.

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) that identified individual fish based on the unique pattern of

4

intervals within a burst of pulses emitted from acoustic transmitters at pseudo-random intervals of 45-90 s. Since the Sacramento River is the primary migration route, the ith telemetry station within this route is denoted as B_i from the release site to the last telemetry station in the Delta at Chipps Island (B_8). Steamboat and Sutter sloughs (A_1) diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of B_6. Telemetry stations within Georgiana Slough and the interior Delta were labeled as C_i where Georgiana Slough diverges from the mainstem Sacramento River at the second river junction (C_1) until the convergence of the interior Delta with the Sacramento River at C_3. For the Delta Cross Channel, stations were labeled with D_i beginning at the second river junction (D_1) and ending when these river channels converge at C_2.. Following this hierarchy, Routes A, B, C, and D contained 1, 8, 3, and 2 telemetry stations, respectively for a total of 15 telemetry stations within the Delta. Numerous telemetry stations were located in San Francisco Bay (B_9) downstream of B_8, and detections at any of these stations were used as the last sampling station in our model. Parameter subscripting and coding of detection histories followed this hierarchical structure (see **Model Development** section below).

Fish Tagging and Release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (approximately 340 km upriver of release sites near Sacramento, CA). For the first release in December, we used a 1.44-g tag (Vemco Ltd., Model V7-1L-R64K, 40-d expected battery life) and for the second release in January we used 1.58-g tag (Vemco Ltd., Model V7-2L-R64K-2, 95-d expected battery life). Except for a minimum size criteria of 140-mm fork length, fish were randomly selected for tagging resulting in a mean fork length 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. 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. All fish

survived the recovery period, and we observed no aberrant physiological or behavioral effects of tagging.

To conduct releases, fish were transported to release sites in the Sacramento River near Sacramento, CA (22 km upstream of B_2; Figure 1). Fish were then transferred to net pens 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 them 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 migrating through junction l (Figure 2). In addition, the parameter ω_{open} estimates the probability 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 Steamboat or Sutter Slough (stations A_1; Figure 1) were pooled to estimate a single route entrainment probability. Thus the parameter ψ_{A1} estimates the probability of being entrained into either Steamboat or Sutter Slough at the first river junction (Figure 2).
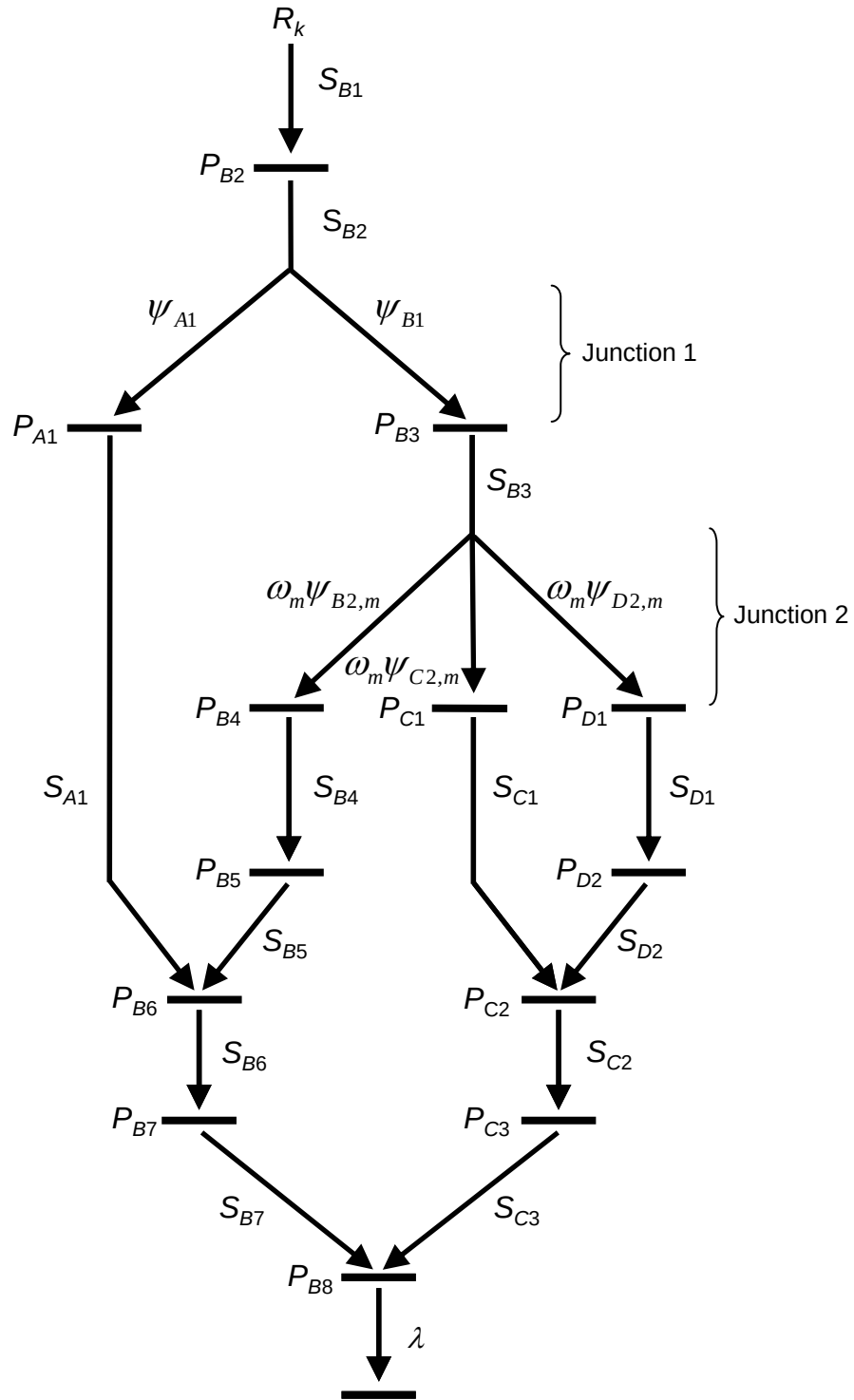
Figure 2.—Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), and route entrainment (ψ_{hl}) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made on 5 December 2006 and 17 January 2007.

