Effect of Tides, River Flow, and Gate Operations on Entrainment of Juvenile Salmon into the Interior Sacramento–San Joaquin River Delta

Russell W. Perry[a], Patricia L. Brandes[b], Jon R. Burau[c], Philip T. Sandstrom[df] & John R. Skalski[e]

[a] U.S. Geological Survey, Western Fisheries Research Center, 5501A Cook-Underwood Road, Cook, Washington 98605, USA

[b] Stockton Fish and Wildlife Office, 850 Guild Avenue, Suite 105, Lodi, California 95240, USA

[c] U.S. Geological Survey, California Water Science Center, 6000 J Street, Placer Hall, Sacramento, California 95819, USA

[d] Biotelemetry Laboratory, Department of Wildlife, Fish, and Conservation Biology, University of California, 1334 Academic Surge, Davis, California 95616, USA

[e] School of Aquatic and Fishery Sciences, University of Washington, 1325 Fourth Avenue, Suite 1820, Seattle, Washington 98101-2509, USA

[f] Present address: Washington Department of Fish and Wildlife, 1111 Washington Street Southeast, Olympia, Washington 98501, USA.
Published online: 08 Apr 2015.

PLEASE SCROLL DOWN FOR ARTICLE

ARTICLE

Effect of Tides, River Flow, and Gate Operations on Entrainment of Juvenile Salmon into the Interior Sacramento–San Joaquin River Delta

Russell W. Perry*

U.S. Geological Survey, Western Fisheries Research Center, 5501A Cook-Underwood Road, Cook, Washington 98605, USA

Patricia L. Brandes

Stockton Fish and Wildlife Office, 850 Guild Avenue, Suite 105, Lodi, California 95240, USA

Jon R. Burau

U.S. Geological Survey, California Water Science Center, 6000 J Street, Placer Hall, Sacramento, California 95819, USA

Philip T. Sandstrom[1]

Biotelemetry Laboratory, Department of Wildlife, Fish, and Conservation Biology, University of California, 1334 Academic Surge, Davis, California 95616, USA

John R. Skalski

School of Aquatic and Fishery Sciences, University of Washington, 1325 Fourth Avenue, Suite 1820, Seattle, Washington 98101-2509, USA

Abstract

Juvenile Chinook Salmon *Oncorhynchus tshawytscha* emigrating from natal tributaries of the Sacramento River, California, must negotiate the Sacramento–San Joaquin River Delta (hereafter, the Delta), a complex network of natural and man-made channels linking the Sacramento River with San Francisco Bay. Fish that enter the interior and southern Delta—the region to the south of the Sacramento River where water pumping stations are located—survive at a lower rate than fish that use alternative migration routes. Consequently, total survival decreases as the fraction of the population entering the interior Delta increases, thus spurring management actions to reduce the proportion of fish that are entrained into the interior Delta. To better inform management actions, we modeled entrainment probability as a function of hydrodynamic variables. We fitted alternative entrainment models to telemetry data that identified when tagged fish in the Sacramento River entered two river channels leading to the interior Delta (Georgiana Slough and the gated Delta Cross Channel). We found that the probability of entrainment into the interior Delta through both channels depended strongly on the river flow and tidal stage at the time of fish arrival at the river junction. Fish that arrived during ebb tides had a low entrainment probability, whereas fish that arrived during flood tides (i.e., when the river's flow was reversed) had a high probability of entering the interior Delta. We coupled our entrainment model with a flow simulation model to evaluate the effect of nighttime closures of the Delta Cross Channel gates on the daily probability of fish entrainment into the interior Delta. Relative to 24-h gate closures, nighttime closures increased daily entrainment probability by 3 percentage points on average if fish arrived at the river junction uniformly throughout the day and by only 1.3 percentage points if 85% of fish arrived at night. We illustrate how our model can be used to evaluate the effects of alternative water management actions on fish entrainment into the interior Delta.

*Corresponding author: rperry@usgs.gov
[1]Present address: Washington Department of Fish and Wildlife, 1111 Washington Street Southeast, Olympia, Washington 98501, USA.

