Individual-, Release-, and Route-Specific Variation in Survival of Juvenile Chinook Salmon Migrating Through the Sacramento–San Joaquin River Delta

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Abstract

Previous studies have developed an analytical framework for quantifying survival of juvenile salmon migrating through the Sacramento-San Joaquin Delta (Perry, 2010a; Perry, 2010b; Perry and Skalski, 2008, 2009). This report builds on this past work by 1) estimating survival and migration route probabilities of acoustic-tagged late-fall Chinook salmon smolts for the 2008-2009 migration year (hereafter, "2009"), 2) comparing interannual variability in route-specific survival for migration years 2007 through 2009, and 3) quantifying mechanisms explaining variability in survival across years. For the 2009 migration year, population-level survival through Delta was 0.386 (SE = 0.038) and 0.330 (SE = 0.035), respectively, for releases made in December and January. Although the December release group was intended to pass the Delta Cross Channel when its gates were open, long travel times caused nearly half of this release group to pass the cross channel after its gates had closed. Consequently, the fraction of fish entering each migration routes did not differ appreciably between releases. As in previous years, survival for fish entering migration routes leading to the interior Delta was lower than for fish migrating within the Sacramento River.

We found that survival was positively related fork length and positively related to discharge of the Sacramento River for fish migrating through the Sacramento River and Sutter and Steamboat Sloughs. Discharge covariates for the interior Delta failed to explain variation in survival for fish migrating through the interior Delta. Although fork length and river discharge explained significant variation in survival, we found substantial variation in survival among release groups that could not be explained by environmental variables. This analysis takes an important step towards quantifying mechanisms affecting route-specific survival of juvenile salmon. Furthemore, our modeling approach provides a framework within which managers can quantify of the effects of water management actions on both route-specific survival and population-level survival of juvenile salmon.

Table of Contents

Table of Figures

Table of Tables

Acknowledgements

Introduction

Previous studies have developed an analytical framework for quantifying survival of juvenile salmon migrating through the Sacramento-San Joaquin Delta (Perry, 2010a; Perry, 2010b; Perry and Skalski, 2008, 2009). Key aspects of this framework include estimating survival of fish migrating through different pathways in the Sacramento-San Joaquin River Delta (hereafter, "the Delta") and quantifying the fraction of the population using each migration route. Such an approach quantifies how survival through each migration route contributes to population-level survival. We applied this framework to acoustic tagging data from two migration seasons (2006/2007 and 2007/2008, hereafter "2007" and "2008") and found that survival of fish migrating through the Interior Delta was significantly lower than survival of fish remaining in the Sacramento River (Perry, 2010a; Perry and Skalski, 2008, 2009). While differences among routes remained similar between years, survival through all routes in 2008 was considerably lower than in 2007. In addition, we found that the distribution of fish among migration routes generally followed the distribution of river flow, but sizeable deviations from this relationship suggested that factors other than mean river flow also affect fish routing. This report focuses on quantifying the mechanisms responsible for variability in survival. Factors affecting the fraction of fish using different migration routes are detailed in Perry et al. (2010b).

Past studies examining the relation between environmental variables and survival in the Delta have identified Sacramento River flow, water temperature, tides, position of the Delta Cross Channel gates, salinity, and to a lesser extent, water exports as important factors affecting survival (Kjelson and Brandes, 1989; Newman and Rice, 2002; Newman, 2003, 2008, Newman and Brandes, 2010). These experiments have provided critical information to develop water management actions that aid in the recovery of endangered salmon. One limitation, however, is that the response variable has often been the ratio of recapture rates of coded-wire-tagged fish (CWT) between different release locations, which reduces to the ratio of survival probabilities under the assumption of equal capture probabilities. Ratios of recapture rates have then been modeled as a function of covariates (e.g., exports). When modeling ratios, it is impossible to disentangle the relation of the covariate with each of the underlying survival rates, and therefore, inference about the effect of the covariate on survival is indirect. In contrast, acoustic telemetry data allow for direct modeling of the survival probabilities for each migration route as a function of the relevant environmental variables. Since population-level survival is driven by the relative differences in survival among routes, explicitly modeling survival rates within migration routes is critical to understand how differences among routes arise. In this report, we capitalize on these advantages of acoustic tags to understand differences in survival among migration routes and factors affecting survival within routes.

This report unfolds as follows: First we use the multistate mark-recapture model presented in earlier works to estimate survival and migration route probabilities from acoustic tagged fish migrating through the Delta during winter 2008/2009 (hereafter, "2009"). This analysis proceeds much as in Perry and Skalski (2008, 2009), but excludes most of the methods already presented these reports. Readers interested in detailed methods for the multistate mark-recapture model should see Perry and Skalski (2008, 2009) and Perry (2010). We then examine patterns of variation in route-specific survival over all years (2007–2009). Last, to explain variability in survival, we undertake an analysis of this three-year data set along with additional acoustic tag data from a study conducted by UC Davis and NOAA fisheries. Since this report focuses on survival, we simplified the mark-recapture framework by excluding route entrainment probabilities, and then used a Cormack-Jolly-Seber mark-recapture model to examine effects of covariates. We incorporate both group-level covariates (migration route, study, release group, year) and individual covariates (river flow, fish size), then select among a set of alternative models to identify factors responsible for variation in survival.

Methods

Survival and migration route probabilities in 2009

We used a modified version of the multistate mark-recapture model presented in previous reports to estimate survival and migration route probabilities for the 2009 migration year. Since statistical methods were presented extensively in previous chapters and experimental design remained largely unchanged, here we present only details of the 2009 study that differed from previous years. Other details of the 2009 study, such as model schematic and reach-specific parameter estimates, can be found in the appendix.

Release timing, release locations, and telemetry system design closely followed the design used in 2008 (Perry and Skalski, 2009). A number of telemetry stations used in 2008 were not implemented in 2009 (Figure 1), but since these stations divided reaches within routes, the model structure remained essentially unchanged from that presented in Perry and Skalski (2009). Release timing and release locations were similar to 2008, with fish released at Sacramento and also in Georgiana Slough to increase sample sizes of fish migrating through the Interior Delta (Table 1). All fish were surgically implanted with VEMCO acoustic tags at Coleman National Fish Hatchery and transported to release sites where they were held in-river for 24 h prior to release. At each location, fish were released in early December and again in mid-January (Table 1).
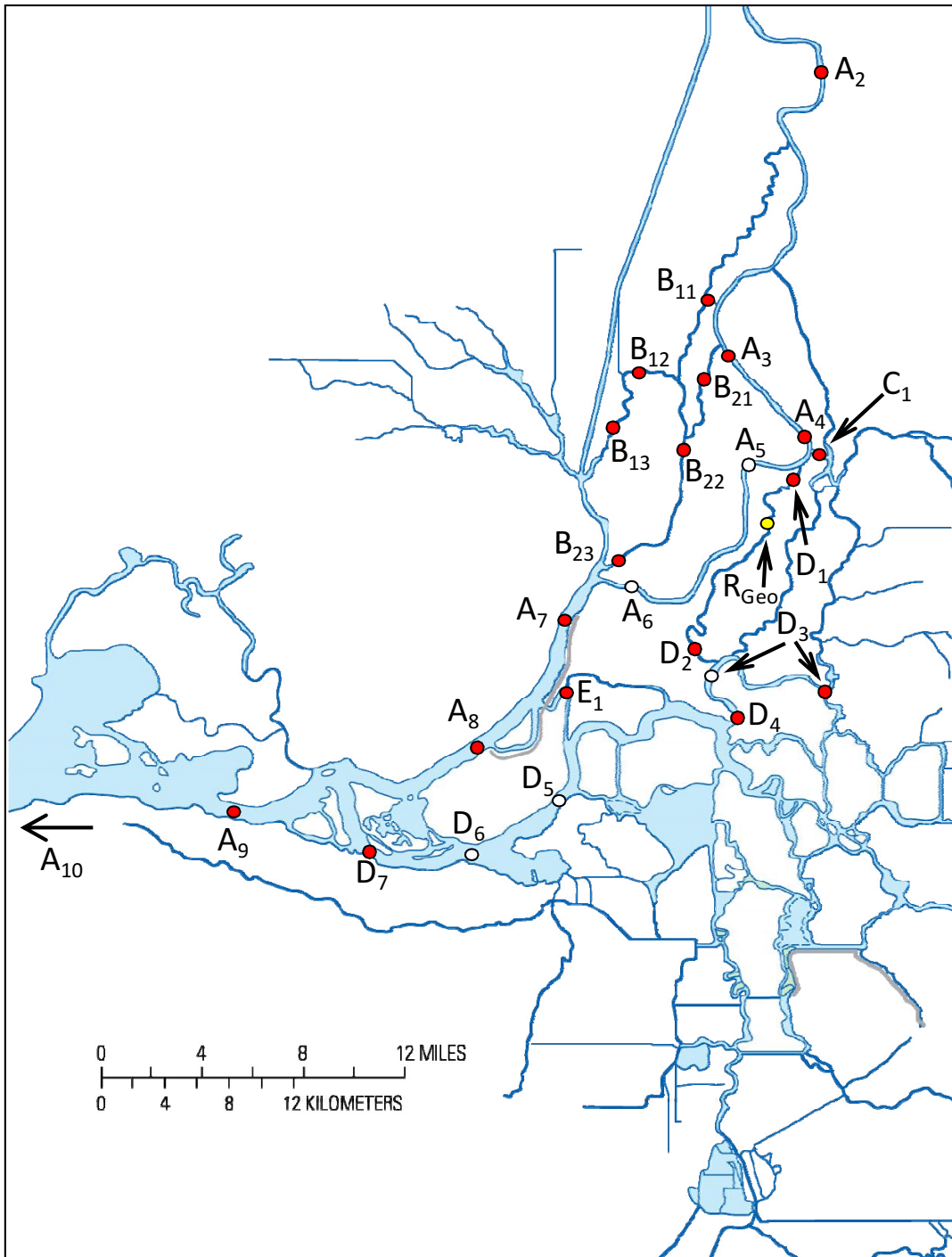
Figure 1.—Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2009. Red-filled circles labeled as h_i show the location of telemetry station i with route h. Locations denoted by unfilled circles show telemetry stations used in 2008 but not 2009. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The Sacramento release site was 19 river kilometers upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

3

The first release group was intended to pass the Delta Cross Channel when the cross channel gates were open, and the second release group when the gates were closed; but a substantial fraction of the first release group passed the Delta Cross Channel after the gates had closed. Therefore, as presented in Perry et al. (2010a), we incorporated a parameter to estimate the probability of fish passing this river junction when the gates were open (ω_{open}). We then estimated route entrainment probabilities conditional on gate position (i.e., $\Psi_{hl,open}$ and $\Psi_{hl,closed}$). Route-specific survival was estimated for each release as described in Perry and Skalsi (2009). Thus, for the first release group, route-specific survival represents the average survival over conditions experienced by this release-group; that is, with the Delta Cross Channel gates both open and closed.

Table 1.—Summary of release dates, release locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2009.

Release dates	Release number	Release location	Sample size
Nov 30 –Dec 4	1	Sacramento	192
Dec 2 –Dec 6	1	Georgiana Slough	100
Jan 13 – Jan 17	2	Sacramento	192
Jan 15 – Jan 19	2	Georgiana Slough	100

Multiyear analysis of route-specific survival

To quantify factors affecting survival over the three-year duration of this study, we incorporated covariates into a Cormack-Jolly-Seber (CJS) model that focused on a subset of the Delta (Cormack, 1964; Jolly, 1965; Seber, 1965). The CJS model was constructed to estimate survival to the exit of the Delta at Chipps Island from entry points into three major migration routes: 1) Sutter and Steamboat sloughs, 2) the Sacramento River, and 3) the interior Delta.

We examined a subset of the full multistate model for three reasons: First, the telemetry system differed in each year of study, resulting in year-specific multistate models that varied in their level of the spatial resolution. Second, our goal was to examine factors affecting survival at the migration-route scale, rather than at the scale of reaches within routes. In Perry and Skalski (2009), we found that changes in survival between releases occurred simultaneously for all reaches within a route (e.g., Sutter and Steamboat sloughs). This finding suggested that processes affecting survival acted at the migration-route scale. Last, we wanted to model survival as a function of individual covariates but imperfect detection probabilities for stations in the lower Delta made it impossible to use individual covariates due to missing covariate values for many fish. Rather, focusing the model on key entry points into migration routes

where detection probabilities were nearly perfect allowed us to incorporate individual covariates without estimation and bias problems associated with missing covariate values (Catchpole et al., 2008).