Conversely, $1-\psi_{A1}=\psi_{B1}$ 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 ψ_{B2}, ψ_{D2}, and $1-\psi_{B2}-\psi_{D2}=\psi_{C2}$ estimate the probabilities of remaining in the Sacramento River (Route B), being entrained into the Delta Cross Channel (Route D), and entering Georgiana Slough (Route C) at junction 2 (Figure 2). Since fish from a given release could pass junction 2 when the Delta Cross Channel was either open or closed, route entrainment probabilities at junction 2 are conditional on the position of the Delta Cross Channel gate (Figure 2).

While some survival probabilities estimate survival within a given river channel from telemetry station i to $i+1$ (e.g., S_{B2}), others represent survival of fish migrating through a number of possible migration pathways. For example, fish entering Steamboat or Sutter Slough at A_1 may migrate through a northern or a southern channel (Figure 1). Thus, the parameter S_{A1}, estimating survival between sites A_1 and B_6, represents an average of survival weighted by the proportion of fish using each route. Note, however, that to separately estimate the underlying components of S_{A1}, additional telemetry stations would need to be placed at key channel junctions within this route. Similar survival probabilities include S_{D1} and S_{C2}, 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, 5 route entrainment probabilities, ω_{open}, and λ, the joint probability of surviving and being detected at telemetry stations downriver of B_8 (Figure 2).

Parameter Estimation

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. The records of tag-detections were first processed to eliminate false positive detections using methods similar to those described by Skalski et al. (2002). In the lower Sacramento River (sites B_6–B_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. Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, the history 1B0BBBBBB indicates a fish was released ("1"), detected in

8

the Sacramento River at B_2 ("B"), not detected in the Sacramento River at B_3 ("0"), and then subsequently detected at every other telemetry station in the Sacramento River ("BBBBB"). 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 forms one of the 912 cell probabilities of a multinomial distribution where each cell probability is defined as a function of the detection, survival, and route entrainment probabilities. For example, the probability of history 1B0BBBBBB can be expressed as:

$$S_{B1}P_{B2}S_{B2}\psi_{B1}(1\text{-}P_{B3})S_{B3}\omega_{open}\psi_{B2}P_{B4}S_{B4}P_{B5}S_{B5}P_{B6}S_{B6}P_{B7}S_{B7}P_{B8}\lambda$$

In words, the probability of this detection history is the joint probability of surviving the first reach (S_{B1}) and being detected at B_2 (P_{B2}); surviving the second reach (S_{B2}), remaining in the Sacramento River at junction 1 (ψ_{B1}), and not being detected at B_3 ($1-P_{B3}$); and surviving the third reach (S_{B3}), remaining in the Sacramento River at junction 2 (ψ_{B2}) 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:

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

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 (θ). 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., $\psi_{C2} = 1 - \psi_{B2} - \psi_{D2}$). Uncertainty in parameter estimates is presented both as standard errors and 95% profile likelihood confidence intervals.

