

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}_{Delta} was 0.174 ($\hat{\text{SE}}=0.031$) and for January 2008, \hat{S}_{Delta} was 0.195 ($\hat{\text{SE}}=0.034$), 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 $\leq 35.2\%$ ($\hat{\text{SE}} \leq 0.11$) 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

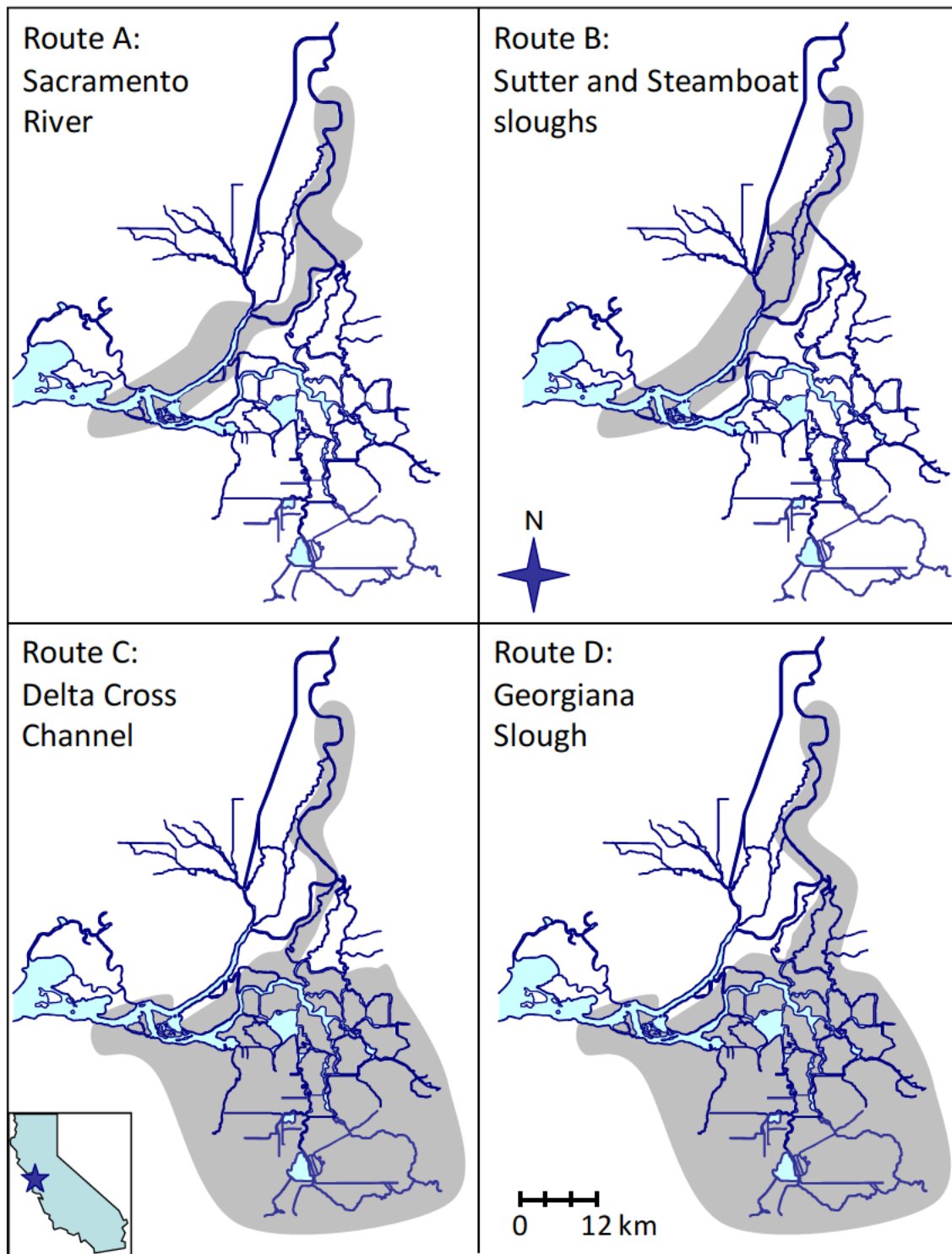


Figure 1.—Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. For routes C and D, the interior Delta is the large shaded region at in southern-most section of the migration route.

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 salmon smolts 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).