Detections at key telemetry stations formed virtual "release" points where survival was modeled from the point of entry into each route. Virtual release points were formed from telemetry stations at the entry to Sutter and Steamboat sloughs (stations B_{11} and B_{21}), the Sacramento River at its junction with the Delta Cross Channel and Georgiana Slough (station A_4), and the lower Mokulemne River where it enters the San Joaquin River (station D_4; Figure 1). Since detection probabilities at these locations were nearly perfect (See Perry and Skalski, 2008, 2009) and Appendix Table 3), conditioning the analysis on only detected fish resulted in little loss of information. Survival was then modeled for a single reach from each of these stations to Chipps Island. Reach length via the shortest possible pathway was 41.9 km for the interior Delta, 50.3 km for Sutter and Steamboat sloughs, and 51.9 km for the Sacramento River.

Reaches not included in this analysis are the Sacramento River from the release point at Sacramento to station A_4, the Delta Cross Channel from its junction with the Sacramento River to station D_4, and Georgiana Slough from the release location or from its junction with the Sacramento River to station D_4 (Figure 1). The upper reaches in the Sacramento River were excluded because telemetry stations were not implemented consistently in all years and survival in these reaches remained relatively high over all years of study (Perry and Skalski, 2008, 2009 and Appendix Table 3). The short reaches comprising Georgiana Slough, the Delta Cross Channel, and the North and South forks of the Mokelumne River were excluded so that survival of fish from both routes could be estimated simultaneously after they converge at the mouth of the Mokelumne River.

In addition to the USFWS study on which previous works are based, we also incorporated telemetry data from a CALFED-funded study (http://californiafishtracking.ucdavis.edu/, accessed June 2010). Telemetry data from both studies consisted of fish released during the winters of 2007, 2008, and 2009 from 11 release groups (Table 2). The CALFED and USFWS studies collaborated on tagging efforts, and the same personnel surgically implanted transmitters for both studies using methods described in Perry et al. (2010a). All juvenile salmon were monitored with same system of VEMCO telemetry stations. Although release sites and release methods varied among studies and years, all fish in the Sacramento River were released a minimum of 40 km upstream of entry points to migration routes used in the CJS model. By combining data from both studies, 932 fish were included in the analysis: 381 for the Sacramento River, 264 for Sutter and Steamboat sloughs, and 287 for the Interior Delta (Table2).

Table 2.—Route-specific sample sizes used in the CJS model for release groups of juvenile late-fall Chinook salmon implanted with acoustic tags during the winters of 2007 – 2009. Migration year includes the November and December of the previous calendar year (e.g., releases in December, 2006 occurred in migration year 2007).

Study	Migration year	Release group	Release dates	Sacramento River	Steamboat and Sutter Slough	Interior Delta
USFWS	2007	1	Dec 5 – Dec 6	18	16	7
CALFED		2[*]	Jan 16–Feb 2	8	1	2
USFWS		3[*]	Jan 17 – Jan 18	33	29	2
USFWS	2008	4	Dec 4 – Dec 5	44	45	53
CALFED		5	Dec 7	22	12	8
USFWS		6	Jan 15 –Jan 16	52	23	73
CALFED		7	Jan 17	32	18	12
USFWS	2009	8	Nov 30 –Dec 4	56	48	48
CALFED		9	Dec 13	38	20	17
CALFED		10	Jan 11	19	15	6
USFWS		11	Jan 13 –Jan 17	59	37	59
All groups				381	264	287

[*]These release groups were pooled for analysis because sample sizes for release group 2 were inadequate for estimating route- and release-specific survival.

Incorporating covariates into the CJS model

The CJS model had two sampling occasions with four possible captures histories (111, 110, 101, and 100). The two occasions were formed from detections at station A_9 (Chipps Island) and station A_{10} (seaward of Chipps Island; Figure 1). We structured the negative log-likelihood of the CJS model following the approach of Skalski et al. (1993) where each individual's contribution to the likelihood is explicit:

$$\ln L\left(S_i, p_i, \lambda_i \mid \mathbf{Y}\right) = -\sum_{i=1}^{n} y_{i,111} \ln\left(S_i p_i \lambda_i\right) + y_{i,110} \ln\left(S_i p_i (1 - \lambda_i)\right)$$
$$+ y_{i,101} \ln\left(S_i (1 - p_i)\lambda_i\right) + y_{i,100} \ln\left(1 - S_i + S_i (1 - p_i)(1 - \lambda_i)\right). \quad (1)$$

Here, y_{ij} is an indicator variable resolving to 1 if the ith fish has the jth capture history, and zero otherwise, S_i is the probability of the ith fish surviving to Chipps Island from one of three starting points in the Delta, p_i is the detection probability of the ith fish at Chipps Island, and λ_i is the joint probability of the ith fish surviving and being detected at telemetry stations in San Francisco Bay. This model is overparameterized, and parameters for each individual are estimable only when constrained as a function of group-level or individual covariates.

We used the framework of generalized linear models (glm; McCullough and Nelder, 1989) to link a linear function of the CJS parameters, $g(\theta)$, to the covariates. We used a logit link function for all parameters:

$$g\left(\theta_i\right) = \ln\left(\frac{\theta_i}{1+\theta_i}\right) = \beta_0 + \beta_1 x_{i1} + \ldots + \beta_p x_{ip} = \boldsymbol{\beta}' \mathbf{x}_i \tag{2}$$

where $\theta_i = S_i$, p_i, or λ_i; β_0 is the intercept; and β_j is the slope parameter for $j = 1, \ldots, p$ covariates, x_{ij}. The covariates were introduced into the negative log-likelihood using the inverse logit function:

$$\theta_i = \frac{\exp\left(\boldsymbol{\beta}' \mathbf{x}_i\right)}{1+\exp\left(\boldsymbol{\beta}' \mathbf{x}_i\right)} \tag{3}$$

and the likelihood was iteratively minimized using optimization routines in the R statistical computing platform (R Development Core Team, 2008) to estimate the vector of β parameters. The variance-covariance matrix was estimated as the inverse of the observed Hessian matrix.

Defining group and individual covariates

We modeled survival through the Delta as function of both group-level and individual covariates. Individual covariates consisted of fork length and route-specific river discharge when individuals entered each route. Group-level covariates consisted of study (USFWS or CALFED), migration route, migration year, and mean river discharge for each release group and migration route.

We hypothesized that the 3-d period after fish entered a migration route was a critical period during which hydraulic conditions of the river could affect survival. Thus, individual covariates for river discharge were defined by mean discharge for the 3-d period after each fish entered the reach of interest. This time period was based on median travel times to the lower Sacramento River at Rio Vista (station A_7; Figure 1) from virtual release points in the Sacramento River (median = 2.4 d) and Sutter and Steamboat sloughs (median = 3.1 d). For the Interior Delta, we also focused on a 3-d period, hypothesizing that river conditions shortly after fish enter the San Joaquin River would influence their probability of moving towards the ocean or towards pumping stations in the southern Delta, which in turn, could affect survival.

For fish migrating through the Sacramento River, we modeled survival as a function of Sacramento River discharge just downstream of Georgiana Slough (Q_S, between stations A_4 and A_5 in Figure 1; also see Figure 6?). Since the Delta Cross Channel diverts river flow upstream of this location, this gauging station measures flow remaining in the Sacramento River in response to operation of the cross channel gates. To capture the effect of tidal fluctuations on survival, we also considered the

7

standard deviation of 15-min discharge over the 3-d period as a possible covariate. However, we found that the mean and standard deviation of discharge were highly correlated ($r = -0.864$, Figure 2). As inflow increases, tidal fluctuations are dampened; therefore, we used only mean discharge in the model because it quantifies both the effect of river inflow and the effect of inflow on tidal fluctuations.
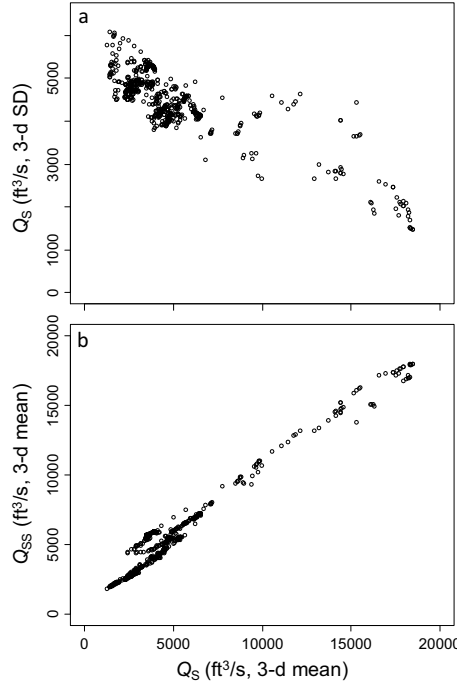
Figure 2.—Relation between mean Sacramento River discharge measured downstream of Georgiana Slough (Q_S) with a) the standard deviation of Q_S, and b) the mean discharge entering Sutter and Steamboat sloughs (Q_{SS}). Means and standard deviations were calculated from 15-min flow data during the 3-d period following detection of tagged fish entering the Sacramento River and Sutter and Steamboat sloughs.

We also used Q_S for Sutter and Steamboat sloughs because 1) Q_S was highly correlated with discharge entering Sutter and Steamboat Slough ($r = 0.98$, Figure 2), 2) fish from both routes migrate through a common reach in the lower Sacramento River (Figure 1), and 3) using the same flow covariate allowed us to test whether the slope coefficients differed between migration routes. Specifically, the effect of Q_S on survival was modeled with the following structure (excluding the other covariates for clarity):

$$g(S) = \beta_1(I_{Sac} + I_{SS})Q_S + \beta_2 I_{SS}Q_S$$

where I_{Sac} and I_{SS} are dummy variables resolving to one when fish enter the Sacramento River (Sac) or Sutter and Steamboat sloughs (SS), and zero otherwise. With both terms in the model, the first estimates the slope for the Sacramento River and the second estimates the difference in slopes between the

8

Sacramento River and Sutter and Steamboat sloughs. Thus, the null hypotheses $\beta_2 = 0$ explicitly tests whether the effect of Q_S on survival differs between migration routes.

River flow and migration routing in the interior Delta is more complex than the other migration routes. Once fish exit the Mokelumne River and enter the San Joaquin River, their probability of surviving may depend on whether they move seaward or inland towards the pumping stations. The probability of fish moving towards the pumps likely depends on the balance of flows exiting the Mokelumne River and the San Joaquin River relative to water exports at the pumping stations. Thus, individual covariates for the interior Delta were defined as mean 3-d discharge of water exports at the pumping stations (Q_E), of the Mokelumne River where fish enter the San Joaquin River (Q_M, near station D_4), and of the San Joaquin River at Jersey Point (Q_J, near station D_5, Figure 1).

We formed group-level covariates for river flow by averaging the individual covariates over each release group and migration route. This approach is equivalent to a weighted average with weights proportional to the distribution of entry times to each reach. All covariates were standardized by subtracting the mean from each observation and then dividing by the standard deviation.

Model selection

We used a three-phase approach to determine factors affecting route-specific survival: We first identified the best-fit model for p and λ and used this model as a basis fitting covariates to survival. Second, we modeled group-level covariates using analysis of deviance (ANODEV). Last, we selected among models with individual covariates using likelihood-ratio tests (LRT) and Akaike's Information Criterion (AIC; Burnham and Anderson, 2002).

We used ANODEV because it explicitly accounts for overdispersion and replication at the route- and release group-level. Since the analysis consisted of only 10 release groups (after pooling release groups 2 and 3) and 3 reaches, ANODEV "penalizes" for this low level of replication through the effects of the "source" and "error" degrees of freedom on the F test. Furthermore, the error mean deviance quantifies overdispersion (release-to-release variability unexplained by covariates in the model), ensuring that test statistics for model selection remain unbiased. Because likelihood ratio tests (LRT) account for only multinomial sampling variability, they too often reject the null hypothesis of no covariate effect in the presence of variability that is unrelated to the group covariates (Skalski et al., 1993). In contrast, we used LRT for the individual covariates because LRT remains unbiased for individual covariates in the presence of extra variability unrelated to the covariate (Skalski et al., 1993).