9

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, $P_{B3} = 0$ because station B_3 was not operational, rendering limited ability to uniquely estimate the parameters S_{B2}, ψ_{A1}, and S_{B3}. However, S_{B2} and ψ_{A1} can be estimated under the assumption that $S_{B2} = S_{B3}$, which was supported by the similarity of S_{B2} and S_{B3} measured during the second release (for R_2: $\hat{S}_{B2} = 0.959$, $\widehat{SE} = 0.024$; $\hat{S}_{B3} = 0.976$, $\widehat{SE} = 0.025$). The Delta Cross Channel gate was closed for the second release, so ω_{open} and ψ_{D2} were set to zero, which eliminated P_{D1}, S_{D1}, P_{D2}, and S_{D2} 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_{C1} and S_{C2} could not be estimated for the first release, but the product $S_{C1}S_{C2}$ was estimable as a single parameter. Likewise, for the second release only the product $S_{C1}S_{C2}S_{C3}$ 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 B_2 (Freeport) to the exit of the Delta at station B_8 (Chipps Island). Population-level survival through the Delta was estimated from the individual components as:

$$S_{Delta} = \sum_{h=A}^{D} \psi_h S_h \tag{1}$$

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:

$$\psi_A = \psi_{A1} \tag{2}$$

$$\psi_B = \psi_{B1}\psi_{B2} \tag{3}$$

$$\psi_C = \psi_{B1}\psi_{C2} \tag{4}$$

$$\psi_D = \psi_{B1}\psi_{D2} \tag{5}$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route D). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{B1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{D2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (ψ_D) is the product of these route entrainment probabilities, $\psi_{B1}\psi_{D2}$. For release 1, when the Delta Cross Channel was both open and closed,

$$\psi_{h2} = \omega_{open}\psi_{h2,open} + \left(1 - \omega_{open}\right)\psi_{h2,closed}.$$

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 B_2 and B_8 (Figure 1, Figure 2):

$$S_A = S_{B2}S_{A1}S_{B6}S_{B7} \tag{6}$$

$$S_B = S_{B2}S_{B3}S_{B4}S_{B5}S_{B6}S_{B7} \tag{7}$$

$$S_C = S_{B2}S_{B3}S_{C1}S_{C2}S_{C3} \tag{8}$$

$$S_D = S_{B2}S_{B3}S_{D1}S_{D2}S_{C2}S_{C3} \tag{9}$$

Since each of these components of S_{Delta} measures survival between the same beginning and end points, comparison of these route-specific survival estimates yields direct insight about the effect of different migration routes on survival through the entire Delta. Furthermore, the migration route probabilities show 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 to deconstruct survival through the Delta and understand how each component affects population-level survival through the Delta.

We also compared our estimates of S_{Delta} described above to estimates produced by a standard three-station CJS model. We included telemetry stations B_2, B_8, and B_9 in this model. Here, S_{Delta} is estimated directly from the model as survival from station B_2 to B_8. We compared the two approaches to ensure they produced similar estimates and to examine the standard errors produced under each approach. Given that the CJS model contained many fewer parameters (4

for R_1 and 5 for R_2), we suspected that the CJS model might yield more precise estimates of S_{Delta}.

Results

River Conditions

For the first release in December, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport (near station B_2; Figure 1) increased from 12,900 $ft^3 \cdot s^{-1}$ to 24,100 $ft^3 \cdot s^{-1}$ (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 12,000 $ft^3 \cdot s^{-1}$ when fish from the December release were migrating through the lower reaches of the study area (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 12,000 $ft^3 \cdot s^{-1}$ until 9 February, after which discharge increased to 39,000 $ft^3 \cdot s^{-1}$. 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 and averaged 10,789 $ft^3 \cdot s^{-1}$ for the December migration period and 6,823 $ft^3 \cdot s^{-1}$ for the January study period (Figure 3).