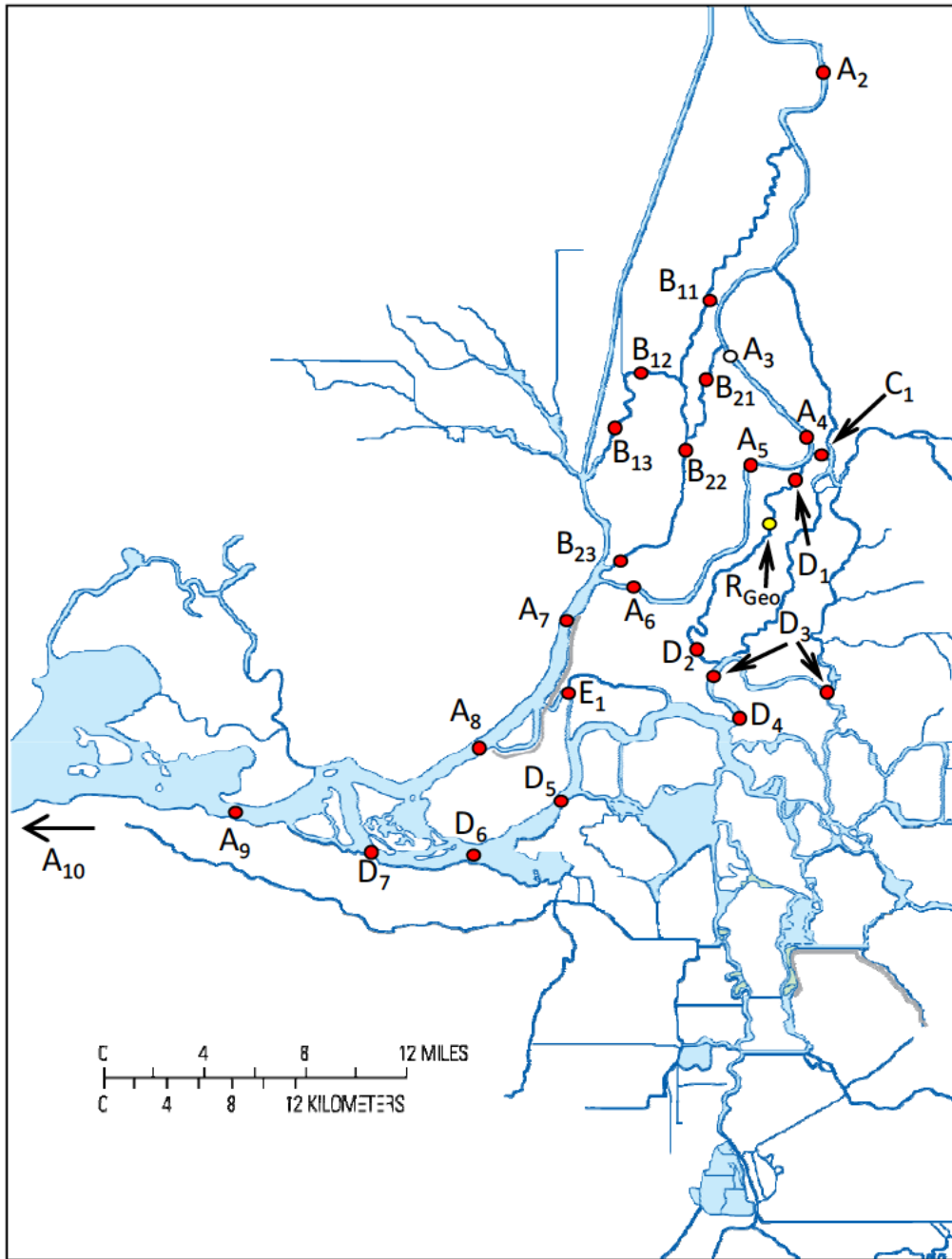


Figure 2.—Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2007/2008. Red-filled circles labeled as h_i show the location of telemetry station i with route h . The Delta extends from station A₂ at Freeport to station A₉ at Chipps Island. The first river junction occurs where Sutter Slough (B₁₁) and Steamboat Slough (B₁₂) diverge from the Sacramento River at location A₃. Location A₃ 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 (C₁) and Georgiana Slough (D₁) diverge from the Sacramento River at station A₄. Station A₁₀ pools all telemetry stations in San Francisco Bay downstream of A₉. The two site labeled D₃ were treated as a single station in the mark-recapture model. The Sacramento release site was 19 river kilometers upriver of station A₂, 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 A₈ and D₇) 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 (A₉), we formed one additional telemetry station by pooling detections from numerous stations downstream of A₉ 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 A₂) or Georgiana slough (about 5 km downstream from D₁; 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 A₇ in the Sacramento River may enter Three Mile