The fully saturated model estimated a unique p and λ for each release group and unique survival probabilities for each release group and migration route. Using the glm framework, this model was

9

parameterized by including a main effect of release group for p and λ; and release group, route, and a release:route interaction for S (where ':' denotes interaction) . Given this saturated model, we evaluated reduced models for p and λ that consisted of year-specific parameters and constant p and λ over all years. We first selected the best model for λ and then fit models for p under the best λ model. The best-fit λ and p models were selected on the basis of LRT and AIC.

At the group level, we fit a model with all covariates which included route, year, study, Q_S for the Sacramento River and Sutter and Steamboat sloughs, and Q_M, Q_J, and Q_E for the Interior Delta. we then constructed an ANODEV table analogous to ANOVA tables that partition the variance among different sources of error (Skalski et al., 1993). To select variables for inclusion in the model, we used stepwise selection, adding variables to the ANODEV table in order of the largest reduction in negative log-likelihood (NLL; Skalski et al., 1993). Interaction terms were always added to the model with their corresponding main effects. This approach results in a sequential ANODEV table where the F test for a given variable includes all other covariates previously added to the model.

For individual covariates, we added fork length (L) and flow variables to the saturated model for survival (i.e. to the model with route, release group, and route:release group). First, to test for differences in slopes among release groups, we considered interactions between release group and individual covariates. However, when simultaneously including all possible two-way interactions in the model, maximization of the likelihood became unstable and many parameters became inestimable, which was likely due to small sample size for some of the releases and routes (Table 2). Instead, prior to forming a full model, we added each covariate separately to the saturated model, crossed the covariate with release group, fixed inestimable slope parameters to zero, and then compared this model against the corresponding model lacking an interaction. None of the interactions were significant using LRT at $\alpha =$ 0.05, so they were not included in the full model. Therefore, the full model with individual covariates estimated unique intercepts for each release group-route combination, but a common slope over all release groups.

Only the individual covariates were considered for model selection, keeping route, release, and route:release group in all models. The intent here was twofold: first, our goal was to explain within-release variation in survival over and above that accounted for by route and release group. Second, maintaining group-level structure ensured that group differences in survival were not wrongly attributed to the individual covariate. When covariate values do not overlap among groups, and group survival differs due to factors other than the covariate, LRT may falsely attribute a covariate effect to the group differences in survival (Hoffman and Skalski, 1995). However, Hoffman and Skalski (1995) showed that the LRT was unbiased when individual covariates were added to the fully saturated model. We used

reverse elimination of covariates to identify the best-fit model, dropping terms one-at-a-time from the full model, eliminating the variable that least explained variation in survival (using LRT and AIC), re-fitting the reduced model, and then eliminating the next variable. Covariates were eliminated until no variable could be dropped without resulting in a significantly poorer fit based on a substantial increase in AIC and evaluation of LRT at $\alpha = 0.05$.

Results

Migration routing and survival in 2009

Sacramento River discharge was less than 10,000 ft^3/s for much of the study period, and travel times of the first release group were substantially longer than observed in previous years (Figures 3 and 6). For the December release group, the median travel time to junction 2 (Stations A_4, C_1, and D_1; Figure 1) was 13 days, and the central 80% of this release group took 25 days to pass the second river junction. The January release group exhibited much shorter travel times to river junction 2 (median = 4.1 days) and a more compressed distribution, despite flows remaining low (Figure 3). These findings suggest that the first release group may not have been actively migrating smolts at the time of release. Travel times of the first release group to the outlet of the Delta were substantially longer than the second release group and their arrival distributions overlapped. For the first release group, the median travel time to Chipps Island was 25 days, but arrival at Chipps Island was distributed over nearly two months. For the second release group, the median travel time was 10.9 days and arrival times between the 10th and 90th percentile were distributed over 32 days. All fish exited the Delta with the onset of a freshet in late February. Migration route probabilities varied according to the position of the Delta Cross Channel gate. The first release group was supposed to pass the Delta Cross Channel while its gates were open, but long travel times caused 45% of fish to pass the Cross Channel when the gates were closed (See ω_{open}, Appendix Table 3). For this release group, fish that passed when the Delta Cross was open distributed in thirds among the Sacramento River, Sutter and Steamboat Slough, and interior Delta (via the Delta Cross Channel or Georgiana Slough; Table 3). For routes leading to the interior Delta, 22.4% of the population entered through the Delta Cross Channel, whereas 12.4% entered through Georgiana Slough (Table 3). In contrast, of the fish from the first release group that passed the Delta Cross Channel when the gates were closed, 46.6% remained in the Sacramento River and 21.2% entered the Interior Delta. Since the Delta Cross Channel was closed, migration route probabilities for the second release group were similar to those of the first release group that encountered a closed gate (Table 4). Closing the Delta Cross Channel increases discharge in both the Sacramento River and Georgiana Slough. Coincident with this increase in

11

flow, migration route probabilities for both releases indicate that the fraction of fish in both Georgiana Slough and the Sacramento River increased when the gate was closed. Chapter 6 of Perry (2010) expands on these findings to explicitly quantify entrainment probabilities as a function of discharge entering each route.
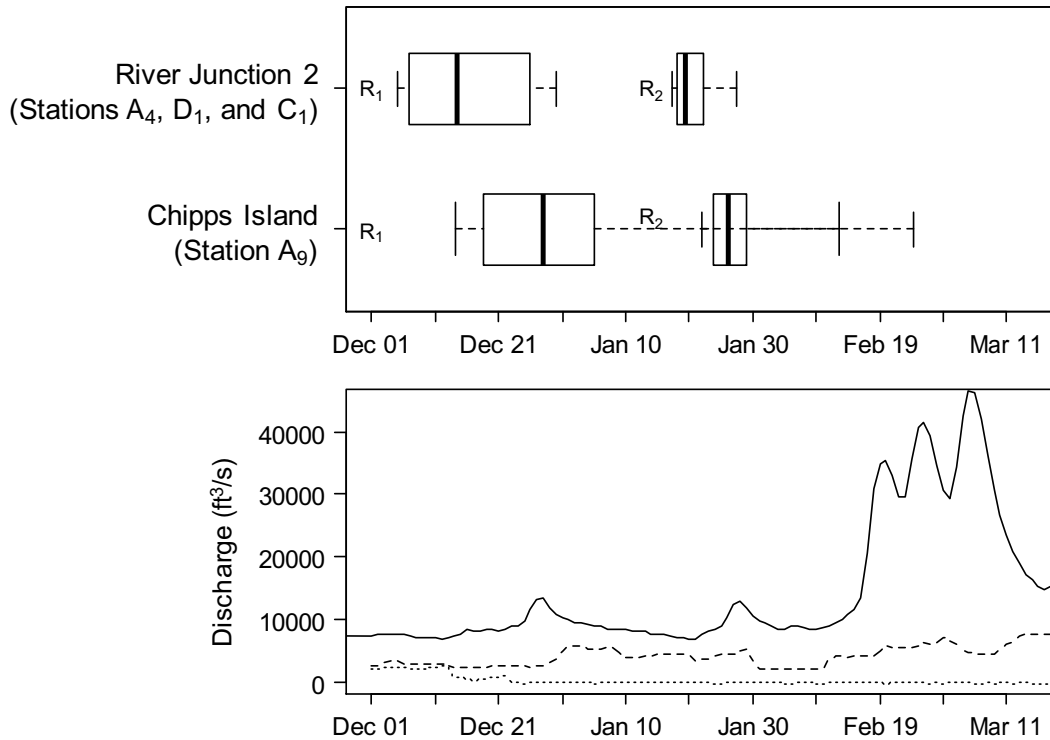
 Figure 3.—River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during the winter of 2009. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A_4, C_1, and D_1) and at Chipps Island, the terminus of the Delta (telemetry station A_9). Release dates are shown as R_1 and R_2. 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. For Chipps Island, whiskers have different widths to distinguish the overlap in arrival distributions. 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.

12

Table 3.—The probability of migrating through each route (Ψ_h) for acoustically tagged late fall-run juvenile Chinook salmon released in December 2008 as a function of gate position when fish passed the Delta Cross Channel.

Migration route	Cross Channel Open		Cross Channel Closed	
	$\hat{\Psi}_h$ ($\widehat{SE}$)	95% Profile likelihood interval	$\hat{\Psi}_h$ ($\widehat{SE}$)	95% Profile likelihood interval
A) Sacramento R.	0.331 (0.050)	0.238 , 0.431	0.466 (0.054)	0.360, 0.569
B) Sutter & Steamboat S.	0.321 (0.037)	0.251 , 0.397	0.321 (0.037)	0.251, 0.397
C) Delta Cross Channel	0.224 (0.045)	0.145 , 0.318	NA	
D) Georgiana S.	0.124 (0.036)	0.065 , 0.206	0.212 (0.049)	0.128, 0.315

Survival through the Delta was comparable between release groups even though the first release group had substantially longer travel times. Survival through the Delta was 0.386 for the first release group and 0.339 for the second release group (Table 4). Since half of the first release group encountered a closed Delta Cross Channel gate, migration route probabilities did not differ drastically between releases, resulting in similar contributions of route-specific survival to population-level survival. Among routes, fish migrating in the Sacramento River and Sutter and Steamboat sloughs exhibited the highest survival probabilities whereas fish migrating through the Delta Cross Channel and Georgiana Slough had lower survival (Table 4). For both releases, survival probabilities for the Sacramento River and Sutter and Steamboat sloughs ranged from 0.394 to 0.448. In contrast, survival probabilities ranged from 0.117 to 0.315 for fish migrating through the Interior Delta (Table 4).

The ratio of survival through each route relative to the Sacramento River (θ_h) indicated that fish entering the Interior Delta had significantly lower survival for two of the three survival probabilities. Fish entering the Delta Cross Channel exhibited significantly lower survival than the Sacramento River, as did fish entering Georgiana Slough from the second release group (Table 5). Although $\hat{\theta}_D = 0.70$ indicated lower survival of fish entering Georgiana Slough for the first release group, the 95% confidence interval encompassed one. For Sutter and Steamboat sloughs combined, θ_B was not different from one during either release. However, considering these routes separately, fish from the first release group entering Sutter Slough exhibited significantly lower survival but fish entering Steamboat Slough had significantly higher survival than the Sacramento River. For the second release group, fish within each of these routes experienced similar survival as fish remaining in the Sacramento River (Table 5).

13

Interannual patterns in route-specific survival

We observed substantial variation in the magnitude of within-route survival among years, yet stable patterns of survival across routes over all years. Among years, 2008 stands out as having the lowest survival at both the route scale and the Delta scale (Figure 4 and 5). Survival through the Delta was <0.20 for 2008, but > 0.33 for all other years and releases. In contrast, given that fish experienced the lowest flows in 2009 (Figure 5.6), estimates of S_{Delta} for 2009 were substantially higher than might be expected when compared relative to S_{Delta} for 2008 (Figure 4). Over all years, estimates of S_{Delta} exceeded 0.40 for only one release group (Dec. 2006 in migration year 2007), and only during 2007 did observed estimates of S_{Delta} differ between releases.

Although rankings of route-specific survival vary somewhat across releases, one pattern remained constant: survival probabilities for the Sacramento River were always greater than survival for migration routes through the Interior Delta (via Georgiana Slough and the Delta Cross Channel; Figure 4). In addition, Sutter and Steamboat sloughs exhibited either similar survival to the Sacramento River (typically for January releases) or lower survival than the Sacramento River (typically for December releases). Except for the December release group in the 2007 migration year, observed survival estimates for Sutter and Steamboat Sloughs were greater than for routes leading to the Interior Delta. These findings clearly show that migration routes leading to the Interior Delta will reduce population survival proportional to the fraction of the population entering the interior Delta.