Survival through the Delta

Overall, the estimate of survival through the Delta for the December release was lower than for January (for R_1: $\hat{S}_{Delta} = 0.351$, $\widehat{SE} = 0.101$; for R_2: $\hat{S}_{Delta} = 0.543$, $\widehat{SE} = 0.070$, Table 1). The CJS model produced nearly the same point estimates and standard errors (for R_1: $\hat{S}_{Delta} = 0.351$, $\widehat{SE} = 0.101$; for R_2: $\hat{S}_{Delta} = 0.536$, $\widehat{SE} = 0.070$). 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 $\hat{S}_{Delta}$. Relative to the small sample size of this study, precision was favorable due to high detection probabilities at most telemetry stations ($\hat{P}_{hi} \geq 0.941$ for all stations except B_6, B_8, and C_2, Appendix Table 2).
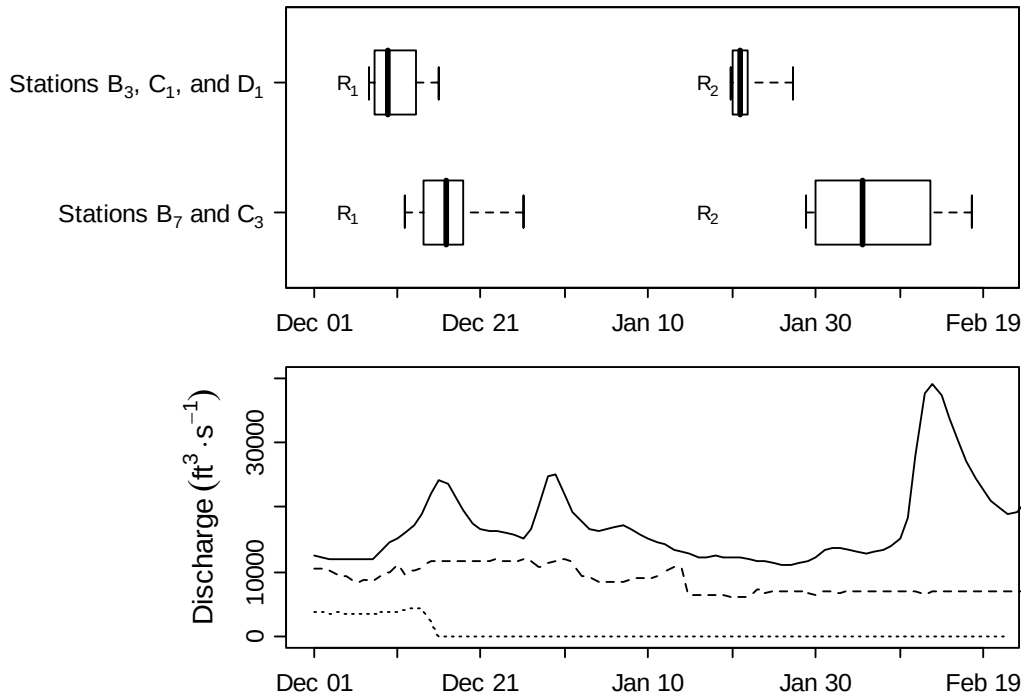
Figure 3.—River discharge, water exports, and Delta Cross Channel discharge (lower panel) during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2006/2007 (upper panel). Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations B_3, C_1, and D_1) and near the exit of the Delta (telemetry stations B_7 and C_3). The two release dates are shown as R_1 = 5 December 2006 and R_2 = 17 January 2007. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median. River discharge (solid line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station B_6), 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.

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 Steamboat and Sutter sloughs (for R_1: $\hat{\psi}_{A1} = 0.296$, $\widehat{SE} = 0.062$; for R_2: $\hat{\psi}_{A1} = 0.414$, $\widehat{SE} = 0.059$, Appendix Table 2). For the December release, most fish remaining in Sacramento River encountered the second river junction when the Delta Cross Channel was open ($\hat{\omega}_{open} = 0.861$, $\widehat{SE} = 0.058$), and 39% percent of these fish were entrained into the Delta Cross Channel ($\hat{\psi}_{D2,open} = 0.387$, $\widehat{SE} = 0.087$). Regardless of release group or position of the Delta Cross Channel gate, similar fractions of fish

13

passing junction 2 were entrained into Georgiana Slough (for R_1: $\hat{\psi}_{C2,open} = 0.161$, $\widehat{SE} = 0.066$; $\hat{\psi}_{C2,closed} = 0.200$, $\widehat{SE} = 0.179$; for R_2: $\hat{\psi}_{C2,closed} = 0.150$, $\widehat{SE} = 0.056$). The remaining 45% of fish passing junction 2 when the Delta Cross Channel was open stayed in the Sacramento River ($\hat{\psi}_{B2,open} = 0.452$, $\widehat{SE} = 0.089$), whereas nearly twice that fraction remained in Sacramento River when the Delta Cross Channel was closed (for R_1: $\hat{\psi}_{B2,closed} = 0.800$, $\widehat{SE} = 0.179$; for R_2: $\hat{\psi}_{B2,closed} = 0.850$, $\widehat{SE} = 0.056$).

A substantial proportion of fish migrating past junction 2 entered the interior Delta through the Delta Cross Channel and Georgiana Slough, but the effect of these routes on the population was reduced by the fraction of fish migrating through Sutter and Steamboat sloughs (Figure 1). Thus, accounting for population distribution among all routes, 23.5% were entrained into the Delta Cross Channel ($\hat{\psi}_D$), 11.7% entered Georgiana Slough ($\hat{\psi}_C$), and 35.2% migrated within the Sacramento River ($\hat{\psi}_B$) for the December release when the Delta Cross Channel was open during much of the migration period (Table 1). In contrast, in January when the Delta Cross Channel was closed, 8.8% migrated through Georgiana Slough and 49.8% remained in the Sacramento River (Table 1). Because Steamboat and Sutter sloughs rejoin the Sacramento River upstream of telemetry station B_6 (Figure 1), much of this migration route through the Delta consists of the mainstem Sacramento River. Thus for the December release, 64.8% of fish took migration routes largely consisting of the Sacramento River ($\hat{\psi}_A + \hat{\psi}_B$) 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, with 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) were generally proportional to 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 (station B_2), upstream of the two river junctions. Steamboat and Sutter Slough diverted 33.4% and 37.6% of the mean flow of the Sacramento River during the December and January migration period, accounting for the large

