

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

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

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

salmon is therefore critical to devising effective recovery strategies for these populations.

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

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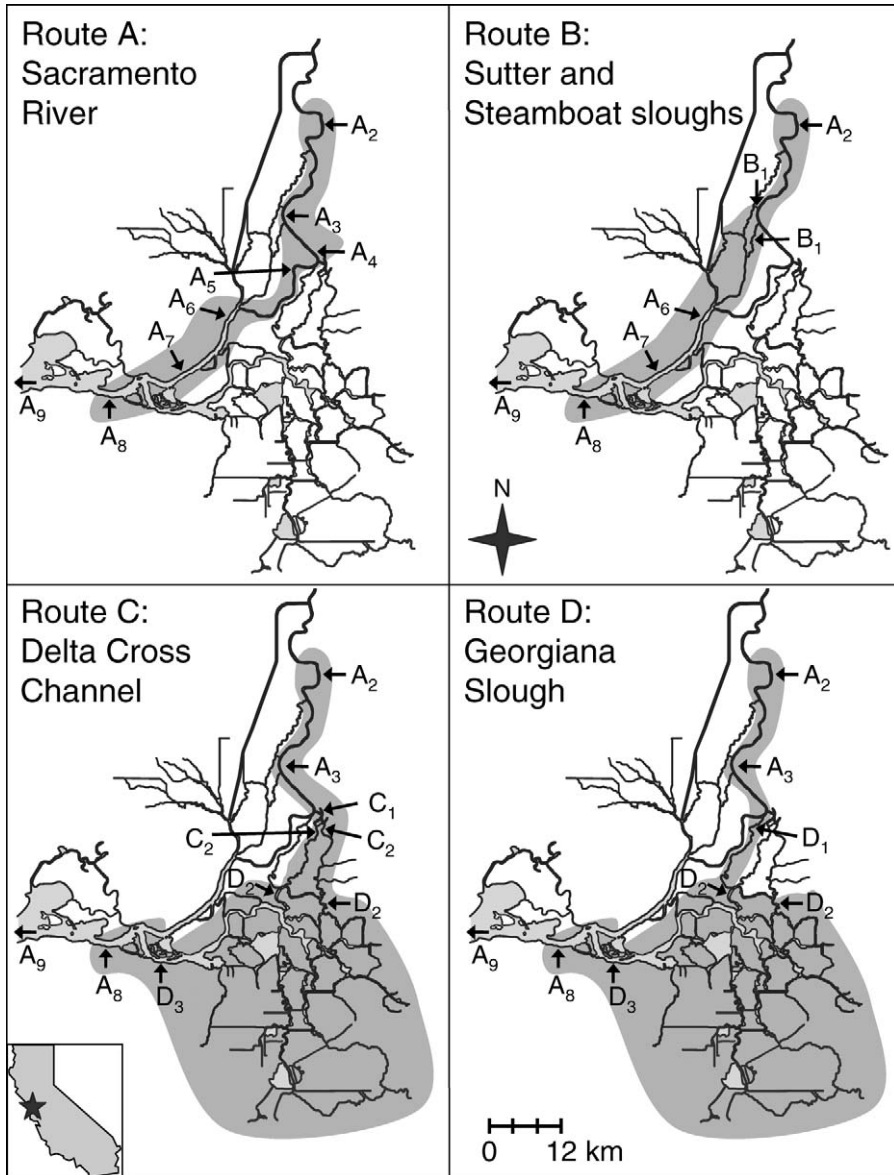


FIGURE 1.—Maps of the Sacramento–San Joaquin River Delta, with shaded regions showing the river reaches that comprise four different migration routes. Arrows show the locations of the telemetry stations specific to each route. The delta extends from station A<sub>2</sub> at Freeport to station A<sub>8</sub> at Chipps Island. The first river junction occurs where Sutter and Steamboat sloughs (B<sub>1</sub>) diverge from the Sacramento River at station A<sub>3</sub>. The second junction occurs where the Delta Cross Channel (C<sub>1</sub>) and Georgiana Slough (D<sub>1</sub>) diverge from the Sacramento River at station A<sub>4</sub>. For routes C and D, the interior delta is the large shaded region to the south of station D<sub>2</sub>. Telemetry stations with the same label (B<sub>1</sub>, C<sub>2</sub>, and D<sub>2</sub>) were pooled as one station in the mark–recapture model. Station A<sub>3</sub> was not operational during the first release in December 2006. Station A<sub>9</sub> pools all of the telemetry stations in San Francisco Bay downstream of A<sub>8</sub>. The release site (rkm 92) was 19 rkm upriver of station A<sub>2</sub> (rkm 73).