Table 4.—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 late-fall juvenile Chinook salmon released in December 2008 (R_1) and January 2009 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{SE}$)	95% Profile likelihood interval	$\hat{\Psi}_h$ ($\widehat{SE}$)	95% Profile likelihood interval
R_1: December 2008				
A) Sacramento R.	0.448 (0.053)	0.348, 0.553	0.392 (0.040)	0.354, 0.458
B) Sutter & Steamboat S.	0.394 (0.056)	0.296, 0.507	0.321 (0.037)	0.251, 0.397
B$_1$) Sutter S.	0.281 (0.061)	0.172, 0.407	0.217 (0.033)	0.157, 0.288
B$_2$) Steamboat S.	0.632 (0.059)	0.509, 0.741	0.104 (0.025)	0.062, 0.158
C) Delta Cross Channel	0.117 (0.048)	0.044, 0.228	0.224 (0.045)	0.145, 0.318
D) Georgiana S.	0.315 (0.054)	0.216, 0.426	0.164 (0.164)	0.112, 0.226
S_{Delta} (All routes)	0.386 (0.038)	0.315, 0.463		
R_2: January 2009				
A) Sacramento R.	0.398 (0.051)	0.308, 0.484	0.459 (0.043)	0.404, 0.498
B) Sutter & Steamboat S.	0.432 (0.067)	0.394, 0.514	0.253 (0.036)	0.188, 0.328
B$_1$) Sutter S.	0.426 (0.086)	0.271, 0.468	0.096 (0.024)	0.055, 0.151
B$_2$) Steamboat S.	0.436 (0.075)	0.372, 0.518	0.158 (0.030)	0.105, 0.222
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.163 (0.033)	0.146, 0.204	0.288 (0.040)	0.219, 0.361
S_{Delta} (All routes)	0.339 (0.035)	0.310, 0.379		

Table 5.—The ratio (θ_h) of survival through route h (S_h) to survival through the Sacramento River (S_A) for acoustically tagged late fall-run juvenile Chinook salmon released in December 2008 and January 2009.

| Migration route | R_1: December 2008 | | R_2: January 2009 | |
	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile likelihood interval	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile likelihood interval
B) Sutter & Sutter S.	0.879 (0.131)	0.644, 1.170	1.086 (0.199)	0.872, 1.251
B$_1$) Sutter S.	0.626 (0.139)	0.383, 0.925	1.070 (0.239)	0.832, 1.227
B$_2$) Steamboat S.	1.410 (0.144)	1.148, 1.728	1.096 (0.215)	0.977, 1.443
C) Delta Cross Channel	0.260 (0.109)	0.098, 0.527	NA	
D) Georgiana S.	0.703 (0.139)	0.466, 1.014	0.409 (0.094)	0.374, 0.449
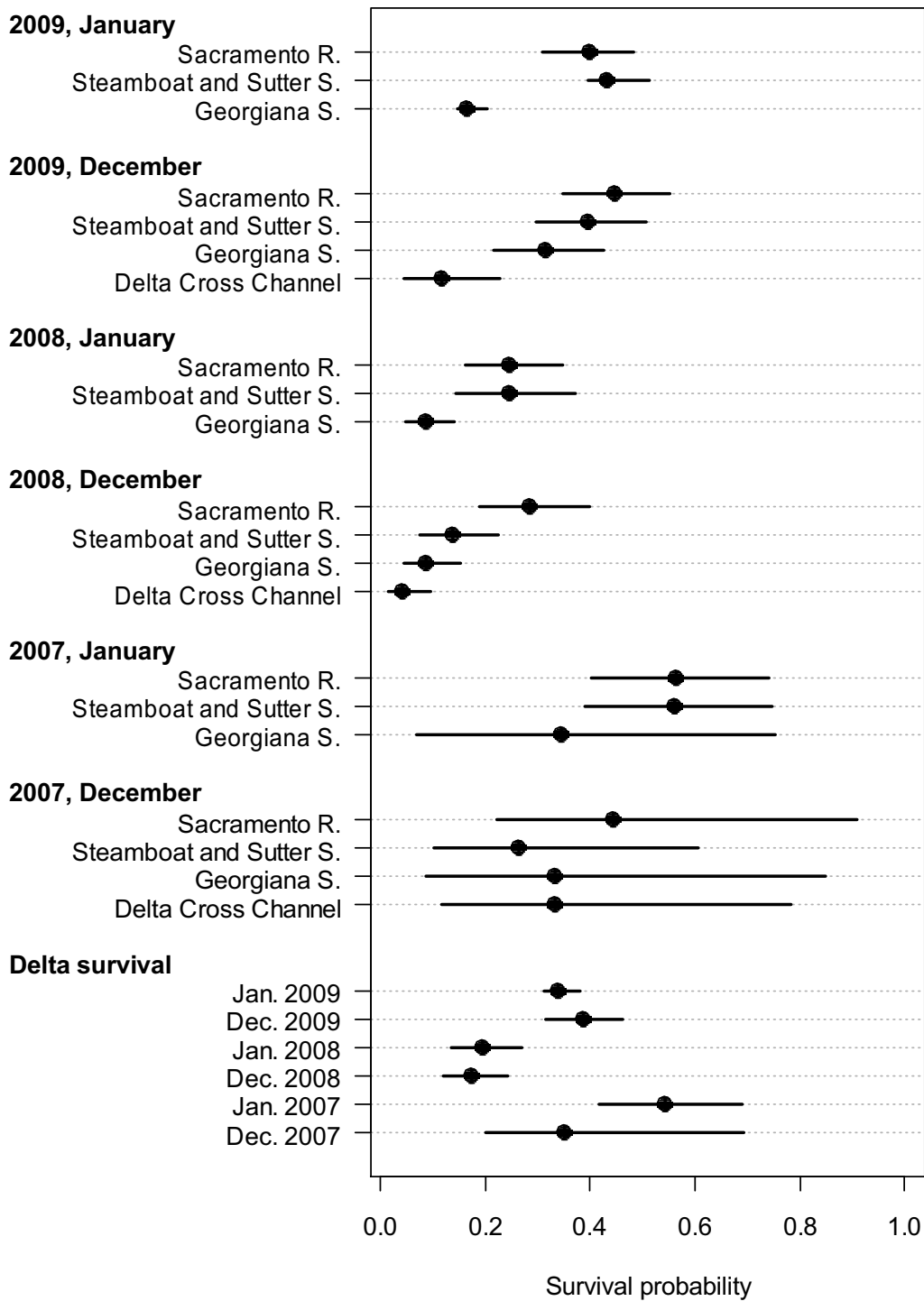
Figure 4.—Summary of route-specific survival probabilities during migration years 2007–2009. Data points are organized by release group to facilitate comparison among routes within each release Migration years are shown next to release months (e.g., "Dec. 2007" refers to releases in December, 2006 in migration year 2007).

16
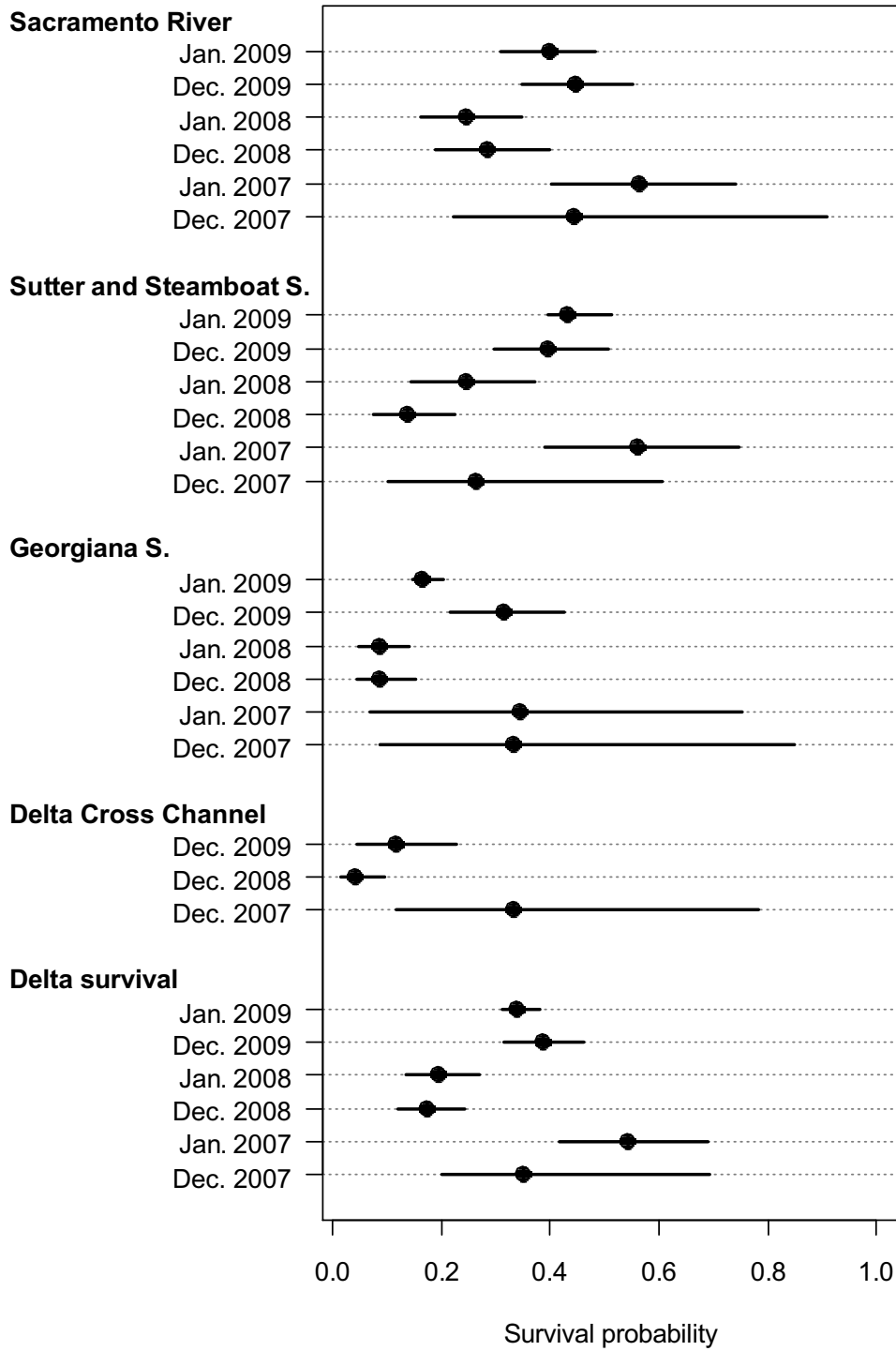
Figure 5.—Summary of route-specific survival probabilities during migration years 2007–2009. Data points are organized by migration route to facilitate comparison among releases within each route. Migration years are shown next to release months (e.g., "Dec. 2007" refers to releases in December, 2006 in migration year 2007).
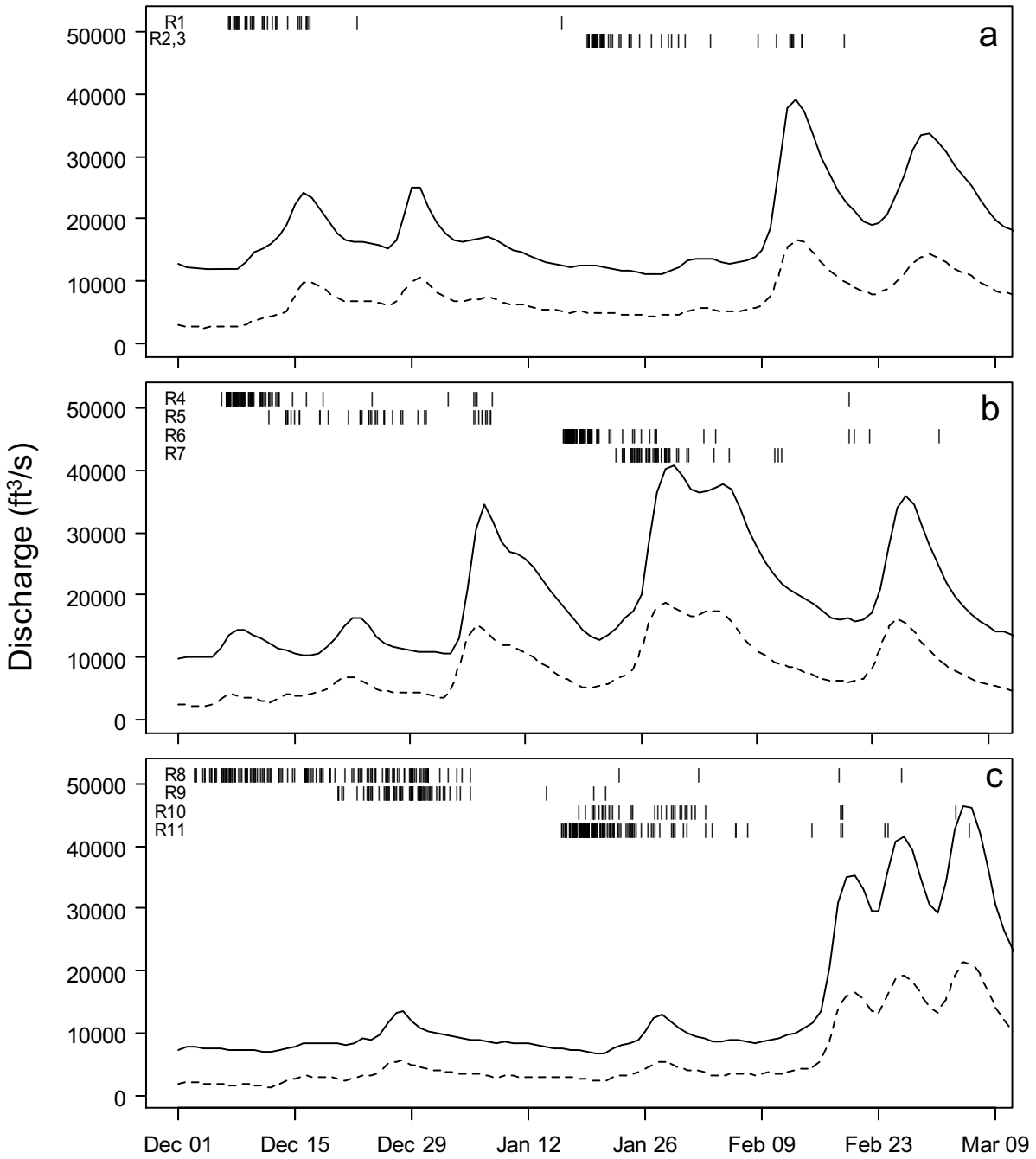
Figure 6.—River conditions experienced by acoustic-tagged late-fall Chinook salmon smolts migrating through the Sacramento–San Joaquin River Delta during migration years a) 2007, b) 2008, and c) 2009. The solid line is mean daily discharge of the Sacramento River at Freeport and the dashed line is mean daily discharge of the Sacramento just downstream of Georgiana Slough. Tick marks show when tagged fish from each release group ($R_1 - R_{11}$) were detected at telemetry stations defining entry into migration routes used in the CJS survival model.