proportion of 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, with flow in the Sacramento River downstream of junction 2 representing 25.6% of its total discharge when the Delta Cross Channel was open (December release) compared to 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. However, for both releases the proportion of fish migrating within the Sacramento River was about 10 percentage points higher than the fraction of flow remaining in the Sacramento River (Figure 4).

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 (R_1) and 17 January 2007 (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	$\hat{S}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval	$\hat{\psi}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval
R_1: December 2006				
A) Steamboat & Sutter S.	0.263 (0.112)	0.102, 0.607	0.296 (0.062)	0.186, 0.426
B) Sacramento R.	0.443 (0.146)	0.222, 0.910	0.352 (0.066)	0.231, 0.487
C) Georgiana S.	0.332 (0.179)	0.087, 0.848	0.117 (0.045)	0.048, 0.223
D) Delta Cross Channel	0.332 (0.152)	0.116, 0.783	0.235 (0.059)	0.133, 0.361
S_{Delta} (All routes)	0.351 (0.101)	0.200, 0.692		
R_2: January 2007				
A) Steamboat & Sutter S.	0.561 (0.092)	0.388, 0.747	0.414 (0.059)	0.303, 0.531
B) Sacramento R.	0.564 (0.086)	0.403, 0.741	0.498 (0.060)	0.383, 0.614
C) Georgiana S.	0.344 (0.200)	0.067, 0.753	0.088 (0.034)	0.036, 0.170
D) Delta Cross Channel	NA		0.000	NA
S_{Delta} (All routes)	0.543 (0.070)	0.416, 0.691		
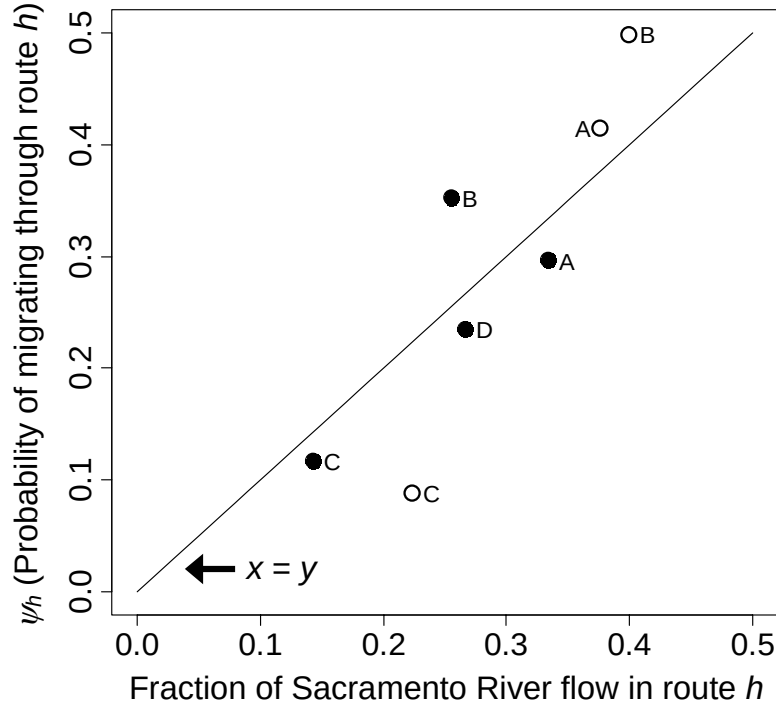
Figure 4.—The probability of migrating through route h (ψ_h) as a function of the proportion of total river flow in route h for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (filled symbols) and 17 January 2007 (open symbols). Data labels A–D represent Steamboat and Sutter sloughs, the Sacramento River, Georgiana Slough, and the Delta Cross Channel, respectively. The reference line shows where the fraction migrating through each route is equal to the proportion of flow in each route.