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

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the delta. Inflow into the

delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the delta, water distribution is affected by two water pumping projects in the southern delta (the State Water Project and Central Valley Project). These

projects pump water from the delta for agricultural and municipal uses, and can export up to 50% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior delta (see  $C_1$  in route C, Figure 1). In addition to these human influences on water flow through the delta, natural processes include seasonal rainfall and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and biweekly time scales.

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

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

level approach that quantifies dispersal of the population among migration routes and that measures survival within these routes to better understand the influence of management actions on population-level survival.

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

## Methods

### *Telemetry system*

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

Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 1). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco, Ltd.; Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. Since the Sacramento River is the primary migration route, the  $i$ th telemetry station within this route was denoted

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

#### *Fish tagging and release*

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (rkm 431). For the first release in December, we used a 1.44-g tag (Vemco, Ltd.; Model V7-1 L-R64K, 40-d expected battery life), and for the second release in January we used a 1.58-g tag (Vemco, Ltd.; Model V7-2 L-R64K-2, 95-d expected battery life). Except for a minimum size criterion of 140-mm fork length (FL), fish were randomly selected for tagging, resulting in a mean FL of 164.6 mm (SD = 10.9) and mean weight of 53.5 g (SD = 12.6). The tag weight represented 2.7% of the mean fish weight

(range = 1.3–3.8%) for the December release and 3.0% (range = 1.9–4.9%) for the January release. Although recommendations for maximum tag-to-body weight ratios have varied (Jepsen et al. 2004), we followed Adams et al. (1998) guidance for a maximum tag-to-body weight ratio of 5%. Fish were fasted for 24 h prior to surgery to ensure they were in a postabsorptive state. To surgically implant transmitters, fish were anesthetized in 90 mg/L tricaine methanesulfonate (MS-222) until they lost equilibrium. A fish was then placed in a light anesthetic bath (30 mg/L MS-222), ventral side up, and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4–0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for 7 d prior to release. All fish survived the recovery period. We observed no aberrant physiological or behavioral effects of tagging, based on laboratory studies examining growth, wound healing, and tag retention of late-fall Chinook salmon (A. Ammann, unpublished data).