18

Factors affecting route-specific survival

For the CJS model, both λ and p varied among years, but not among releases within years. A model with a constant λ was not supported by AIC or LRT (Table 6). For constant p across years, the likelihood ratio test was significant at $\alpha = 0.10$, but not at $\alpha = 0.05$. However, since AIC increased with a 2-parameter decrease between models, we elected to use the year-specific p model for as the basis of model selection of group-level and individual-covariates (Table 6).

Table 6.—Results of model selection to identify the best-fit CJS model for λ and p.

Parameter modeled	Model[*]	Number of parameters	AIC	NLL	LR	P
λ	S(rt*rel) p(rel) λ(rel)	49	1897.9	900.0		
	S(rt*rel) p(rel) λ(yr)	42	1889.2	902.6	5.3	0.63
	S(rt*rel) p(rel) λ(.)	40	1892.6	906.3	7.4	0.02
P	S(rt*rel) p(yr) λ(yr)	35	1879.1	904.6	5.8	0.57
	S(rt*rel) p(.) λ(yr)	33	1880.2	907.1	5.1	0.08

[*]Model notation is as follows: rel = release group, rt = route, and yr = migration year. An asterisk between variables indicates inclusion of both main effects and their interaction, and a period indicates an intercept-only model.

For group-level covariates, a nearly saturated model with route, year, study, and all possible interactions explained 85% of the discrepancy between the fully saturated and null models, whereas a model with only migration route and flow covariates explained 42%. These findings indicated that year and study shared common deviance with the flow covariates. The full covariate model explained 75.7% of the discrepancy in deviance between the saturated and null models, with year, study, and Q_S explaining most of this discrepancy (Table 7). We also found evidence of overdispersion as suggested by a mean error deviance of 1.5. Thus, even after accounting for the covariates, release-to-release variability was still greater than that expected by multinomial sampling variation. Year and study reduced the deviance more than any other variables and therefore appeared first in the ANODEV table (Table 7). Although route was not significant, it was entered next since the remaining flow variables were crossed with migration route indicator variables. Adding $(I_{Sac}+I_{SS}):Q_S$ to the model explained significant deviance over that explained by route, year, and study, but none of the other flow variables were significant. Thus, the final model consisted of route, year, study, and $(I_{Sac}+I_{SS}):Q_S$. The inclusion of year and study in the final model shows that river flow could not fully account for differences in survival among years or between studies.

Individual covariates added six parameters to the saturated model but decreased AIC by 11 units, indicating that individual covariates explained considerable within-release variation in survival (Table 8).

Model selection for individual covariates paralleled that for group-level covariates: flow variables for the interior Delta survival were not significant, nor was there a difference in slopes for Q_S between the Sacramento River and Sutter and Steamboat Sloughs (Table 8). However, when either fork length or $(I_{Sac}+I_{SS}):Q_S$ were dropped from the model, model fit worsened considerably (Table 9). Thus, the best fit model with individual covariates consisted of release group, route, route:release group, $(I_{Sac}+I_{SS}):Q_S$, and fork length. Despite the individual covariate model having 24 more parameters than the best-fit group covariate model, AIC for the individual covariate model (AIC = 1862.8) was 6.3 units less than for the group covariate model (AIC = 1869.1), indicating that individual covariates explained more variation in survival than group covariates alone.

Table 7.—Analysis of deviance table for group covariates in the CJS model. Survival was modeled with year-specific p and λ. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Source	Degrees of freedom	Deviance	Mean deviance	F	P-value
Total (saturated model)	29[*]	904.6			
Intercept (null model)	1	960.8			
Corrected total	28	112.4			
Covariate total	10	85.0	8.5	5.59	<0.001
Study	1	21.9	21.9	14.43	0.001
Year	2	33.9	16.9	11.15	<0.001
Route	2	4.5	2.2	1.47	0.255
$(I_{Sac}+I_{SS}):Q_S$	1	18.1	18.1	11.94	0.003
$I_{ID}:Q_M$	1	4.8	4.8	3.15	0.092
$I_{ID}:Q_E$	1	1.1	1.1	0.70	0.414
$I_{SS}:Q_S$	1	0.7	0.7	0.45	0.512
$I_{ID}:Q_J$	1	0.1	0.1	0.07	0.800
Error	18	27.3	1.5		

[*]Release groups 2 and 3 were pooled as one group, and for this release group survival for the Interior Delta was fixed to 1 because all fish survived. For the saturated model, this led to 10 release groups, 3 routes, and 1 fixed parameter for a total of 10(3) - 1 = 29 degrees of freedom.

Table 8.—Results of model selection for the effect of individual covariates on survival. Survival was modeled with year-specific p and λ. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Model or covariate dropped	Number of parameters	AIC	NLL	LR	P-value
Route*Release + all covariates	41	1869.2	893.6		
Route*Release – all covariates	35	1879.1	904.6	21.9	0.001
$I_{ID}:Q_J$	40	1867.2	893.6	0.0	1.000
$I_{SS}:Q_S$	39	1865.2	893.6	<0.1	0.888
$I_{ID}:Q_E$	38	1863.4	893.7	0.22	0.639
$I_{ID}:Q_M$	37	1862.8	894.4	1.41	0.235

Table 9.—Likelihood ratio tests and AIC when each variable is dropped from the best fit model with individual covariates. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Variable dropped	Number of parameters	NLL	Likelihood Ratio	AIC	ΔAIC	*P*-value
None (best fit)	37	894.4		1862.8	0.0	
Fork length	36	898.8	8.8	1869.6	6.8	0.003
$(I_{Sac}+I_{SS}):Q_S$	36	899.9	11.0	1871.8	9.0	0.001

Parameter estimates and predicted survival probabilities

Significant effects of study and year indicated that differences in survival among release groups could not be fully accounted for by my migration route and river flow (Table 10). A negative coefficient of -0.37 suggests that on average, release groups for the USFWS study exhibited lower survival than for the CALFED study. For example, predicted survival of the reference group (Sacramento R., 2009, CALFED study) is $logit^{-1}(0.71) = 0.67$ at the mean flow of 5127 ft^3/s, whereas for the USFWS, predicted survival is $logit^{-1}(0.71-0.37) = 0.58$. Among years, 2008 had a large negative coefficient, suggesting lower survival than in 2009. For example, relative to the reference group at the mean flow, predicted survival for 2007 and 2008 is $logit^{-1}(0.71-0.16) = 0.63$ and $logit^{-1}(0.71-1.19) = 0.38$. Among routes, the interior Delta had the largest negative coefficient despite being the shortest direct route to Chipps Island. Relative to the reference group, predicted survival for the interior Delta is $logit^{-1}(0.71-0.44) = 0.57$. These patterns of variation are consistent with our observations from the multistate model (Figures 4 and 5).

Although flow variables could not account for all variation among release groups, Sacramento River flow still explained significant variability in survival for the Sacramento River and Sutter and Steamboat sloughs. Positive slope estimates under both the group- and individual-covariate models show that survival is positively associated with Q_S (Tables 10 and 11). Under the group covariate model, most of the release groups experienced average flows <8000 ft^3/s, and two data points at higher discharge appear to be driving the relationship (both from release group 7; Figure 7). The individual covariate model strengthens the findings of the group covariate model because individuals from multiple releases experienced river discharge >8000 ft^3/s (Figure 6 and 8). For example, when release group 7 is excluded, Q_S remains statistically significant in the individual covariate model, suggesting that this release group was not driving the relationship. Under both models, predicted survival increases by about 40 percentage points over the observed range of discharge, although the slope is less steep under the individual covariate model (Figures 7 and 8).

21

The individual covariate model also revealed effects of fork length on survival and substantial among-release variation in survival. The slope estimate for fork length was positive, indicating that larger size was associated with higher survival (Table 11). The estimated slope for fork length was about half that of Q_S, and thus, a 1-SD change in fork length, when holding Q_S constant, results in a smaller change in survival than a 1-SD change in flow (when holding length constant; Table 8, Figure 8). For example, at the mean observed discharge, predicted survival increases by about 25 percentage points over the range in fork length, compared to a 40 percentage point change over the range in flow. Despite the relation of survival with fork length and Q_S, considerable release-to-release variation in survival remains. Mechanisms driving this variation remain unknown.

Discussion

Over the three-year duration of this study, we identified substantial variability in survival related to migration route, river flow, and fish size. Although considerable variability in survival remains unexplained, quantifying effects of river flow and migration route on survival helps to understand how water management actions might influence population-level survival. We observed stable patterns of variability in survival across migration routes, with migration routes leading to the interior Delta having lower survival than the Sacramento River or Sutter and Steamboat sloughs. Thus, water management actions affecting routing of fish through the Delta will influence population-level survival. My findings also suggest that decreases in discharge of the Sacramento River could reduce survival of fish migrating in the Sacramento River and Sutter and Steamboat sloughs. By combining both migration routing and survival in a common framework, these relationships form the basis of dynamic models to simulate the effect of water management actions on population-level of survival.

The relation between Sacramento River flow and survival in Sacramento River and Sutter and Steamboat sloughs has important implications for management of water resources in the Delta. Climate change, upstream water withdrawals, and operation of the Delta Cross Channel alter river flow, and in turn, may affect survival of juvenile salmon. For example, at mean total inflows during this study (13,642 ft^3/s at Freeport), flow of the Sacramento River downstream of the Delta Cross Channel increases from 2952 ft^3/s to 4791 ft^3/s upon closing the cross-channel gates (flows estimated from a regression model in Burau et al., 2007). Our analysis suggests that survival would increase by about six percentage points due to this increase in discharge. Although relatively small, this change in survival must be considered simultaneously relative to survival in other routes and the fraction of fish using each migration. Closing the Delta Cross Channel reduces the fraction of fish entering the interior Delta where survival is low, and increases the fraction remaining in the Sacramento River where survival increases due to the increase in

Table 10.—Parameter estimates on the logit scale for group-level covariates best explaining survival and detection probabilities of the CJS model. Parameter estimates for categorical variables (Route, Year, and Study) are estimated as differences from a reference category set as the intercept.