Relative Contributions to S_{Delta}

Estimates of $\hat{S}_{Delta}$ 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 35% of the population migrated through this route ($\hat{\psi}_B$), representing a relatively small contribution to $\hat{S}_{Delta}$ (Figure 5, Table 1). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{Delta}$ and comprised 65% 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 1). For the January release, 91% of the population ($\hat{\psi}_A + \hat{\psi}_B$) migrated through

16

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 1). In comparison, survival for the interior Delta via Georgiana Slough ($\hat{S}_C$) was lower than the other routes, but this route accounted for only 9% of the population ($\hat{\psi}_C$), having little influence on $\hat{S}_{Delta}$ (Figure 5, Table 1).
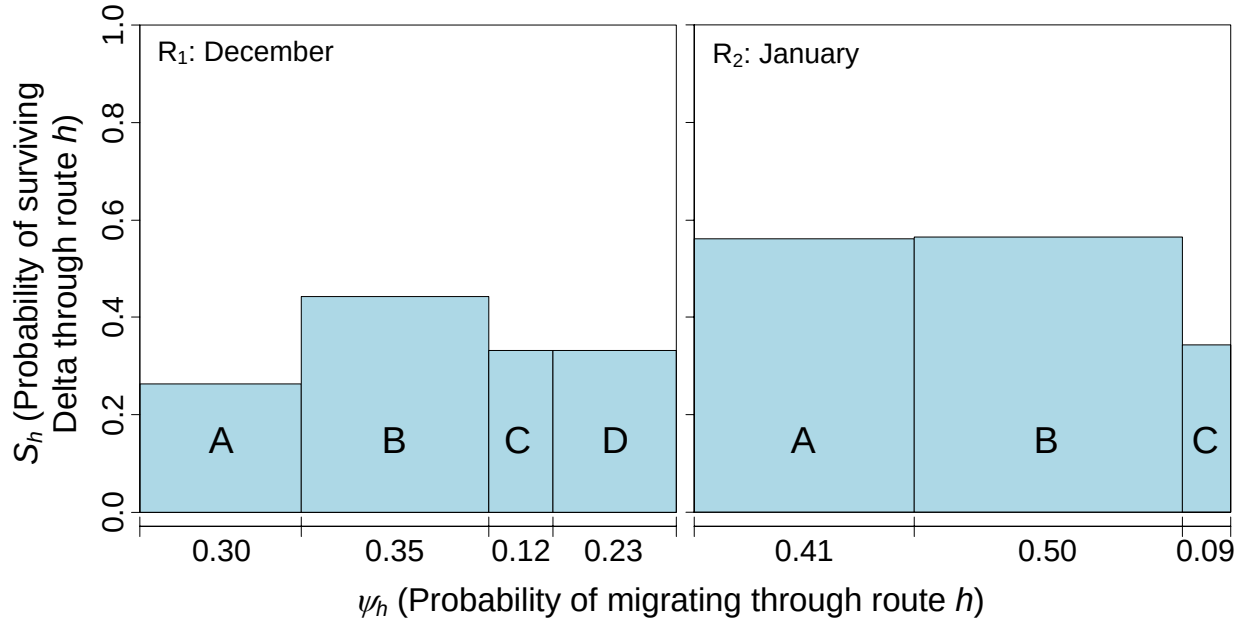
Figure 5.—Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (R_1) and 17 January 2007 (R_2). The width of each bar shows the fraction of fish migrating through each route (ψ_h), and thus, the total area of the bars yields S_{Delta}. Labels A–D represent Steamboat and Sutter sloughs, the Sacramento River, Georgiana Slough, and the Delta Cross Channel, respectively.

The observed difference in $\hat{S}_{Delta}$ between releases can be attributed to 1) a change in the relative contribution of each route-specific survival to $\hat{S}_{Delta}$, 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 ($\hat{S}_B$) during both releases but contributed only 9% for the January release when the Delta Cross Channel was closed ($\hat{\psi}_C + \hat{\psi}_D$), compared to 35% for the December release when the Delta Cross Channel was open (Figure 5, 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, the higher $\hat{S}_{Delta}$ observed for the January release was also a consequence of route-specific survival for the Sacramento River and Sutter and Steamboat sloughs, both of which were higher for the January release compared to 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 migration dispersal through the Delta and survival for given migration routes to understand factors affecting population-level survival through the Delta. Operation of the Delta Cross Channel is a primary water management action thought to affect survival and distribution of juvenile salmon in the Delta (Williams 2006). In our study, closure of the Delta Cross Channel increased population-level survival by reducing the fraction of the population entering the interior Delta and increasing the fraction migrating within the Sacramento River where survival was higher relative to the interior Delta. Closing the Delta Cross Channel increased the relative flow of the Sacramento River which in turn, increased the proportion of fish migrating in the Sacramento River. However, the observed difference in $\hat{S}_{Delta}$ between releases was also influenced by differences in survival within routes, with survival estimates for the January release being higher than for December in both the Sacramento River and Steamboat and Sutter sloughs. 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.