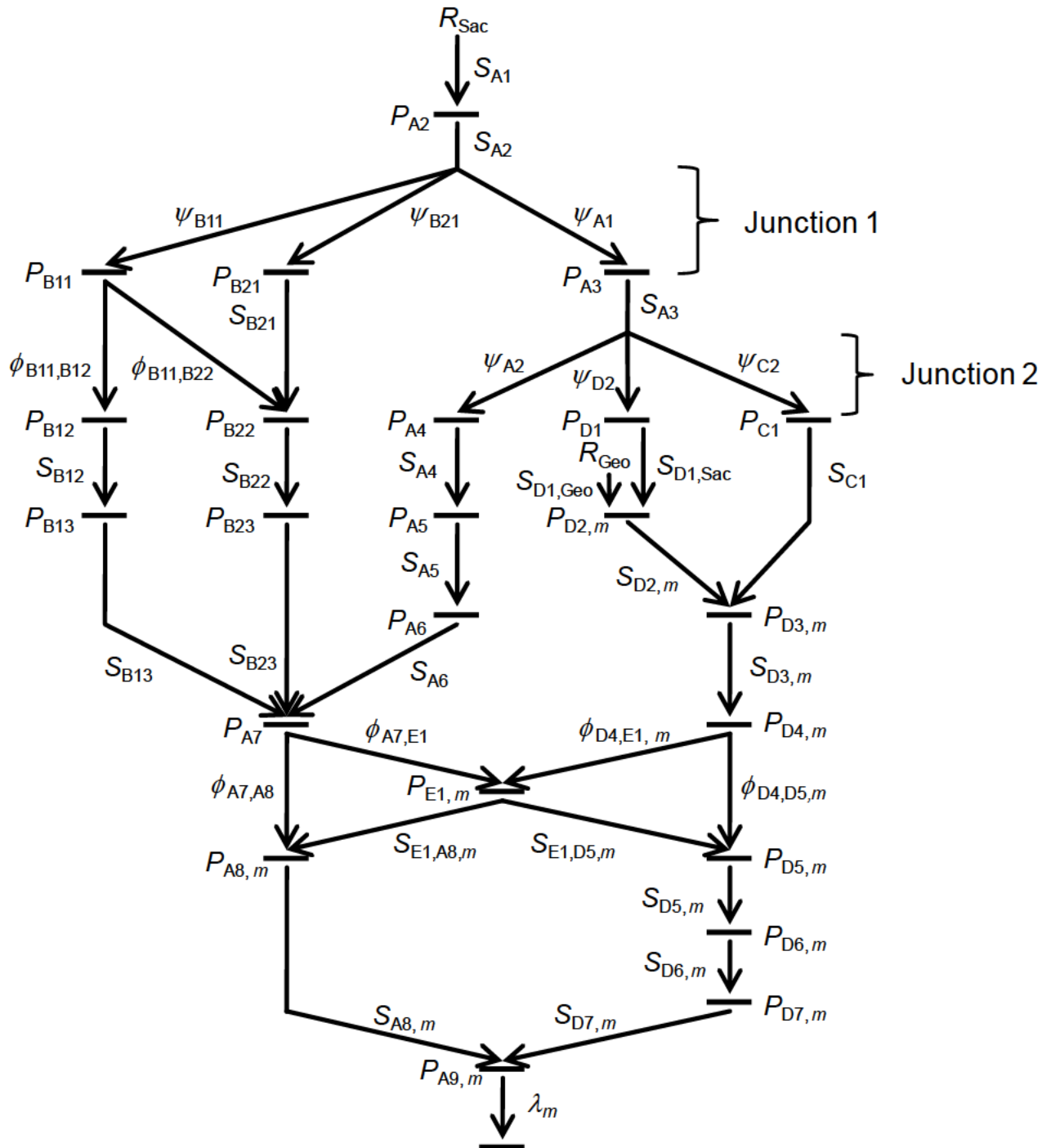


Figure 3.—Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (ψ_{hi}), and joint survival-entrainment ($\phi_{hi,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made December 2007 and January 2008. Release sites are denoted by R_m ($m = \text{Sac}$ (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 ϕ_{A_7,A_8} 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 $\psi_{B_{11}}$ estimates the probability of being entrained into Sutter Slough at station B_{11} and $\psi_{B_{21}}$ 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, $1 - \psi_{B_{11}} - \psi_{B_{21}} = \psi_{A_1}$ 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_{A_2} , ψ_{C_2} , and $1 - \psi_{A_2} - \psi_{C_2} = \psi_{D_2}$ 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_{hi}). However, when telemetry stations are located kilometers downstream of the river junction where fish enter one route or another, then estimates of ψ_{hi} 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, $S_{B11} = \phi_{B11,B12} + \phi_{B11,B22}$, $S_{A7} = \phi_{A7,E1} + \phi_{A7,A8}$, and $S_{D4} = \phi_{D4,E1} + \phi_{D4,D5}$ 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., $S_{D3,m} = S_{D3,Sac}$ or $S_{D3,Geo}$, 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 A₇–A₈ and D₅–D₇), 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 AA0AAAEDDDAA indicates it was released at Sacramento (“A”), detected in the Sacramento River at A₂ (“A”), and not detected in the Sacramento River at A₃ (“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:

$$L_{km}(\underline{\beta} | R_{km}, n_{jkm}) \propto \prod_{j=1}^J \pi_{jkm}^{n_{jkm}}$$

where L_{km} is the likelihood for the k th release group ($k = 1, 2$) at the m th 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 j th detection history in the k th release group at the m th release site, and π_{jkm} is the probability of the j th detection history in the k th release group at the m th release site expressed as a function of the parameters ($\underline{\beta}$). 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 $L_{k,Sac}$ and $L_{k,Geo}$. 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 A₂ (Freeport) to the exit of the Delta at station A₉ (Chipps Island).

Population-level survival through the Delta was estimated from the individual components as:

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

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:

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

$$\psi_B = \psi_{B11} + \psi_{B21} \quad (3)$$

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

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

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, $\psi_{A1}\psi_{C2}$. 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 A₂ and A₉ (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:

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

The bracketed term is the weighted average survival between A₇ (Rio Vista) and A₉ (Chippis Island) with the $\phi_{hi,jk}$ parameters weighting survival of fish that remain in the Sacramento River ($\phi_{A7,A8}S_{A8}$) and survival of fish that finish their migration in the lower San Joaquin after passing through Three Mile Slough ($\phi_{A7,E1}S_{E1,D5}S_{D5}S_{D6}S_{D7}$). 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, $\phi_{A7,E1} \ll \phi_{A7,A8}$ 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:

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

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

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:

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

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

For fish entering Sutter Slough, note that the first bracketed term in S_{B1} accounts for survival of fish taking either Miner Slough ($S_{B12}S_{B13}$) or Steamboat Slough ($S_{B22}S_{B23}$) 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:

$$\theta_h = \frac{S_h}{S_A} \quad h \neq A$$

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 A₄. 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:

$$s_{hi} = \frac{S_{hi}}{x_{hi}}$$

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 B₁₁, A₇, and D₄), 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 D₄ and D₅). 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 ft³/s and 14,000 ft³/s. The central 80% of this release group passed junction 2 (Stations A₄, C₁, and D₁; 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 ft³/s to 14,000 ft³/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 ft³/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).