Parameter modeled	Variable	Group description	$\hat{\beta}$ (SE)	95% Confidence interval (±1.96 SE)
S		Intercept (Sacramento R., CALFED, 2009)	0.71 (0.18)	0.35, 1.06
	Route	Sutter and Steamboat S.	-0.15 (0.18)	-0.49, 0.20
		Interior Delta	-0.44 (0.18)	-0.79, -0.09
	Year	2007	-0.16 (0.28)	-0.70, 0.39
		2008	-1.19 (0.19)	-1.56, -0.82
	Study	USFWS	-0.37 (0.20)	-0.77, 0.03
	$(I_{Sac}+I_{SS})Q_S$		0.74 (0.18)	0.38, 1.09
p	Year	Intercept (2009)	1.58 (0.20)	1.19, 1.96
		2007	-0.85 (0.38)	-1.60, -0.10
		2008	0.09 (0.34)	-0.58, 0.77
λ	Year	Intercept (2009)	1.75 (0.21)	1.34, 2.17
		2007	-0.95 (0.40)	-1.73, -0.18
		2008	-0.78 (0.30)	-1.37, -0.19

Table 11.—Parameter estimates on the logit scale for individual-level covariates best explaining survival probabilities of the CJS model. Parameter estimates for categorical variables (Route and Release Group) are estimated as differences from a reference category set as the intercept. Parameter estimates for Release Group and Route:Release Group interaction terms can be found in Appendix Table 4.4.

Parameter modeled	Variable	Group description	$\hat{\beta}$ (SE)	95% Confidence interval (±1.96 SE)
S		Intercept (Sacramento R., Release group 5)	0.13 (0.50)	-0.84, 1.10
	Route	Sutter and Steamboat S.	-0.01 (0.81)	-1.60, 1.58
		Interior Delta	-0.58 (0.91)	-2.36, 1.20
	Fork length		0.26 (0.09)	0.09, 0.43
	$(I_{Sac}+I_{SS})Q_S$		0.52 (0.18)	0.17, 0.87
p	Year	Intercept (2009)	1.59 (0.20)	1.20, 1.98
		2007	-0.80 (0.37)	-1.53, -0.06
		2008	0.02 (0.35)	-0.67, 0.70
λ	Year	Intercept (2009)	1.77 (0.21)	1.35, 2.18
		2007	-0.90 (0.39)	-1.66, -0.13
		2008	-0.83 (0.30)	-1.43, -0.24
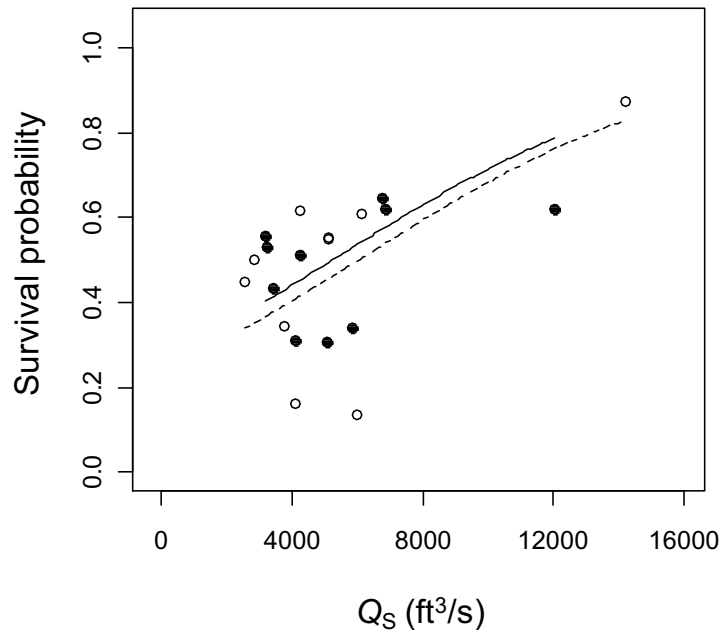
Figure 7.—Predicted survival as a function of Q_S for the Sacramento River (solid line) and Sutter and Steamboat sloughs (dotted line) plotted against survival probabilities for the Sacramento River (filled circles) and Sutter and Steamboat sloughs (open circles). The fully saturated model was used to estimate route- and release group-specific survival probabilities. Predicted survival is plotted at the mean of group-specific intercepts estimated under the best-fit group covariate model.
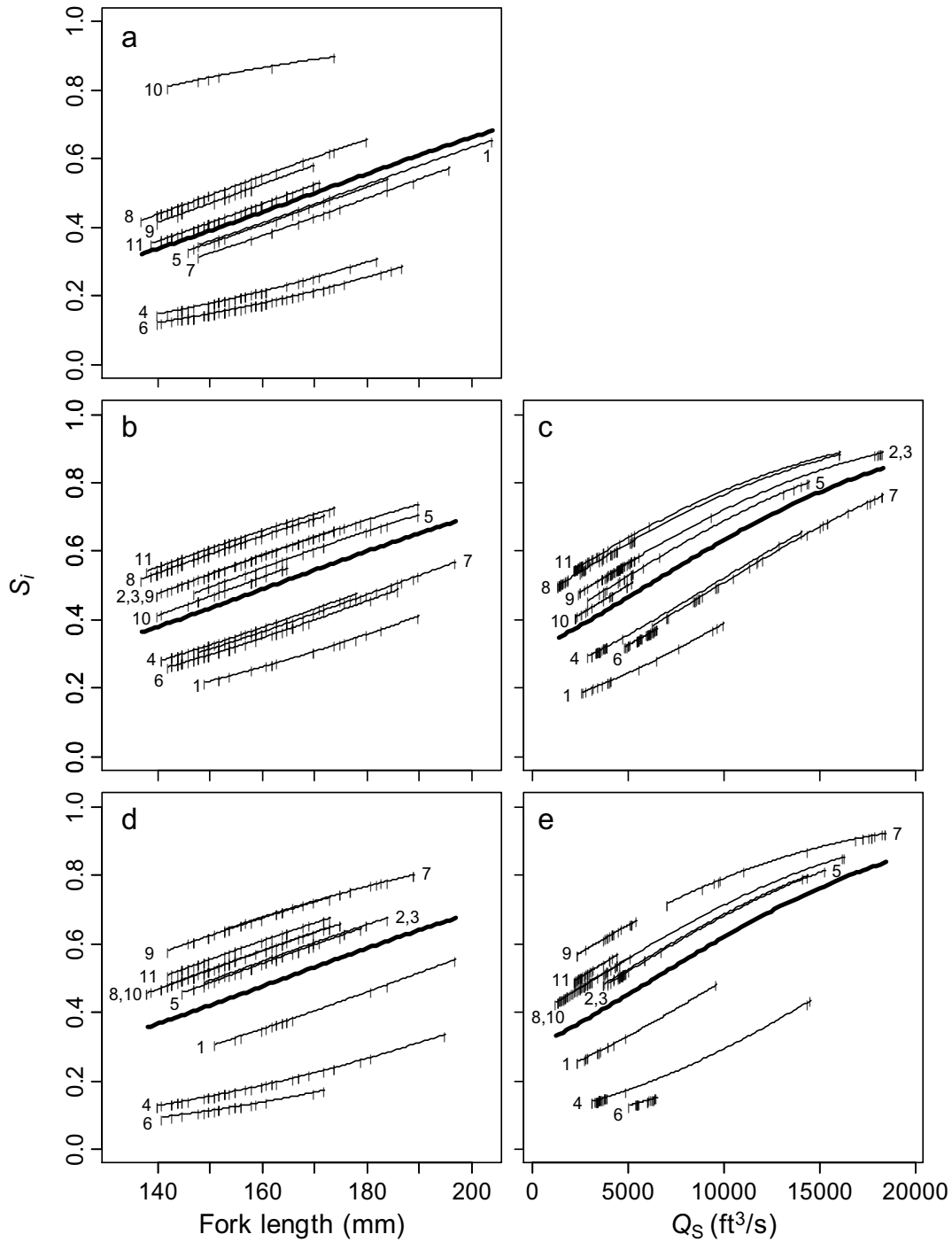
Figure 8.—Predicted individual survival probabilities as a function of fork length (a, b, and d) and Q_S (c and e) for the interior Delta (a), the Sacramento River (b and c), and Sutter and Steamboat sloughs (d and e). Survival probabilities with respect to Q_S are calculated at the mean fork length (156.5 mm) and with respect to fork length are calculated at the mean discharge (5127 ft³/s). Symbols show either observed fork lengths (a, b, and d) or observed flows when each fish entered a migration route (c and e). Each line is labeled by release group as defined in Table 5.2. The heavy line shows predicted survival plotted at the mean of release group-specific intercepts.

25

flow. Thus, water management actions that influence routing of fish as well as survival within routes can have a compounding effect on population survival.

Although smolt survival in two routes was positively associated with river flow, it is important to recognize that other variables correlated to river flow likely also affect survival. For example, tidal fluctuations may affect survival of juvenile salmon by influencing predator encounter rates. As river inflow increases, tidal fluctuations in discharge are dampened (Figure 2). In turn, the point at which the Sacramento River reverses direction on flood tides moves further downstream. These hydrodynamics govern the movements of juvenile salmon by advecting fish upstream on flood tides. Tidal excursions are large when river inflow is low, which increases the distance that fish are advected upstream. Fish pass stationary predators at most once when river discharge is unidirectional, but fish may experience multiple encounters with predators when they are advected upstream with the tides. Thus, although survival decreased with lower discharge, survival was also inversely related to tidal fluctuations. We suspect that the steepness of flow-survival relation is driven by both river inflow and by tidal fluctuations that affect predator encounter rates. Due to the correlation of river flow with other variables that might affect survival, caution should be exercised when using the flow-survival relation to predict survival in response to water management actions. For example, structural changes to the Delta that alter the relation between river flow and tidal dynamics (e.g., levee breaches) could change the relation between river discharge and survival.

Inability to identify a relation between flow and survival for the interior Delta is not unexpected given the small sample size relative to the spatial and hydrodynamic complexity of the interior Delta. Only 287 fish entered the interior Delta whereas 645 fish from both the Sacramento River and Sutter and Steamboat sloughs were used to estimate the relation between survival and Q_S. To detect a significant covariate effect, Hoffman and Skalski (1995) showed that 300 fish were needed to achieve 70% power (α = 0.05) when the individual covariate caused survival to range between 0.5 and 1.0. Baseline survival and capture probabilities in their simulation was on the same order of magnitude observed here, but their study was comprised of three intervals (i.e., reaches), all of which informed the estimate of the slope. In our case, we modeled a single reach and had smaller sample size. Thus, even if an underlying relation existed, power to detect such a relation was likely low.

The interior Delta is a complex environment with multiple alternative migration routes, which also makes it difficult to link mean river flows to survival. Each migration pathway through the interior Delta differs in biotic and abiotic processes that could influence survival. Furthermore, hydrodynamics in the interior Delta are affected not only by river inflow and water exports, but also by tidal dynamics. The particular migration route used by fish migrating through the interior Delta is probably determined more

by hourly-scale flow patterns when fish enter this region, rather than by daily scale mean flows as used in our analysis. In turn, the particular pathway used to migrate through the interior Delta could ultimately determine an individual's probability of surviving. Although the interplay between mean river inputs and exports may influence migration routing and survival, given the complexity of the interior Delta, substantially larger sample sizes over a wide range of conditions will likely be needed to detect such an effect. Newman and Brandes (2010) came to the same conclusion in an analysis of the export effects of survival of coded-wire-tagged juvenile salmon. Similar to our findings, they found that survival of fish through the Interior Delta was substantially lower than fish migrating through the Sacramento River. However, unexplained environmental variability was so large that an effect of exports on survival was not favored over other models that excluded an export effect.

Although a positive relation between survival and fish size is unsurprising, mechanisms driving this relation are less clear. Large juvenile salmon are better able to evade predators and preclude consumption by smaller predators (Sogard, 1997). However, a tag effect could also partially explain size-dependent survival. In this study, fish size was restricted above 140 mm to maintain tag-to-body mass ratios below 5%, a threshold beyond which growth and swimming performance of tagged juvenile salmon declines (Adams et al., 1998a, 1998b). Nonetheless, negative effects of the transmitter may persist: larger fish are better able to carry a tag of a given size. Thus, the magnitude with which size affects survival may be influenced by both predation and the effect of the tag. That is, smaller tagged fish may be less capable of evading predators than similarly sized untagged fish, whereas differences in survival between tagged and untagged fish may disappear as fish size increases. Such an interaction would increase the slope of the relation between fish size and survival relative to that expected for untagged fish. This potential interaction should be kept in mind when interpreting size-dependent survival observed in this study.