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). In general, similar to our study, these authors showed 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. Specifically, recent analysis has shown that the posterior mean of the ratio of survival for Georgiana Slough releases relative to Sacramento River releases was 0.44 with a 95.1% probability of being less than one, indicating significantly lower survival of Georgiana Slough releases. In our study, an analogous estimate is

$S_{C1}S_{C2}S_{C3} / S_{B5}S_{B6}S_{B7}$ (i.e., survival from C_1 to B_8 relative to B_5 to B_8; Figure 1). The estimate of this ratio was 0.625 ($\widehat{SE} = 0.352$) for the December release and 0.591 ($\widehat{SE} = 0.351$) for the January release. Although the standard errors suggest that these estimates do not differ from one, 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 shown that survival differs among migration routes, the effect of route-specific survival on the population could not be quantified because these studies did not estimate the fraction of the population using each migration route. We build on this research by quantifying the relative contribution of route-specific survival to population-level survival, as measured by the fraction of fish migrating through each route (i.e., migration route probabilities, ψ_h). For example, we showed that closure of the Delta Cross Channel decreased the fraction of fish migrating through the interior Delta, thereby reducing the contribution of this route to population-level survival through the Delta. Furthermore, a substantial fraction of the population migrated through Steamboat and Sutter Sloughs. Thus, this route may either reduce population survival, as we observed in December when survival through this route was lower than all others, or increase population survival, as observed for the January release when Steamboat and Sutter sloughs exhibited similar survival to the Sacramento River.

Steamboat and Sutter sloughs also appear to play a key role in population-level survival by influencing the probability of a fish entering the interior Delta. Fish migrating through Steamboat and Sutter sloughs do not encounter the Delta Cross Channel or Georgiana Slough, which directly reduces the fraction of fish entering the interior Delta. This relation is couched explicitly in our model; the probability of migrating through the interior Delta can be expressed as $\psi_C + \psi_D = (1 - \psi_A)(\psi_{C2} + \psi_{D2})$. Note that the fraction entering the interior Delta ($\psi_C + \psi_D$) decreases as the fraction migrating through Steamboat and Sutter sloughs (ψ_A) increases. 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 Steamboat and Sutter sloughs at the first river junction (J.R. Burau, US Geological Survey, 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 Steamboat and Sutter sloughs. However, whether increasing migration through Steamboat and Sutter sloughs improves population-level survival will depend on the difference in survival between these alternative routes.

In general, migration route probabilities were proportional to the fraction of total river discharge in each migration route, with some deviations for specific routes (e.g., the Sacramento River). We are uncertain whether this pattern will hold over a wider range of conditions, as fish in our study migrated past river junctions over a short time period. Flow distribution among the river channels at each junction is known to vary with the tides on hourly time scales (Blake and Horn 2003). Thus, the migration route probabilities in our study represent the integration over time of individual-specific route entrainment probabilities that likely depend on the flow distribution at the specific time and date when each individual passed the river junctions. In addition, research is beginning to show that juvenile late-fall Chinook salmon preferentially migrate at night through riverine stretches of the Sacramento River (Wilder and Ingram 2006; Burau et al. 2007; Chapman et al. 2007). In our study, for the December and January release respectively, 88% and 94% of fish migrated past the first river junction during night, and 69% and 95% migrated past the second river junction at night. Since fish migrated past the two river junctions over only a 5–7-d period (Figure 3) and predominantly at night, they were likely exposed to a narrow range of hydraulic conditions when passing the two river junctions. We hypothesize that changes in the distribution of average river flow at river junctions will effect coincident changes in average migration route probabilities, but variability in these migration route probabilities will be driven by the interaction between migration behavior and hourly-scale changes in flow distribution at the river junctions. These fine-scale processes are an active area of research in the Delta and should provide new insights into the migration dynamics of juvenile salmon.

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. 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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Appendix

Appendix Table 1.—Counts of detection histories for the full model shown in Figure 2 for a release of $R_1 = 64$ fish on 5 December 2006 and $R_2 = 80$ fish on 17 January 2007. 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), with a "0" indicating a fish was not detected. Since some routes contained fewer telemetry stations than others, the "*" notation acts as a place holder to maintain information about the jth telemetry station in the jth position of the detection history. In the fourth position of the detection history, the history for junction 2, a capital letter indicates a fish passed junction 2 when the Delta Cross Channel was open, and a lower-case letter indicates the Delta Cross Channel was closed when a fish passed junction 2.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
1BA**BBBB	1	1BA**BBBB	4
1BA**BB0B	2	1BA**0BBB	2
1BA**BBB0	2	1BA**00BB	1
1BA**B000	1	1BA**BB0B	4
1BA**0000	10	1BA**0B0B	1
1B0BB0BBB	1	1BA**BBB0	1
1B0BB0B0B	1	1BA**0BB0	2
1B0BBBBB0	1	1BA**BB00	3
1B0BBBB00	4	1BA**B000	1
1B0BBB000	3	1BA**0000	10
1B0BB0000	3	1BBbBBBBB	5
1B0B00000	1	1B0bBBBBB	1
1B0000000	5	1BBbB0BBB	3
100000000	7	10BbB0BBB	1
1B0bBBBBB	2	1BBbB00BB	1
1B0b00000	2	1BBbBBB0B	4
1B0C*C0BB	1	1BB0BBB0B	1
1B0C*C000	2	1BBbBBBB0	1
1B0C*0000	2	1BBbB0BB0	2
1B0c*0000	1	1BBbBBB00	1
1B0DDC00B	1	1BBbB0B00	1
1B0DD000B	1	1BBbBB000	2
1B0DDC0B0	1	1BBbB0000	10
1B0DD00B0	1	1BBb00000	1
1B0DDC000	2	1BB000000	1
1B0DD0000	5	1B0000000	3
1B0D00000	1	100000000	7
		1BBc***BB	1
		1BBc***B0	1
		1BBc***00	4
Total released (R_k)	64		80