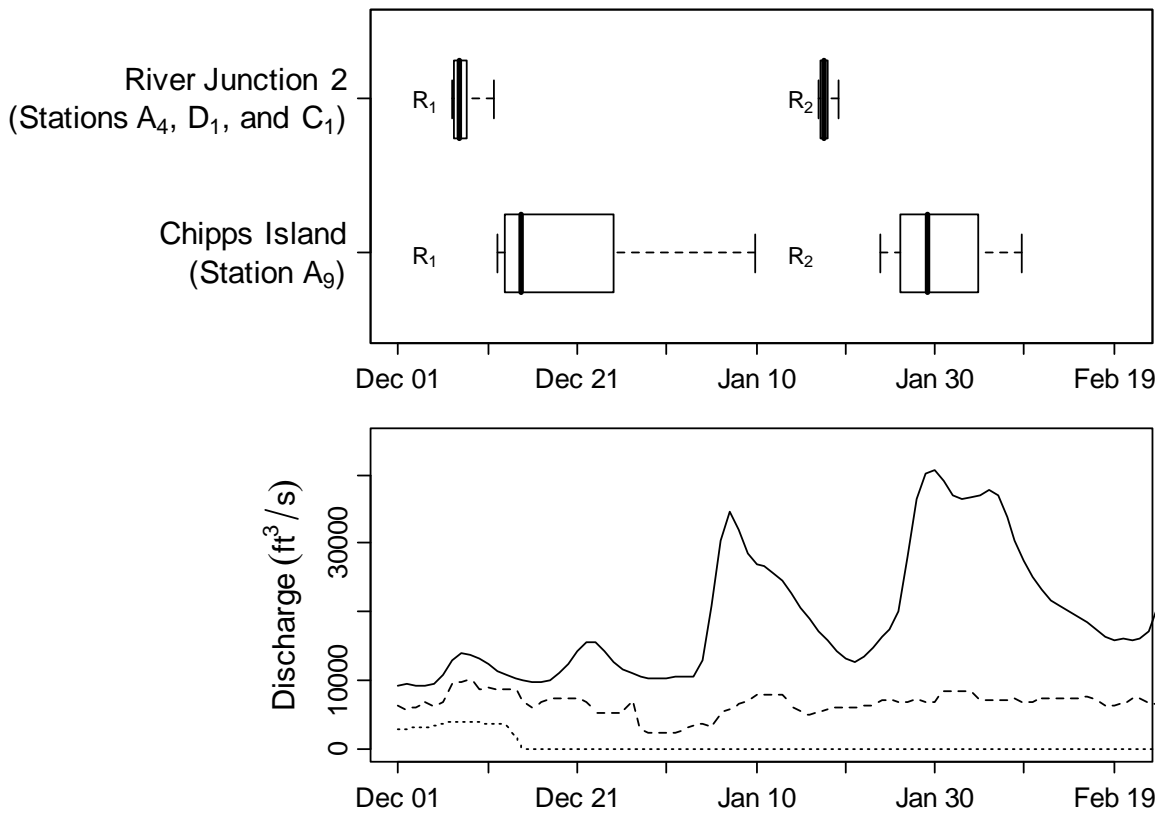


Figure 4.—River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2007/2008. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento 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 R₁ = 4 December 2006 for a release size of 149 tagged fish and R₂ = 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 (SE)	95% Profile Likelihood Interval	$\hat{\psi}_h$ (SE)	95% Profile Likelihood Interval
<i>R</i> 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		
<i>R</i> 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		