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

#### *Model development*

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

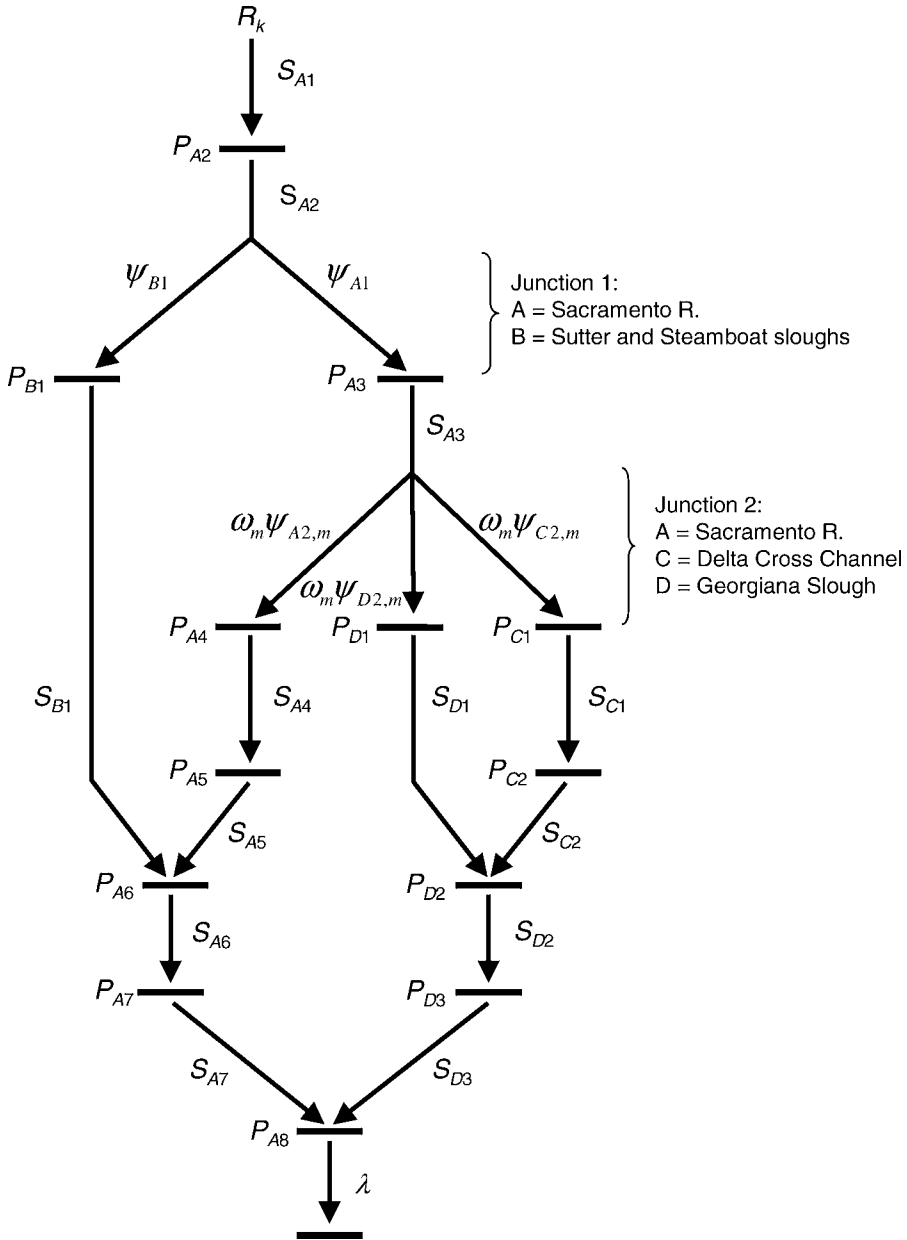


FIGURE 2.—Schematic of the mark–recapture model used to estimate survival ( $S_{hi}$ ), detection ( $P_{hi}$ ), and route entrainment ( $\psi_{hi}$ ) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made on 5 December 2006 and 17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

of fish passing junction 2 when the Delta Cross Channel was open. This model can be classified as a generalization of the standard Cormack–Jolly–Seber (CJS) mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) and a special case of a multistate mark–recapture model where the route entrainment probabilities represent a constrained matrix of state

transition probabilities (Lebreton and Pradel 2002; Williams et al. 2002). Statistical assumptions associated with a model of this structure are detailed in Burnham et al. (1987) and Skalski et al. (2002).

The first river junction was modeled as a two-branch junction where detections at the entrance to either Sutter or Steamboat Slough (station B<sub>1</sub>; Figure 1) were

pooled to estimate a single route entrainment probability. Thus, the parameter  $\psi_{B1}$  estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Figure 2). Conversely,

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

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

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

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

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

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

#### Parameter estimation

Prior to parameter estimation, the records of tag detections were processed to eliminate false-positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False-positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given

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

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

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

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

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

and being detected at  $A_2$  ( $P_{A_2}$ ); surviving the second reach ( $S_{A_2}$ ), remaining in the Sacramento River at junction 1 ( $\psi_{A_1}$ ), and not being detected at  $A_3$  ( $1 - P_{A_3}$ ); and surviving the third reach ( $S_{A_3}$ ), remaining in the Sacramento River at junction 2 ( $\psi_{A_2,open}$ ) when the Delta Cross Channel was open ( $\omega_{open}$ ), and surviving and being detected at all remaining stations in the Sacramento River (Figure 2).

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

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

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

Parameters were estimated separately for each release, but the model for each release was reduced from the full model because not all parameters could be estimated from the tag detection data. For the first release in December,  $P_{A_3}$  equaled 0 because station  $A_3$  was not operational, rendering limited ability to uniquely estimate the parameters  $S_{A_2}$ ,  $\psi_{B1}$ , and  $S_{A_3}$ . However,  $S_{A_2}$  and  $\psi_{B1}$  can be estimated under the assumption that  $S_{A_2}$  equals  $S_{A_3}$ , which was supported by the similarity of  $S_{A_2}$  and  $S_{A_3}$  measured during the second release (for  $R_2$ :  $\hat{S}_{A_2} = 0.959$ ,  $SE = 0.024$ ;  $\hat{S}_{A_3} = 0.976$ ,  $SE = 0.025$ ). The Delta Cross Channel gate was closed for the second release, so  $\omega_{open}$  and  $\psi_{C2}$  were set to zero, which eliminated  $P_{C1}$ ,  $S_{C1}$ ,  $P_{C2}$ , and  $S_{C2}$  from the model. For both releases, a number of detection probabilities were set to 1 because of perfect detection data. Last, due to low detection frequencies in the interior delta, the parameters  $S_{D1}$  and  $S_{D2}$  could not be estimated for the first release, but the product  $S_{D1}S_{D2}$  was estimable as a single parameter. Likewise, for the second release only the product  $S_{D1}S_{D2}S_{D3}$  was estimable as a single parameter.