Regulated rivers are managed to balance human demands (e.g., electricity generation and water withdrawal) with the maintenance of functioning aquatic ecosystems. In rivers supporting depressed populations of anadromous salmonids, this balance often involves assessing water management actions that can improve the survival of seaward-migrating juvenile salmon at the expense of using water for human benefits (Williams 2006). For example, passing water over spillways at dams increases the total survival of juvenile salmon by diverting fish away from high-mortality turbines, but this comes at the cost of foregone electricity generation (Williams 2008). Although such tradeoffs are fundamental to the management of natural resources, understanding how fish behave in response to their environment can aid in developing water management actions that provide ecosystem services while reducing negative effects on fish populations.

The Sacramento–San Joaquin River Delta (hereafter, the Delta) in California is a complex network of channels that has been highly altered to convey water for domestic and agricultural uses via two large pumping stations in the interior Delta (Nichols et al. 1986; Figure 1). Threatened populations of juvenile salmonids emigrating from the Sacramento River distribute among these channels and use multiple migration routes on their seaward journey (Perry et al. 2010). Migration routes vary in width and length as well as in biotic and abiotic factors, all of which influence the survival of juvenile salmon. For instance, juvenile Chinook Salmon *Oncorhynchus*

tshawytscha that migrate through the interior Delta survive at lower rates than fish that migrate within the Sacramento River (Figure 1), likely due to high predation rates, longer migration times, and entrainment into water pumping stations (Newman and Brandes 2010; Perry et al. 2010, 2013). Because the survival of juvenile salmon in the interior Delta is lower than that in other routes, the total survival of smolts decreases as the fraction of the smolt population entering the interior Delta increases (Perry et al. 2013).

Juvenile Chinook Salmon enter the interior Delta via two channels that diverge from the Sacramento River (Figure 1). Fish first migrate past the Delta Cross Channel, a man-made, gated channel that is used to divert water into the interior Delta to reduce salinities at the pumping stations. Fish that remain in the Sacramento River then encounter Georgiana Slough, a natural channel that is located 1 km downstream from the entrance to the Delta Cross Channel. Up to 50% of juvenile Chinook Salmon encountering these two channels may be entrained into the interior Delta, exposing a substantial fraction of the population to low survival probabilities (Perry 2010). Consequently, the Delta Cross Channel is operated in a precautionary manner by closing the gates during the emigration period of endangered winter-run juvenile Chinook Salmon; this strategy is employed under the assumption that fish entrainment into the Delta Cross Channel is directly proportional to the mean fraction of river flow that is diverted to the interior Delta (SWRCB 1995; Low et al. 2006). However, the validity of this assumption is unclear,
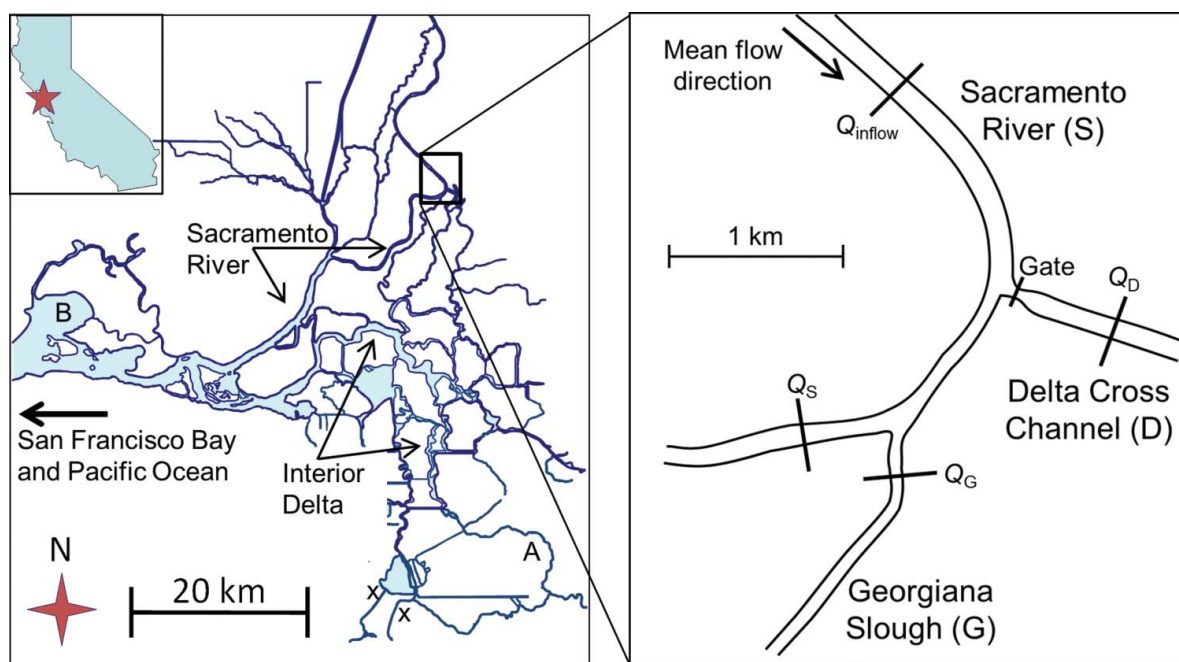
FIGURE 1.   Map of the Sacramento–San Joaquin River Delta, with exploded view showing the junction of the Sacramento River with the Delta Cross Channel and Georgiana Slough. Discharge gauging stations in each channel are labeled as Q_j (Q_S = Sacramento River gauging station; Q_D = Delta Cross Channel gauging station; Q_G = Georgiana Slough gauging station). Other labels as follows: A = San Joaquin River; B = Suisun Bay; Gate = Delta Cross Channel gate; and X = water pumping stations in the southern Delta. [Figure available online in color.]