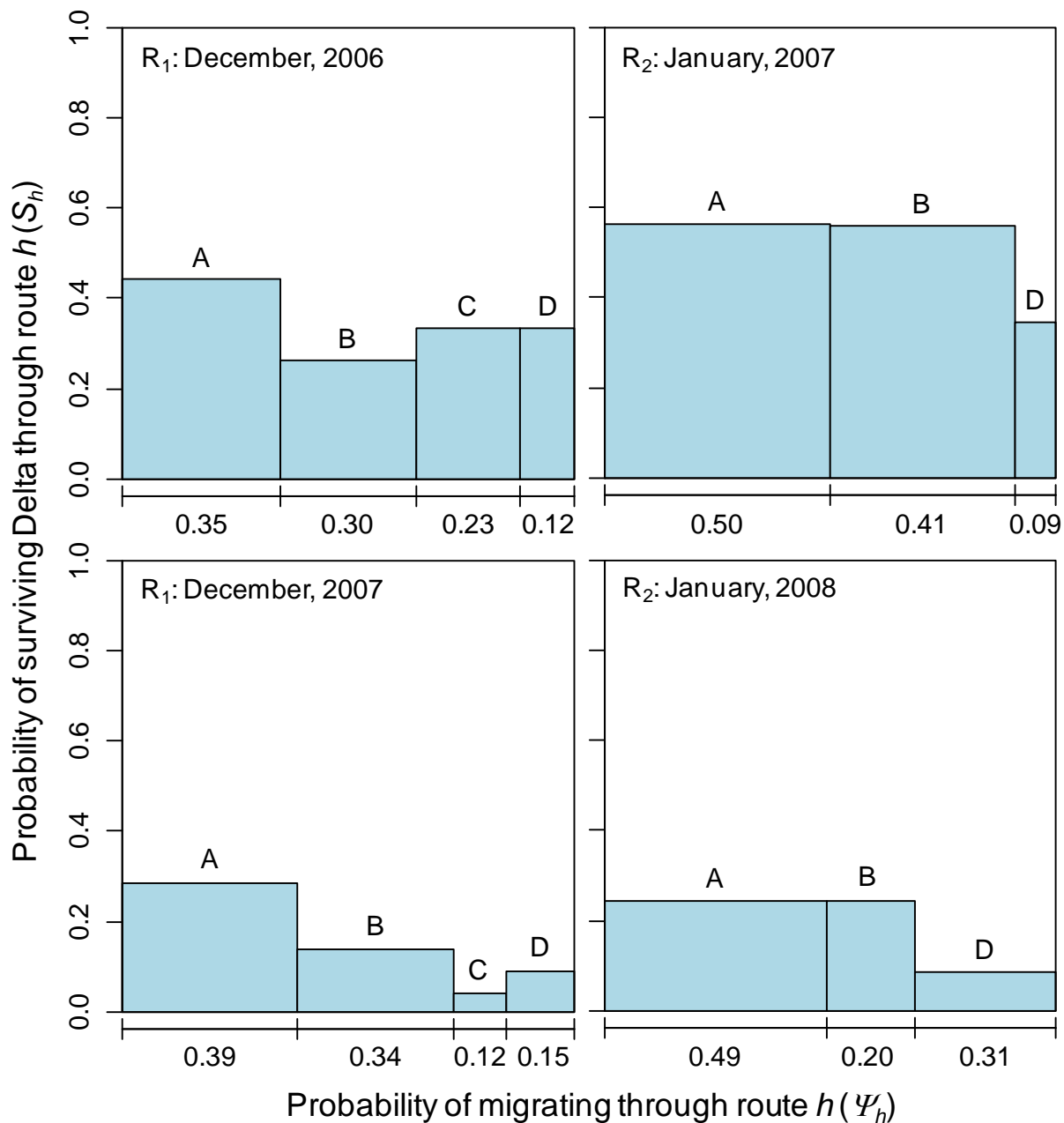


Figure 5.—Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon emigrating from the Sacramento River. The width of each bar shows the fraction of fish migrating through each route (ψ_h), and 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.

Migration route	<u>R₁: December 2007</u>		<u>R₂: January 2008</u>	
	$\hat{\theta}_h$ (SE)	95% Profile Likelihood Interval	$\hat{\theta}_h$ (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 ($\hat{\psi}_B$, 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 $\hat{\psi}_B$ between releases occurred at the entrance to Sutter Slough (Table 2). In December, twice the fraction of fish entered Sutter Slough ($\hat{\psi}_{B11} = 0.230$) as compared to Steamboat Slough ($\hat{\psi}_{B21} = 0.115$), 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.

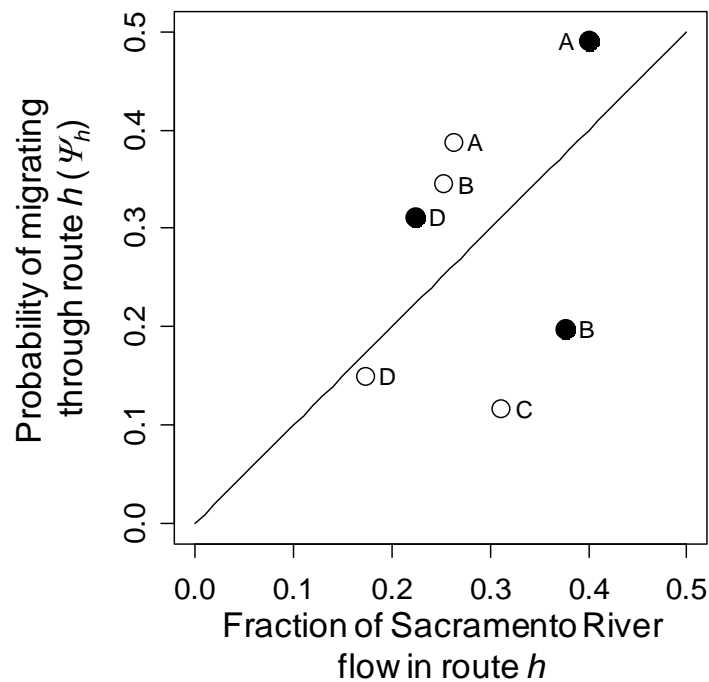


Figure 6.—The probability of migrating through route h (ψ_h) as a function of the proportion of total river flow in route h for tagged late-fall juvenile Chinook salmon released in December 2007 (open circles) and January 2008 (filled circles). Data labels A–D represent the Sacramento River, Steamboat 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}_{Delta} for both releases in 2008 (Table 2) was lower than in 2007; \hat{S}_{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}_{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., = 0.867¹⁰ = 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 B₁₃, B₂₃, and A₆ (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 $\geq 0.96 \text{ km}^{-1}$. 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 $< 0.96 \text{ km}^{-1}$. 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