*Survival through the delta.*—Our model estimates

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

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

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

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

$$\psi_A = \psi_{A1}\psi_{A2} \tag{2}$$

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

$$\psi_C = \psi_{A1}\psi_{C2} \tag{4}$$

$$\psi_D = \psi_{A1}\psi_{D2} \tag{5}$$

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  $\psi_{A1}$ , after which it enters the Delta Cross Channel at the second river junction with probability  $\psi_{C2}$ . Thus, the probability of a fish migrating through the delta via the Delta Cross Channel ( $\psi_C$ ) is the product of these route entrainment probabilities,  $\psi_{A1}\psi_{C2}$ . For release 1, when the Delta Cross Channel was both open and closed,  $\psi_{h2} = \omega_{open}\psi_{h2,open} + (1 - \omega_{open})\psi_{h2,closed}$ .

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

$$S_A = S_{A2}S_{A3}S_{A4}S_{A5}S_{A6}S_{A7} \tag{6}$$

$$S_B = S_{A2}S_{B1}S_{A6}S_{A7} \tag{7}$$

$$S_C = S_{A2}S_{A3}S_{C1}S_{C2}S_{D2}S_{D3} \tag{8}$$

and

$$S_D = S_{A_2} S_{A_3} S_{D_1} S_{D_2} S_{D_3}. \quad (9)$$

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

## Results

### *River Conditions and Migration Timing*

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

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

19.1 d;  $n = 5$ ). For the January release, travel times were similar for fish migrating through the Sacramento River (median = 18.1 d; interquartile range = 13.2–23.9 d;  $n = 19$ ) and Sutter and Steamboat sloughs (median = 17.8 d; interquartile range = 12.7–27.3 d;  $n = 17$ ). We obtained travel times through the interior delta for only one fish in the January release, which took 33.9 d to travel from release to the lower delta.

### *Migration Routing*

As juvenile salmon migrated past the first river junction, a large proportion of both release-groups left the Sacramento River and migrated through Sutter and Steamboat sloughs (for  $R_1$ :  $\hat{\psi}_{B_1} = 0.296$ ; for  $R_2$ :  $\hat{\psi}_{B_1} = 0.414$ ). For the December release, most fish remaining in Sacramento River encountered the second river junction when the Delta Cross Channel was open ( $\hat{\omega}_{\text{open}} = 0.861$ ; SE = 0.058), and 39% percent of these fish were entrained into the Delta Cross Channel ( $\hat{\psi}_{C_2, \text{open}} = 0.387$ ; SE = 0.087). Regardless of release-group or position of the Delta Cross Channel gate, similar fractions of fish passing junction 2 were entrained into Georgiana Slough (for  $R_1$ :  $\hat{\psi}_{D_2, \text{open}} = 0.161$ , SE = 0.066;  $\hat{\psi}_{D_2, \text{closed}} = 0.200$ , SE = 0.179; for  $R_2$ :  $\hat{\psi}_{D_2, \text{closed}} = 0.150$ , SE = 0.056). The remaining 45% of fish passing junction 2 when the Delta Cross Channel was open stayed in the Sacramento River ( $\hat{\psi}_{A_2, \text{open}} = 0.452$ ; SE = 0.089), whereas nearly twice that fraction remained in Sacramento River when the Delta Cross Channel was closed (for  $R_1$ :  $\hat{\psi}_{A_2, \text{closed}} = 0.800$ , SE = 0.179; for  $R_2$ :  $\hat{\psi}_{A_2, \text{closed}} = 0.850$ , SE = 0.056).