as fish passing the Delta Cross Channel may be subsequently entrained into Georgiana Slough.

Quantifying the factors that affect migration routing at this river junction is challenging because fish behavior and complex physical processes may interact to cause the entrained fraction of fish to deviate from the mean fraction of flow entering the interior Delta. Tidal forcing causes the Sacramento River to reverse direction twice daily at river flows less than about 566 m³/s (as measured at Freeport, U.S. Geological Survey station number 11447650). This tidal forcing causes the relative distribution of flows among the three channels to vary over hourly time scales. For example, nearly all of the river's flow is diverted into the Delta Cross Channel and Georgiana Slough during reverse-flow flood tides, whereas little discharge enters the Delta Cross Channel during ebb tides. Given this hourly variation, the probability of fish entry into a given channel (i.e., entrainment probability) will depend on the hydraulic conditions that the fish encounter when migrating past each channel's entrance (Steel et al. 2013). In addition, late-fall Chinook Salmon smolts have been shown to exhibit nocturnal migration behavior in the Sacramento River (Chapman et al. 2013), and spring–neap cycles during winter cause larger-magnitude flood tides during the day and smaller tides at night. Consequently, the diel activity patterns of juvenile salmon may interact with tidal cycles to decouple the mean fraction of fish entering the interior Delta from the mean proportion of flow diverted into the interior Delta.

These complex interactions between behavioral and physical processes pose challenges for understanding the response of fish populations to management actions. Therefore, our objective was to develop a model that could be used to quantify the effects of various water management actions on entrainment of juvenile salmon into the interior Delta. First, we developed an entrainment model that was fitted to a multiyear telemetry data set describing tagged juvenile late-fall Chinook Salmon. This model estimated individual probabilities of entrainment into the Delta Cross Channel and Georgiana Slough as a function of time-dependent hydraulic conditions in each river channel. We illustrate how this model can be used to inform management actions by simulating fish entrainment into the interior Delta under alternative scenarios of gate operations and diel migration patterns. For this application, we hypothesized that opening the Delta Cross Channel gates during the daytime but closing them at night would allow water to be diverted while minimizing the risk of juvenile salmon entrainment. By simulating alternative management actions, we were able to gain insights into the potential effects of management actions for which outcomes would be highly uncertain and costly to implement in practice.

METHODS

Telemetry data.—To model entrainment probabilities at the Delta Cross Channel and Georgiana Slough, we compiled telemetry data on late-fall Chinook Salmon smolts from three acoustic telemetry studies. Detailed methods about telemetry systems, data processing, and tagging procedures for these studies are provided by Vogel (2008), Perry et al. (2010, 2013), and Singer et al. (2013). In total, 1,873 acoustic-tagged smolts were released in 13 discrete groups during the winters of 2007–2009 (Table 1). All fish were released into the Sacramento River a minimum of 40 km upstream of the Delta Cross Channel. To detect tagged fish as they entered each route, detection arrays consisting of one or more hydrophones were situated just downstream of the entrances to the Delta Cross Channel, Georgiana Slough, and the Sacramento River. The

TABLE 1. Sample sizes for release groups of juvenile late-fall Chinook Salmon that received acoustic tags during the winters of 2007–2009 (DCC = Delta Cross Channel). "Number detected with DCC open" indicates the number of fish that were detected at the river junction while the DCC gates were open.