Among release groups, we identified systematic differences in survival among years and between studies. Mechanisms driving release-, year- and study-specific differences in survival remain unknown, but we present three alternative hypotheses: 1) episodic events related to handling and release of tagged fish, 2) differences in expression of post-release mortality experienced by fish released at different locations, and 3) environmental factors that may have influenced survival but were not included in the model. First, the nature of mark-recapture studies requires that animals be handled, tagged, transported, and released; therefore, such studies are subject to unforeseen events that may subsequently compromise the survival of tagged animals. For example, release group 1 may have experienced handling mortality due to buckling of the net pen in which fish were held (P. Brandes, USFWS, personal communication), but the extent of this mortality is unknown.

A second possible mechanism explaining study-specific differences in survival is initial culling of unfit hatchery fish that occurs shortly after release. On average, fish released for the USFWS study exhibited lower survival, but were also released into the Sacramento River >176 km downstream of fish from the CALFED study. Since late-fall Chinook used in this study were obtained directly from a hatchery, all fish were naïve to the natural river environment and likely underwent some period of acclimation during which they could have been subject to higher mortality. If fish released further upriver experienced such mortality prior to arrival in Delta whereas fish released downriver had not yet fully expressed this mortality upon entering the Delta, then differences in route-specific survival might be expected. Such differential mortality among groups of fish released in different locations has been suspected in the both the Columbia River (Muir et al., 2001; Skalski et al., 2009) and the Sacramento River (Newman, 2003). Although a plausible explanation, this hypothesis is not supported by observed survival estimates for 2009. Release locations in 2009 were the same as in 2008 yet survival estimates between studies were similar (Figure 8).

A third explanation is that we failed to include critical variables that would explain the remaining variability among release groups not accounted for by migration route, river flow, or fish size. Since predation is a major source of juvenile salmon mortality in the Delta (Lindley and Mohr, 2003), mechanisms influencing predation rates could account for unexplained variability in survival. For example, turbidity can affect predation rates by affecting the reaction distance at which predators can detect prey (Gregory and Levings, 1998), and recapture ratios of juvenile salmon in the Delta have been positively associated with turbidity (Newman, 2003). In addition, since arrival timing at entry points to migration routes did not completely overlap among release groups, shifts in the spatial distribution of predators could cause differential mortality among release groups over and above that expected from river flow. High temperature has also been shown to negatively affect survival of juvenile salmon in the Delta (Baker et al., 1995; Newman and Rice, 2002; Newman, 2003), but fish migrating between December and February experience a much lower and narrower range of temperatures (about 6 – 12 °C) than observed in these studies (e.g., mean temperature was 18.7°C in Newman's 2003 analysis). These hypotheses remain fruitful avenues of exploration to explain release-to-release variation in survival not explained by migration route, river flow, and fish size.

In a system complex as the Delta, management models are needed to understand how human- and natural-caused changes to the Delta influence dynamics of endangered fish populations. However, parameterizing such models with empirical data is difficult precisely due to the Delta's complexity. Our analysis has taken an important step by providing a modeling framework and quantifying important mechanisms affecting survival. We found that survival differed among migration routes and was

influenced by fish size and route-specific river flow. These relationships can be incorporated into the multistate framework to quantify population-level survival in response to survival in different migration routes. Although route-specific survival is clearly an important component of population survival, understanding the dynamics of migration routing is also critical. Given dynamic relationships for both migration routing and survival, managers can begin to understand how both components change simultaneously to drive survival of juvenile salmon emigrating through the Delta.

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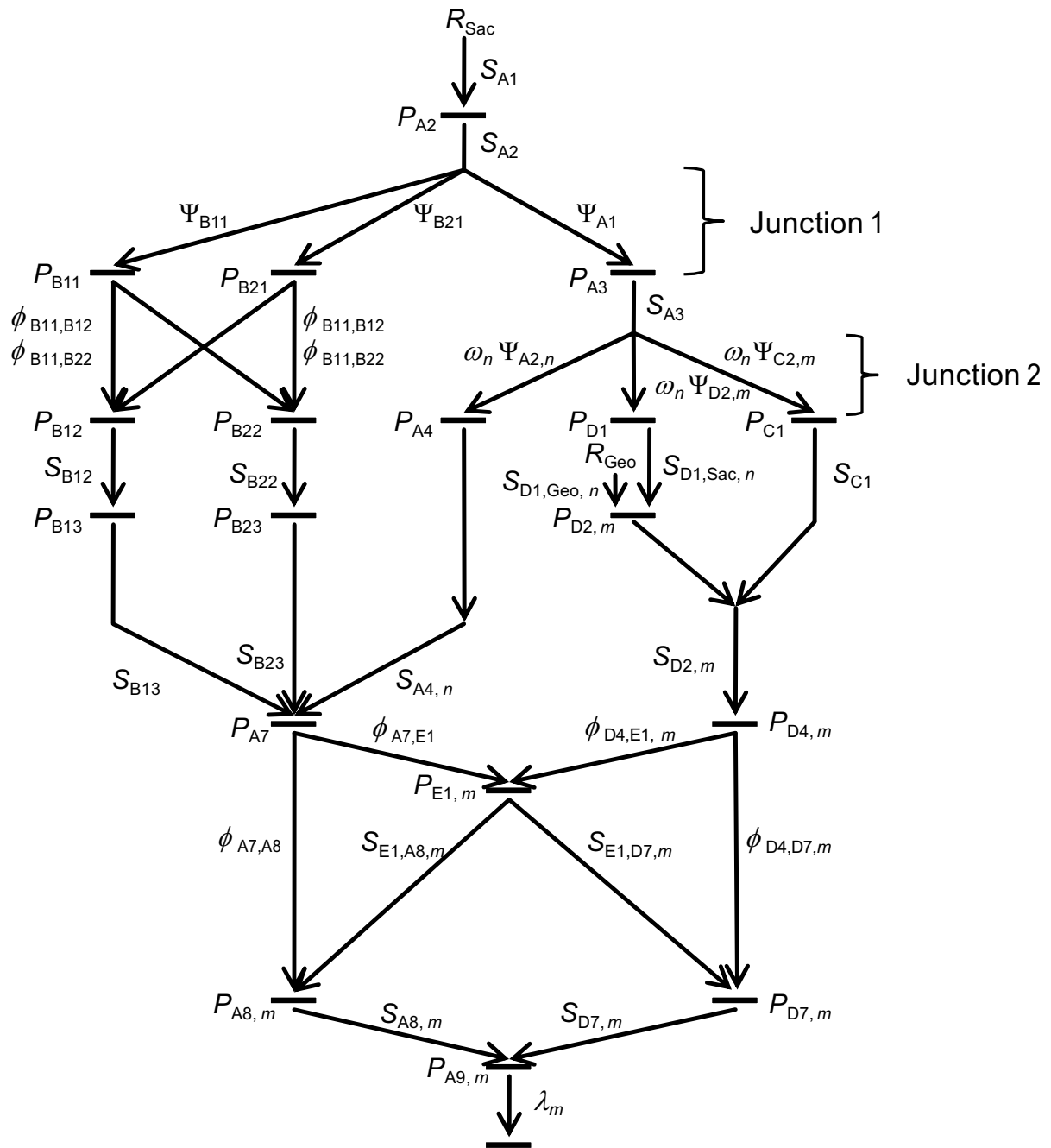
Appendix Figure 1. Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (Ψ_{hl}), and joint survival-entrainment ($\phi_{hi,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made in December 2008 and January 2009. Release sites are denoted by R_m (m = Sac (Sacramento) and Geo (Georgiana Slough)), parameters subscripted by n are conditional on the position of the Delta Cross Channel gate, and m denote parameters which can be estimated separately for each release site.

Appendix Table 1. Counts of detection histories for the model shown in Figure 4.2 for a release of R_1 = 208 fish on 4 December 2007 and R_2 = 211 fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A "0" indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with "0 0 0 D" indicate fish released in Georgiana Slough whereas those beginning with "A" are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0	67	0 0 0 D 0 0 0 0 0 0	42
0 0 0 D D 0 0 0 0 0	7	0 0 0 D D 0 0 0 0 0	19
0 0 0 D D 0 D 0 0 0	1	0 0 0 D D D 0 0 0 0	17
0 0 0 D D D 0 0 0 0	11	0 0 0 D D D 0 0 0 A	1
0 0 0 D D D 0 0 A A	1	0 0 0 D D D 0 0 A A	4
0 0 0 D D D D 0 0 0	2	0 0 0 D D D D 0 A 0	2
0 0 0 D D D D 0 0 A	4	0 0 0 D D D D 0 A A	11
0 0 0 D D D D 0 A A	4	0 0 0 D D D DE 0 0 0	1
0 0 0 D D D DE 0 0 0	1	0 0 0 D D D DE EA 0 0	1
0 0 0 D D D DE EA A A	2	0 0 0 D D D DE EA A A	2
A 0 0 0 0 0 0 0 0 0	21	A 0 0 0 0 0 0 0 0 0	23
A 0 A a 0 0 0 0 A A	1	A 0 A d D D 0 0 A A	1
A 0 A a 0 0 A 0 0 0	1	A 0 B2 0 0 0 0 0 0 0	1
A 0 A a 0 0 A 0 A A	1	A 0 B2 B2 0 0 0 0 0 0	1
A 0 A a 0 A 0 0 0 A	1	A A 0 0 0 0 0 0 0 0	23
A 0 A a 0 A 0 0 A 0	1	A A A 0 0 0 0 0 0 0	13
A 0 B1 0 B2 A AE 0 0 0	1	A A A a 0 0 0 0 0 0	24
A A 0 0 0 0 0 0 0 0	14	A A A a 0 0 0 0 0 A	3
A A 0 0 B2 A A 0 A 0	1	A A A a 0 0 0 0 A 0	1
A A 0 d D D 0 0 0 0	1	A A A a 0 0 0 0 A A	1
A A 0 B2 0 0 A 0 0 0	1	A A A a 0 0 A 0 0 A	2
A A A 0 0 0 0 0 0 0	8	A A A a 0 0 A 0 A A	10
A A A 0 0 0 A 0 0 0	1	A A A a 0 A 0 0 0 0	1
A A A A 0 0 0 0 0 0	11	A A A a 0 A 0 0 0 A	3
A A A A 0 0 A 0 A A	4	A A A a 0 A A 0 0 0	2
A A A A 0 A 0 0 0 0	3	A A A a 0 A A 0 A 0	1
A A A A 0 A A 0 0 0	2	A A A a 0 A A 0 A A	11
A A A A 0 A A 0 0 A	1	A A A d 0 0 0 0 0 0	13
A A A A 0 A A 0 A 0	2	A A A d D 0 0 0 0 0	4
A A A A 0 A A 0 A A	3	A A A d D D 0 0 0 0	12
A A A C 0 0 0 0 0 0	13	A A A d D D D 0 0 0	2
A A A C 0 D 0 0 0 0	2	A A A d D D D 0 A A	4
A A A C 0 D D 0 0 A	1	A A A d D D DE EA 0 0	1
A A A C 0 D D 0 A 0	1	A A B1 0 0 0 0 0 0 0	3
A A A C 0 D D 0 A A	1	A A B1 B1 0 0 0 0 0 0	1
A A A D 0 0 0 0 0 0	1	A A B1 B1 B1 0 0 0 0 0	1
A A A D D 0 0 0 0 0	1	A A B1 B1 B1 0 A 0 0 A	1
A A A D D D 0 0 0 0	4	A A B1 B1 B1 A 0 0 0 A	1
A A A D D D D 0 A A	3	A A B1 B1 B1 A 0 0 A A	1