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



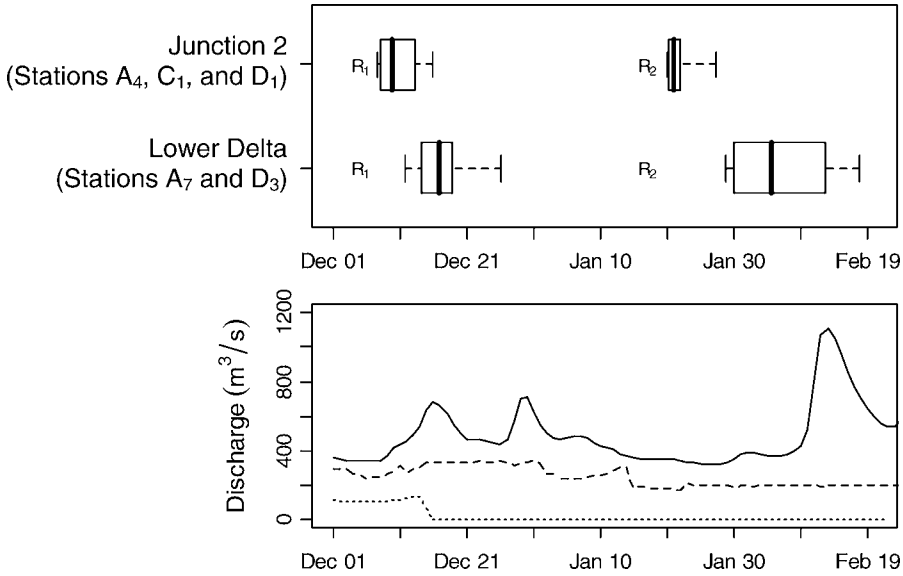


FIGURE 3.—In the upper panel are box plots showing the distribution of arrival dates at junction 2 on the Sacramento River and near the exit of the delta. The two release dates shown are 5 December 2006 ( $R_1$ ; 64 tagged fish) and 17 January 2007 ( $R_2$ ; 80 fish). The whiskers represent the 10th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

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

We found that migration route probabilities ( $\psi_h$ ) corresponded well with the fraction of total river

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

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

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

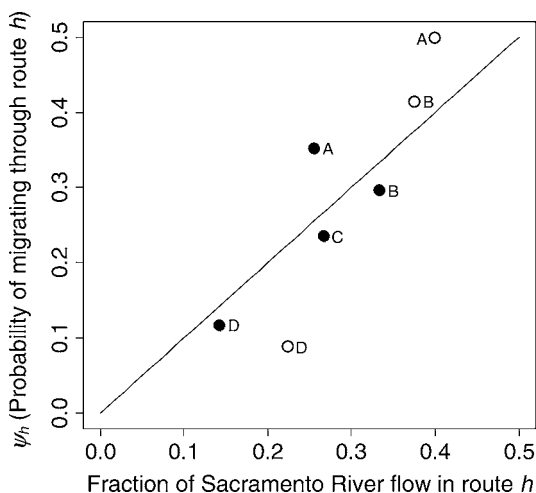


FIGURE 4.—The probability of migrating through route  $h$  as a function of the proportion of total river flow in route  $h$  for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (filled symbols) and 17 January 2007 (open symbols). Data labels A–D represent the Sacramento River, Steamboat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

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

#### Survival through the Delta

Overall, the estimate of survival through the Delta for the December release was lower than for January (for  $R_1$ :  $\hat{S}_{\text{delta}} = 0.351$ ; for  $R_2$ :  $\hat{S}_{\text{delta}} = 0.543$ ; Table 1) despite higher discharge and shorter travel times through the delta for the December release (Figure 2). The CJS model produced nearly the same point estimates and SEs (for  $R_1$ :  $\hat{S}_{\text{delta}} = 0.351$ , SE = 0.101; for  $R_2$ :  $\hat{S}_{\text{delta}} = 0.536$ , SE = 0.070). This finding

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

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

supports the validity of our more complex model to reconstruct survival through the delta from the individual components of reach-specific survival and route entrainment probabilities, while also maintaining precision about  $\hat{S}_{\text{delta}}$ . Relative to the small sample size of this study, precision was favorable due to high detection probabilities at most telemetry stations (Table 2).

#### Relative contributions to $S_{\text{delta}}$

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

The observed difference in  $\hat{S}_{\text{delta}}$  between releases can be attributed to (1) a change in the relative contribution of each route-specific survival to  $\hat{S}_{\text{delta}}$ , and (2) differences in survival for given migration

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

### Discussion

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

We show that route-specific survival and movement among migration routes interact to influence population-level survival, but the next challenge is to quantify the mechanisms causing variation in route-specific survival. Within each release, travel times for fish migrating through the interior delta were longer than alternative routes, possibly contributing to lower survival through the interior delta. Relative to the December release, however, survival for the January release was higher for two migration routes (Sacra-

mento River and Sutter and Steamboat sloughs) despite lower discharge and longer travel times through these routes during January (Figure 3). Thus, instantaneous mortality rates (i.e., per time) in these two routes were lower in January than in December, suggesting that factors other than travel time also contribute to variation in survival within and among migration routes. Such factors may include variation in environmental conditions (e.g., water temperature, turbidity, tides) or temporal shifts in the spatial distribution of predators, both of which influence predator-prey interactions. Our study just begins to shed light on this variation, but with replication over a wide range of environmental conditions our framework will allow us to explicitly quantify mechanisms influencing the route-specific components of population survival.