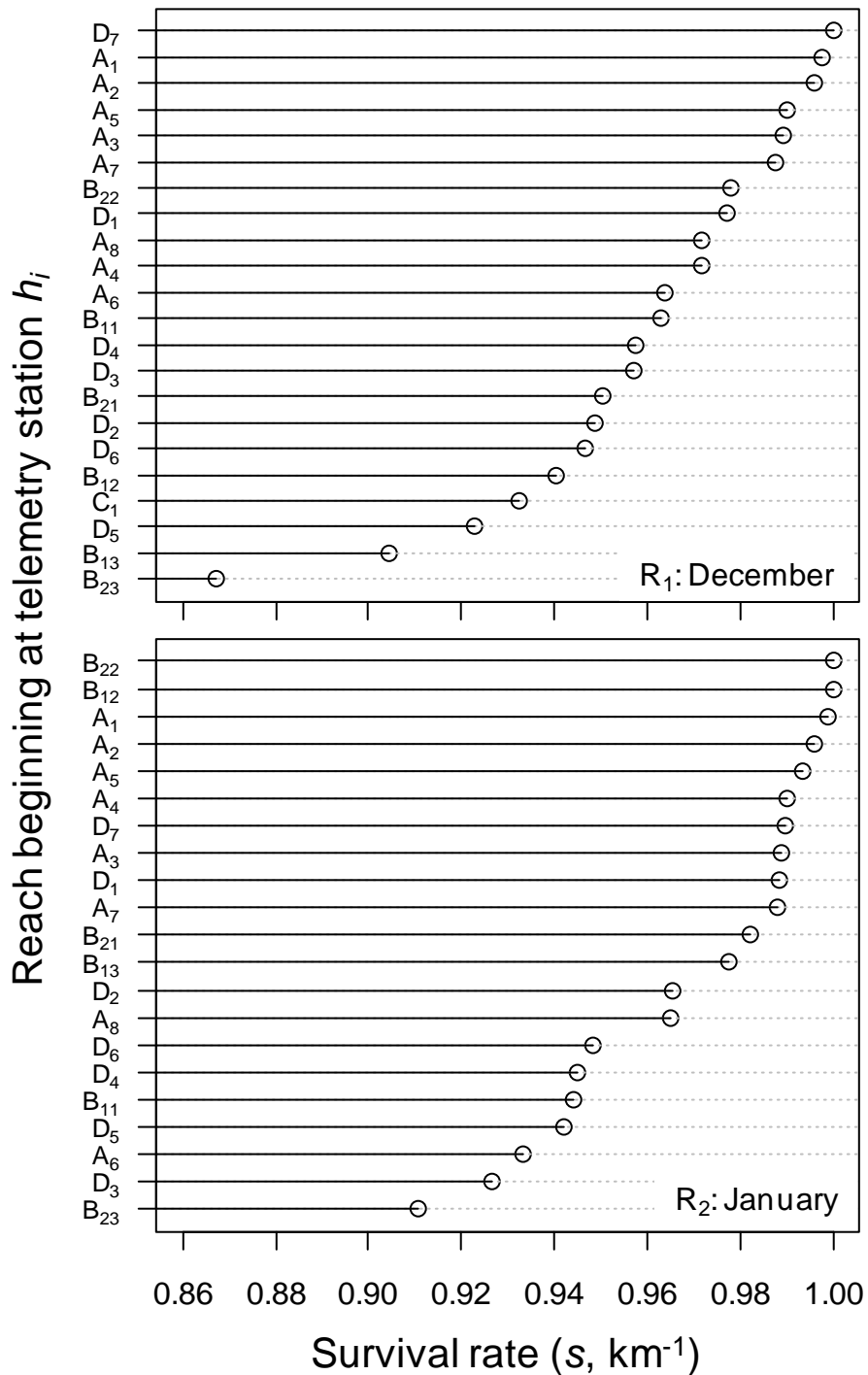


Figure 7.—Reach-specific survival rates plotted in ascending order for tagged late fall Chinook salmon released in December 2007 (top) and January 2008 (bottom). Survival rates scale survival probabilities (S_{hi} , Appendix Table 1.3) to the length of each reach from telemetry station h_i to the next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