34

A A A D D D DE 0 A A	1	A A B1 B1 B1 A A 0 A A	2
A A A a 0 0 0 0 0 0	4	A A B1 B2 0 0 0 0 00	1
A A A a 0 0 0 0 A 0	2	A A B1 B2 B2 0 A 0 A A	1
A A A a 0 0 A 0 0 A	1	A A B1 B2 B2 A 0 0 00	1
A A A a 0 0 A 0 A 0	1	A A B1 B2 B2 A A 0 A A	1
A A A a 0 0 A 0 A A	1	A A B2 0 0 0 0 0 0	3
A A A a 0 0 AE 0 0 0	1	A A B2 B1 0 0 0 0 00	1
A A A a 0 0 AE 0 A A	1	A A B2 B1 B1 0 0 0 A A	1
A A A a 0 A 0 0 0 0	3	A A B2 B1 B1 A 0 0 0 0	1
A A A a 0 A 0 0 A A	3	A A B2 B1 B1 A A 0 A A	1
A A A a 0 A A 0 0 0	2	A A B2 B2 0 0 0 0 00	2
A A A a 0 A A 0 A 0	1	A A B2 B2 B2 0 0 0 00	2
A A A a 0 A A 0 A A	5	A A B2 B2 B2 0 A 0 A A	2
A A A d 0 0 0 0 0 0	1	A A B2 B2 B2 A 0 0 0 A	2
A A A d D 0 0 0 0 0	2	A A B2 B2 B2 A 0 0 A A	1
A A A d D 0 D 0 A A	1	A A B2 B2 B2 A A 0 0 0	1
A A A d D D 0 0 0 0	3	A A B2 B2 B2 A A 0 A 0	2
A A A d D D 0 0 A A	1	A A B2 B2 B2 A A 0 A A	2
A A A d D D D 0 A A	4		
A A A d D D DE EA 0 0	1		
A A B1 0 0 0 0 0 0 0	12		
A A B1 0 B1 A A 0 A A	1		
A A B1 B1 0 0 0 0 00	2		
A A B1 B1 B1 0 0 0 00	5		
A A B1 B1 B1 0 A 0 0 0	1		
A A B1 B1 B1 0 AE ED A A	1		
A A B1 B1 B1 A A 0 0 A	1		
A A B1 B1 B1 A A 0 A A	2		
A A B1 B1 B1 A AE 0 A 0	1		
A A B1 B2 0 A A 0 A A	1		
A A B1 B2 B2 A A 0 00	3		
A A B1 B2 B2 A A 0 A 0	1		
A A B1 B2 B2 A A 0 A A	1		
A A B2 B2 0 0 0 0 00	1		
A A B2 B2 0 A A 0 0 A	1		
A A B2 B2 B2 0 0 0 A A	2		
A A B2 B2 B2 0 A 0 0 A	1		
A A B2 B2 B2 A 0 0 00	1		
A A B2 B2 B2 A 0 0 A A	1		
A A B2 B2 B2 A A 0 A 0	1		
A A B2 B2 B2 A A 0 A A	6		
A A B2 B2 B2 A AE ED 0 0	1		
Total released (R_k)	292		292

Appendix Table 2. Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
$\phi_{B21,B12}$	$= 0$	Ψ_{C2}	$= 0$
$\phi_{B21,B22}$	$= 1$	$\Psi_{A2,open}$	$= 0$
S_{B23}	$= 1$	ω_{open}	$= 0$
$S_{D1,open}$	$= S_{D1,closed}$	$S_{D1,open}$	$= 0$
$P_{E1,Sac}$	$= 1$	$S_{A4,open}$	$= 0$
$P_{E1,Geo}$	$= 1$	S_{C1}	$= 0$
P_{B21}	$= P_{B11}$	$S_{E1,D7}$	$= 0$
P_{B13}	$= 1$	$\phi_{A7,E1}$	$= 0$
P_{C1}	$= 1$	P_{A3}	$= 0$
P_{D1}	$= 1$	P_{A4}	$= 1$
$P_{D2,Sac}$	$= 1$	P_{B11}	$= 1$
$P_{D2,Geo}$	$= 1$	P_{B12}	$= 1$
		P_{B13}	$= 1$
		P_{B21}	$= 1$
		P_{B22}	$= 1$
		P_{B23}	$= 1$
		P_{C1}	$= 0$
		P_{D1}	$= 1$
		$P_{D2,Sac}$	$= 1$
		$P_{D3,Sac}$	$= 1$
		$P_{D4,Sac}$	$= 1$
		$P_{E1,Sac}$	$= 1$
		$P_{D2,Geo}$	$= 1$
		$P_{D4,Geo}$	$= 1$
		$P_{A8,Geo}$	$= 1$
		$P_{E1,Geo}$	$= 1$

Appendix Table 3. Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2008 (R_1) and January, 2009 (R_2). For both release dates, survival in the interior Delta was set equal between release sites (Sacramento, Georgiana Slough) based on lack of significance of likelihood ratios tests. 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 2008 Estimate ($\widehat{SE}$)	95% Profile likelihood interval	R_2: January 2009 Estimate ($\widehat{SE}$)	95% Profile likelihood interval
S_{A1}	0.894 (0.023)	0.844, 0.933	0.883 (0.024)	0.832, 0.924
S_{A2}	0.920 (0.022)	0.870, 0.957	0.861 (0.027)	0.804, 0.908
S_{A3}	0.928 (0.026)	0.867, 0.970	0.881 (0.031)	0.811, 0.933
$S_{A4, open}$	0.600 (0.101)	0.401, 0.785	NA	
$S_{A4, closed}$	0.901 (0.066)	0.744, 1.005	0.616 (0.068)	0.482, 0.746
S_{A7}	0.924 (0.049)	0.815, 1.016	0.944 (0.053)	0.812, 1.030
S_{A8}	0.791 (0.062)	0.658, 0.900	0.902 (0.050)	0.783, 0.979
S_{B11}	0.413 (0.086)	0.256, 0.586	0.674 (0.155)	0.390, 0.980
S_{B12}	0.846 (0.100)	0.596, 0.964	0.818 (0.116)	0.537, 0.967
S_{B13}	0.606 (0.148)	0.321, 0.860	0.923 (0.111)	0.616, 1.063
S_{B21}	1.000	NA	0.826 (0.079)	0.641, 0.942
S_{B22}	0.962 (0.042)	0.829, 1.006	0.789 (0.094)	0.576, 0.929
S_{B23}	1.000	NA	0.900 (0.093)	0.665, 1.037
S_{C1}	0.286 (0.109)	0.113, 0.522	NA	
$S_{D1,Sac}$	0.917 (0.056)	0.764, 0.986	0.649 (0.078)	0.489, 0.789
$S_{D1,Geo}$	0.330 (0.047)	0.243, 0.426	0.580 (0.049)	0.482, 0.674
S_{D2}	0.844 (0.057)	0.722, 0.952	0.720 (0.050)	0.617, 0.809
S_{D4}	0.576 (0.074)	0.431, 0.716	0.518 (0.067)	0.389, 0.648
S_{D7}	0.862 (0.080)	0.676, 0.983	0.919 (0.071)	0.731, 1.014
$S_{E1,D7}$	0.686 (0.198)	0.289, 0.968	0.000	NA
$S_{E1,A8}$	0.847 (0.190)	0.393, 1.065	0.800 (0.179)	0.372, 0.987
ω_{open}	0.550 (0.05)	0.451, 0.646		
Ψ_{A1}	0.679 (0.037)	0.603, 0.749	0.747 (0.036)	0.672, 0.812
Ψ_{B11}	0.217 (0.033)	0.157, 0.288	0.096 (0.024)	0.055, 0.151
Ψ_{B21}	0.104 (0.025)	0.062, 0.158	0.158 (0.030)	0.105, 0.222
$\Psi_{A2,open}$	0.488 (0.068)	0.357, 0.619	0.000	NA
$\Psi_{A2,closed}$	0.687 (0.069)	0.543, 0.810	0.615 (0.050)	0.515, 0.708
Ψ_{C2}	0.329 (0.064)	0.214, 0.460	0.000	NA
$\Psi_{D2,open}$	0.183 (0.052)	0.096, 0.299	0.000	NA
$\Psi_{D2,closed}$	0.313 (0.069)	0.190, 0.455	0.385 (0.050)	0.292, 0.485
$\phi_{B21,B12}$	0.000	NA	0.174 (0.079)	0.058, 0.359
$\phi_{B21,B22}$	1.000	NA	0.652 (0.099)	0.449, 0.823
$\phi_{B11,B12}$	0.413 (0.086)	0.256, 0.586	0.500 (0.134)	0.255, 0.745
$\phi_{B11,B22}$	0.223 (0.073)	0.104, 0.384	0.286 (0.121)	0.099, 0.545
$\phi_{A7,A8}$	0.843 (0.057)	0.724, 0.950	0.944 (0.053)	0.812, 1.030
$\phi_{A7,E1}$	0.081 (0.032)	0.033, 0.158	0.000	NA

Appendix Table 3. Continued.

$\phi_{D4,D7}$	0.479 (0.074)	0.339, 0.624	0.433 (0.066)	0.309, 0.566
$\phi_{D4,E1}$	0.097 (0.041)	0.037, 0.198	0.085 (0.036)	0.031, 0.173
P_{A2}	0.962 (0.015)	0.924, 0.974	0.979 (0.012)	0.948, 1.000
P_{A3}	0.990 (0.010)	0.956, 0.999	1.000	NA
P_{A4}	0.976 (0.024)	0.899, 0.999	1.000	NA
P_{A7}	0.689 (0.056)	0.573, 0.790	0.585 (0.068)	0.451, 0.711
$P_{A8,Sac}$	0.765 (0.059)	0.637, 0.866	0.716 (0.064)	0.582, 0.829
$P_{A8,Geo}$	0.765 (0.059)	0.637, 0.866	1.000	NA
$P_{A9,Sac}$	0.825 (0.048)	0.720, 0.905	0.761 (0.060)	0.633, 0.864
$P_{A9,Geo}$	0.825 (0.048)	0.720, 0.905	0.947 (0.052)	0.787, 1.000
P_{B11}	0.947 (0.036)	0.846, 0.991	1.000	NA
P_{B12}	0.917 (0.080)	0.681, 0.995	1.000	NA
P_{B21}	0.947 (0.036)	0.846, 0.991	1.000	NA
P_{B22}	0.915 (0.057)	0.761, 0.985	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	0.865 (0.072)	0.687, 0.962	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
$P_{D4,Geo}$	0.931 (0.047)	0.802, 0.978	1.000	NA
$P_{D4,Sac}$	0.931 (0.047)	0.802, 0.978	1.000	NA
$P_{D7,Geo}$	0.833 (0.076)	0.654, 0.945	0.707 (0.110)	0.475, 0.883
$P_{D7,Sac}$	0.833 (0.076)	0.654, 0.945	0.836 (0.149)	0.462, 1.000
P_{E1}	1.000	NA	1.000	NA
λ	0.813 (0.049)	0.706, 0.895	0.901 (0.038)	0.810, 0.959

Appendix Table 4. Parameter estimates on the logit scale for the effect Release Group and Route:Release Group on survival for the best-fit individual covariate model.

Coefficient	$\hat{\beta}$ (SE)	95% Confidence interval (± 1.96 SE)
Release 1	-1.24 (0.75)	-2.71, 0.23
Release 2,3	0.15 (0.63)	-1.08, 1.39
Release 4	-0.71 (0.61)	-1.90, 0.49
Release 6	-0.84 (0.58)	-1.98, 0.30
Release 7	-0.76 (0.69)	-2.10, 0.58
Release 8	0.39 (0.59)	-0.76, 1.54
Release 9	0.15 (0.61)	-1.04, 1.34
Release 10	-0.11 (0.70)	-1.48, 1.26
Release 11	0.46 (0.58)	-0.68, 1.60
I_{SS}:Release 1	0.43 (1.14)	-1.81, 2.67
I_{SS}:Release 2,3	-0.18 (0.98)	-2.11, 1.75
I_{SS}:Release 4	-0.96 (0.98)	-2.87, 0.96
I_{SS}:Release 6	-1.19 (1.07)	-3.28, 0.90
I_{SS}:Release 7	1.31 (1.40)	-1.44, 4.06
I_{SS}:Release 8	-0.27 (0.91)	-2.04, 1.51
I_{SS}:Release 9	0.39 (1.00)	-1.57, 2.34
I_{SS}:Release 10	0.24 (1.09)	-1.90, 2.37
I_{SS}:Release 11	-0.21 (0.92)	-2.01, 1.59
I_{ID}:Release 1	1.27 (1.35)	-1.39, 3.92
I_{ID}:Release 4	-0.22 (1.04)	-2.26, 1.82
I_{ID}:Release 6	-0.31 (1.01)	-2.29, 1.67
I_{ID}:Release 7	0.63 (1.20)	-1.72, 2.98
I_{ID}:Release 8	0.19 (1.00)	-1.78, 2.15
I_{ID}:Release 9	0.33 (1.09)	-1.81, 2.47
I_{ID}:Release 10	2.35 (1.60)	-0.77, 5.48
I_{ID}:Release 11	-0.21 (0.99)	-2.16, 1.74