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

Given that 30–40% of the population migrated through Sutter and Steamboat sloughs (Table 1), this migration route plays a key role in population-level

survival by reducing the probability of fish entering the interior Delta. Fish migrating through Sutter and Steamboat sloughs do not encounter the Delta Cross Channel or Georgiana Slough, which directly reduces the fraction of fish entering the interior Delta via these routes. This relation is couched explicitly in our model: the probability of migrating through the interior Delta can be expressed as

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

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

In general, migration route probabilities increased with the fraction of total river discharge in each migration route, but both the form of this relationship and the factors influencing migration route probabilities requires further study. Flow distribution among the river channels at each junction varies with the tides on hourly time scales. Thus, migration route probabilities in our model represent an average of time-specific route entrainment probabilities that depend on the flow distribution when each fish passes a river junction. Furthermore, the spatial distribution of migrating salmon across a river channel may deviate from the spatial distribution of flow, which could cause a disproportionate number of salmon to be entrained into a given river channel relative to the proportion of flow in that channel. For example, in the Columbia River, juvenile salmon pass through shallow spillways at dams in higher proportions than the fraction of flow passing through spillways (Plumb et al. 2003; Zabel et al. 2008) because of the surface-biased distribution of salmon. Similar behavioral processes at river junctions in the delta would manifest as consistently positive or negative deviations from the 1:1 line in Figure 4 (i.e.,

where the proportion of flow = proportion of fish in a given route). Given these processes and our initial findings, we hypothesize that (1) changes in the distribution of average river flow at river junctions will effect coincident changes in average migration route probabilities, (2) consistent deviations in migration route probabilities relative to flow distribution may arise from a mismatch in the spatial distribution of fish relative to flow, and (3) variability in release-specific migration route probabilities will be driven by the interaction between fish arrival timing at a river junction and hourly scale changes in flow distribution at river junctions. Thus, on average, we suspect that closure of the Delta Cross Channel will reduce the proportion of fish entrained into the interior delta by reducing the fraction of mean discharge entering the interior delta. However, hourly scale variation in flow distribution at river junctions will likely magnify release-to-release variation in migration route probabilities, requiring replication over a range of conditions to confirm whether migration route probabilities are indeed positively related to the proportion of average river flow entering a given migration route.

Strictly speaking, inferences from our study population apply directly to the population of hatchery-origin late fall Chinook salmon 140-mm FL or larger migrating through the delta between December and mid-February under the environmental conditions observed during our study. However, four distinct populations of juvenile Chinook salmon (fall, late fall, winter, and spring) of both hatchery and wild origin use the delta to varying degrees at different times of year during different life stages. Although our framework can be applied to any of these populations, inferences from our data should be considered in the context of the similarity of target populations to our study population. Between December and mid-February, most fish captured in midwater trawls in the lower delta at Chipps Island (near station A<sub>8</sub>) range in size from about 110 to 200 mm (Brandes and McLain 2001) and likely represent actively migrating smolts from the late fall and winter run of Chinook salmon (Hedgecock et al. 2001). Fall-run fry (i.e., < 50-mm FL) begin appearing in the delta in January and overlap with the arrival of spring-run parr (>50-mm FL) in March, both of which rear and grow in the delta to sizes smaller than 120-mm FL until complete emigration by late June (as presumed by absence in catch data; Williams 2006 and references therein). Inferences from our data to fall-run fry and spring-run parr are not well supported due to differences in size, seasonal timing, and residence time in the delta. In addition, survival of hatchery-origin fish may differ from that of wild fish (Reisenbichler and McIntyre 1977; Kostow 2004), but

factors influencing relative differences in survival among migration routes (e.g., interior delta relative to Sacramento River) are likely to act similarly on both wild and hatchery populations. Thus, inferences about such relative differences may provide critical information for better understanding mechanisms influencing population-level survival of both hatchery and wild populations.

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

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

level approach will identify the key management actions in the delta that must be rectified if Sacramento River salmon populations are to recover.

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