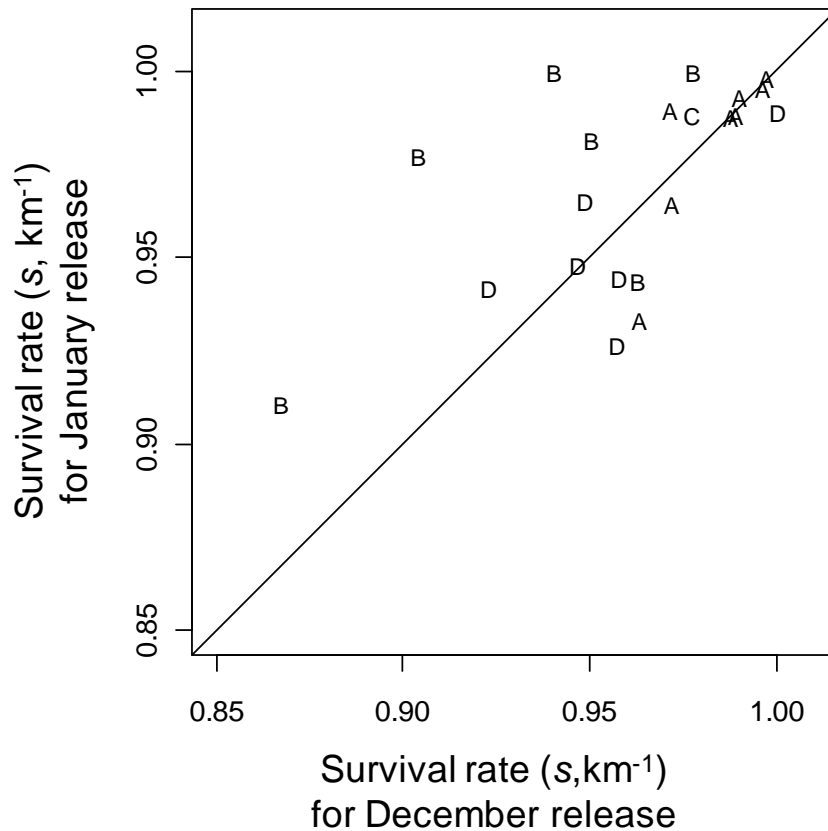


Figure 8.—Reach-specific survival rates for the December 2007 release compared to the January 2008 release for acoustically tagged late fall Chinook salmon migrating through the Sacramento-San Joaquin River Delta. The reference line shows where survival rates are equal between releases. Letters correspond 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 : $\hat{S}_{D_4} = 0.484$, $\overline{SE} = 0.071$; for R_2 : $\hat{S}_{D_4} = 0.395$, $\overline{SE} = 0.080$; 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_{D_4} . 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), $\hat{\phi}_{B_{11},B_{22}}$ was about twice that of $\hat{\phi}_{B_{11},B_{12}}$ 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 : $\hat{\phi}_{A_7,A_8} = 0.837$, $\overline{SE} = 0.074$; for R_2 : $\hat{\phi}_{A_7,A_8} = 0.781$, $\overline{SE} = 0.070$) compared to fish moving from A_7 to E_1 (for R_1 : $\hat{\phi}_{A_7,E_1} = 0.049$, $\overline{SE} = 0.034$; for R_2 : $\hat{\phi}_{A_7,E_1} = 0.109$, $\overline{SE} = 0.046$). 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, $\hat{\phi}_{D_4,E_1} = 0.140$ ($\overline{SE} = 0.049$) and $\hat{\phi}_{D_4,D_5} = 0.351$ ($\overline{SE} = 0.070$), whereas for the second release $\hat{\phi}_{D_4,E_1} = 0.041$ ($\overline{SE} = 0.023$) and $\hat{\phi}_{D_4,D_5} = 0.354$ ($\overline{SE} = 0.079$). 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}_{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}_{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}_{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_{AI} , 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 in Table 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 B₁₃, B₂₃, and A₆ 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.

<u>R_1: December 2006</u>		<u>R_2: January 2007</u>	
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	5
0 0 0 D D 0 0 0 0 0 0 0 0 0	5	0 0 0 D D 0 0 0 0 0 0 0 0 0	4
0 0 0 D D D 0 0 0 0 0 0 0 0 0	7	0 0 0 D D D 0 0 0 0 0 0 0 0 0	21
0 0 0 D D D D 0 0 0 0 0 0 0 0 0	20	0 0 0 D D D D 0 0 0 0 0 0 0 0 0	32
0 0 0 D D D D D 0 0 0 0 0 0 0 0 0	6	0 0 0 D D D D D 0 0 0 0 0 0 0 0 0	4
0 0 0 D D D D E 0 0 0 0 0 0 0 0 0	3	0 0 0 D D D D E 0 0 0 0 0 0 0 0 0	1
0 0 0 D D D D D 0 D 0 0 0 0 0 0 0 0 0	2	0 0 0 D D D D 0 D 0 0 0 0 0 0 0 0 0	1
0 0 0 D D D D D 0 D D A 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D 0 D 0 0 0 0 0 0 0 0 0	2
0 0 0 D D D D E A 0 0 A A 0 0 0 0 0 0 0 0 0	2	0 0 0 D D D D 0 0 D D 0 0 0 0 0 0 0 0 0	1
0 0 0 D D D D D 0 0 D A A 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D 0 0 0 0 0 A 0 0 0 0 0 0 0 0 0	1
0 0 0 D D D D D 0 D D A A 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D E A 0 0 0 A 0 0 0 0 0 0 0 0 0	1
A 0	8	0 0 0 D D D D D 0 D D 0 A 0 0 0 0 0 0 0 0 0 0 0	1
A A 0	18	0 0 0 D D D D 0 0 0 0 0 A A 0 0 0 0 0 0 0 0 0 0 0	1
A 0 B 1 0	1	0 0 0 D D D D D 0 0 0 A A 0 0 0 0 0 0 0 0 0 0 0	1
A A B 1 0	8	0 0 0 D D D D E A 0 0 A A 0 0 0 0 0 0 0 0 0 0 0	1
A A B 2 0	3	0 0 0 D D D D D 0 D 0 A A 0 0 0 0 0 0 0 0 0 0 0	2
A A 0 A 0	7	0 0 0 D D D 0 D 0 0 D A A 0 0 0 0 0 0 0 0 0 0 0	1
A A B 1 B 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	4	0 0 0 D D D D D 0 0 D A A 0 0 0 0 0 0 0 0 0 0 0	1
A A B 1 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1	A 0	6
A 0 B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1	A A 0	16
A A B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2	A A B 1 0	4
A 0 0 C 0	1	A A B 2 0	1
A A 0 C 0	9	A A 0 A 0	3
A A 0 D 0	6	A 0 0 D 0	2
A 0 0 A A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1	A A 0 D 0	4
A A 0 A A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	5	A 0 0 A A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1
A A B 1 B 1 B 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	7	A A 0 A A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	6
A A B 1 B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	4	A 0 B 1 B 1 B 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1
A A B 2 B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2	A 0 B 2 B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1
A A 0 D D 0	1	A A B 2 B 2 B 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	3
A A 0 0 A A 0	1	A A 0 D D 0	3
A A 0 A A A 0	4	A A 0 A A A 0	10
A A 0 D D D 0	1	A 0 0 D D D 0	1

Appendix Table 1.1.—Continued.