Appendix Table 2.—Parameter estimates for the mark-recapture shown in Figure 2 for releases of acoustically tagged late-fall juvenile Chinook salmon made in December, 2006 (R_1) and January, 2007 (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.

Parameter	R_1: December 2006		R_2: January, 2007	
	Estimate ($\widehat{SE}$)	95% Profile likelihood interval	Estimate ($\widehat{SE}$)	95% Profile likelihood interval
S_{A1}	0.389 (0.126)	0.176, 0.645	0.681 (0.093)	0.492, 0.850
S_{B1}	0.891 (0.039)	0.799, 0.951	0.913 (0.032)	0.838, 0.962
S_{B2}	0.947 (0.023)	0.890, 0.981	0.959 (0.024)	0.896, 0.990
S_{B3}	0.947 (0.023)	0.890, 0.981	0.976 (0.025)	0.895, 1.000
S_{B4}	0.833 (0.088)	0.623, 0.956	0.970 (0.030)	0.873, 0.998
S_{B5}	0.830 (0.110)	0.578, 1.000	0.725 (0.085)	0.549, 0.879
S_{B6}	0.750 (0.108)	0.511, 0.915	0.900 (0.059)	0.751, 0.983
S_{B7}	0.952 (0.237)	0.566, 1.000	0.953 (0.077)	0.794, 1.000
S_{C1}	0.648 (0.302)	0.193, 1.000	NA	
$S_{C2}S_{C3}$	0.571 (0.270)	0.166, 1.000	NA	
$S_{C1}S_{C2}S_{C3}$	NA		0.368 (0.213)	0.071, 0.802
S_{D1}	0.917 (0.080)	0.681, 0.995	NA	
S_{D2}	0.707 (0.252)	0.322, 1.000	NA	
ψ_{A1}	0.296 (0.062)	0.186, 0.426	0.414 (0.059)	0.303, 0.531
ψ_{B1}	0.704 (0.062)	0.574, 0.814	0.586 (0.059)	0.469, 0.697
ω_{open}	0.861 (0.058)	0.725 , 0.948	0.000	NA
ω_{closed}	0.139 (0.058)	0.052 , 0.275	1.000	NA
$\psi_{B2,open}$	0.452 (0.089)	0.286 , 0.625	0.000	NA
$\psi_{C2,open}$	0.161 (0.066)	0.061 , 0.315	0.000	NA
$\psi_{D2,open}$	0.387 (0.087)	0.230 , 0.562	0.000	NA
$\psi_{B2,closed}$	0.800 (0.179)	0.372 , 0.987	0.850 (0.056)	0.719, 0.938
$\psi_{C2,closed}$	0.200 (0.179)	0.013 , 0.628	0.150 (0.056)	0.062, 0.281
P_{A1}	1.000	NA	1.000	NA
P_{B2}	1.000	NA	0.986 (0.014)	0.939, 0.999
P_{B3}	1.000	NA	0.975 (0.025)	0.895, 0.999
P_{B4}	1.000	NA	0.970 (0.030)	0.873, 0.998
P_{B5}	1.000	NA	1.000	NA
P_{B6}	0.857 (0.094)	0.621, 0.975	0.641 (0.077)	0.485, 0.779
P_{B7}	1.000	NA	0.941 (0.040)	0.829, 0.990
P_{B8}	0.500 (0.158)	0.218, 0.782	0.655 (0.088)	0.474, 0.810
P_{C1}	1.000	NA	1.000	NA
P_{C2}	0.600 (0.219)	0.199, 0.919	NA	
P_{C3}	1.000	NA	NA	
P_{D1}	1.000	NA	NA	
P_{D2}	1.000	NA	NA	
λ	0.500 (0.158)	0.218, 0.782	0.731 (0.087)	0.544, 0.874