AA0 A A 0A000000	1	AA0 D D D0000000	2
AA B1 B2 B2 0A000000	1	AA B1 B2 B2 0A000000	1
AA B2 B2 B2 0A000000	1	AA B2 B2 B2 0A000000	1
AA0 A A A A000000	2	A00 A A A A000000	1
AA0 C 0 DD000000	3	AA0 A A A A000000	2
AA0 D D DD000000	3	A00 D D DD000000	4
AA B2 B2 B2 00A00000	1	AA0 D D DD000000	12
AA0 A A 0AA00000	1	AA B1 B1 B1 00A00000	1
AA B1 B1 B1 0A A00000	1	A0 B1 B2 B2 00A00000	1
AA B2 B2 B2 0A A00000	1	AA B2 B2 B2 00A00000	1
A00 A A A A A00000	1	AA0 A A A0A00000	2
AA0 A A A A A00000	9	AA0 A A 0A A00000	1
AA0 D D DDD00000	1	AA B1 B1 B1 0A A00000	2
AA0 D D DDE00000	1	AA B2 B2 B2 0A A00000	3
AA0 D D DD00D000	1	A00 A A A A A00000	1
AA0 A A 00A000A0	1	AA0 A A A A A00000	5
AA B1 B2 B2 0A A000A0	1	AA0 D D DDD00000	2
AA B2 B2 B2 0A A000A0	1	AA0 A A A A E00000	2
AA0 A A A A A000A0	2	AA0 A A 0A E0D000	1
AA B1 0 B1 00EDDDA0	1	AA0 A A A A0000A0	1
AA0 0 A 0A00000A	1	AA0 A A A A A000A0	3
AA0 D D DDD0DD0A	2	AA0 A A A A E0D0A0	1
AA0 A A A A EDDDD0A	1	AA0 D D DDD0DDA0	1
AA0 A A A A0000AA	1	AA0 A A 0A A0000A	1
AA B2 B2 B2 00A000AA	1	A00 A A 0A E0D00A	1
AA0 A A A0A000AA	2	AA0 D D DD0000AA	1
AA0 A A 0AA000AA	1	AA0 A A A0A000AA	1
AA B1 B1 B1 0A A000AA	1	AA0 A A 0A A000AA	3
AA B2 B2 B2 0A A000AA	2	A0 B2 B2 B2 0A A000AA	1
AA0 A A A A A000AA	5	AA B2 B2 B2 0A A000AA	2
AA0 C 0 DDEA00AA	1	A00 A A A A A000AA	1
AA0 D D DDD00DAA	1	AA0 A A A A A000AA	5
AA0 D D DDD0DDAA	1	AA0 D D DD000DAA	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.

<i>R</i> ₁ : December 2007		<i>R</i> 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.

Parameter	R_1 : December 2007		R_2 : January 2008	
	Estimate (SE)	95% Profile likelihood interval	Estimate (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.

$\phi_{B11,B12}$	0.482 (0.096)	0.305, 0.674	0.400 (0.155)	0.146, 0.700
$\phi_{B11,B22}$	0.233 (0.077)	0.108, 0.403	0.200 (0.127)	0.036, 0.499
$\phi_{A7,A8}$	0.837 (0.074)	0.679, 0.978	0.781 (0.07)	0.634, 0.914
$\phi_{A7,E1}$	0.049 (0.034)	0.008, 0.143	0.109 (0.046)	0.040, 0.220
$\phi_{D4,D5}$	0.351 (0.070)	0.225, 0.497	0.354 (0.079)	0.225, 0.564
$\phi_{D4,E1}$	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
$P_{A8,Sac}$	0.905 (0.064)	0.734, 0.983	0.950 (0.049)	0.798, 0.997
$P_{A8,Geo}$	1.000	NA	0.950 (0.049)	0.798, 0.997
$P_{A9,Sac}$	0.812 (0.084)	0.618, 0.937	0.846 (0.071)	0.678, 0.949
$P_{A9,Geo}$	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} .

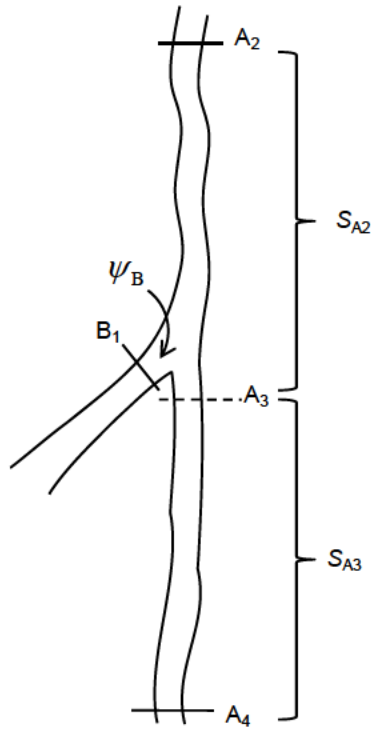
To illustrate the potential bias that might be incurred, we first simplified the problem by assuming a two-branch junction (Appendix Figure 2.1). We were interested not only in bias in ψ_B , but also in bias that might occur in the product $S_{A2}S_{A3}$. This product appears in equations for route specific 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 :

$$\phi_{A2, B1} = S_{A2}\psi_B \quad (\text{A1})$$

$$\phi_{A2, A4} = S_{A2}S_{A3}(1-\psi_B) \quad (\text{A2})$$

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:

$$S_{\text{total}} = \phi_{A2, B1} + \phi_{A2, A4} \quad (\text{A3})$$



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 $1 - \psi_B$.

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 :

$$\tilde{S}_{A2} = \frac{\psi_B - \sqrt{\psi_B^2 - 4S_{\text{total}}(\psi_B - 1)}}{2(\psi_B - 1)} \quad (\text{A4})$$

$$\text{and } \tilde{\psi}_B = \frac{\phi_{A2, B1}}{\tilde{S}_{A2}} \quad (\text{A5})$$

Here, \tilde{S}_{A2} and $\tilde{\psi}_B$ 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 $\phi_{A2, B1}$ 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.

Release	True values				Estimates when assuming $S_{A2} = S_{A3}$		Bias	
	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