Release group	Source	Year	Release dates	Number released	Number detected at junction	Number detected with DCC open
1	Perry et al. (2010, 2013)	2006	Dec 5–6	64	36	32
2	Vogel (2008)		Dec 11–12	96	57	49
3	Perry et al. (2010, 2013)	2007	Jan 17–18	80	39	0
4	Vogel (2008)		Jan 12–23	166	55	0
5	Singer et al. (2013)		Jan 16–Feb 2	200	11	0
6	Perry et al. (2010, 2013)		Dec 4–5	149	76	73
7	Singer et al. (2013)		Dec 7	150	36	3
8	Perry et al. (2010, 2013)	2008	Jan 15–16	130	85	0
9	Singer et al. (2013)		Jan 17	154	49	0
10	Perry et al. (2010, 2013)		Nov 30–Dec 4	192	91	47
11	Singer et al. (2013)		Dec 13	149	57	1
12	Singer et al. (2013)	2009	Jan 11	151	30	0
13	Perry et al. (2010, 2013)		Jan 13–17	192	92	0
All groups				1,873	714	205

fate of each tagged fish was assigned to one of the three river channels based on the time series of detections. Owing to migration through alternative routes and mortality between release sites and the study area, 38% (714 fish) of all released fish were detected at the river junction (Table 1). Of the 714 fish that were detected at the junction, 29% passed the Delta Cross Channel when its gates were open, and the remainder passed the junction after the gates were closed (Table 1).

Entrainment model.—Entrainment probability—the probability that a fish will enter one of the three alternative migration routes—was modeled as a multivariate Bernoulli random variable with the probability distribution

$$\pi_{iD}^{I_{iD}} \pi_{iG}^{I_{iG}} \pi_{iS}^{(1-I_{iD})(1-I_{iG})}, \tag{1}$$

where

π_{iD} = the probability that the ith fish ($i = 1, \ldots, n$) entered the Delta Cross Channel (D);

π_{iG} = the probability that the ith fish entered Georgiana Slough (G);

$\pi_{iS} = 1 - \pi_{iD} - \pi_{iG}$ = the probability that the ith fish entered the Sacramento River (S);

$I_{iD} = \begin{cases} 1 \text{ if the } i\text{th fish entered the Delta Cross Channel} \\ 0 \text{ otherwise; and} \end{cases}$

$I_{iG} = \begin{cases} 1 \text{ if the } i\text{th fish entered Georgiana Slough} \\ 0 \text{ otherwise.} \end{cases}$

When the Delta Cross Channel was closed, π_{iD} was equal to zero, and the probability distribution for an individual fish was reduced to $\pi_{iG}^{I_{iG}} \pi_{iS}^{(1-I_{iG})}$.

To model entrainment probabilities as a function of explanatory variables, we used a generalized linear models framework with a logit link function that was measured relative to a baseline category. The baseline category was selected to be the Sacramento River route such that

$$g(\pi_{ij}) = \log_e\left(\frac{\pi_{ij}}{\pi_{iS}}\right) = \beta_{j0} + \beta_{j1}x_{ij1} + \ldots + \beta_{jp}x_{ijp} = \boldsymbol{\beta}_{ij}'\mathbf{x}_{ij},$$

$$\tag{2}$$

where x_{ijp} is the pth covariate for the ith fish entering the jth channel ($j = $ D or G); and β_{jp} is the slope coefficient for the jth channel and the pth covariate. Entrainment probabilities were expressed as a function of covariates by using the inverse logit function, and the joint likelihood was the product of equation (1) over all observed fish (Agresti 2002). This formulation allowed π_{iD} and π_{iG} to be modeled by a separate set of explanatory variables. The regression coefficients were estimated by maximum likelihood estimation using optimization routines in R (R Development Core Team 2013). Variances were estimated by using the diagonal elements of the inverse Hessian matrix.
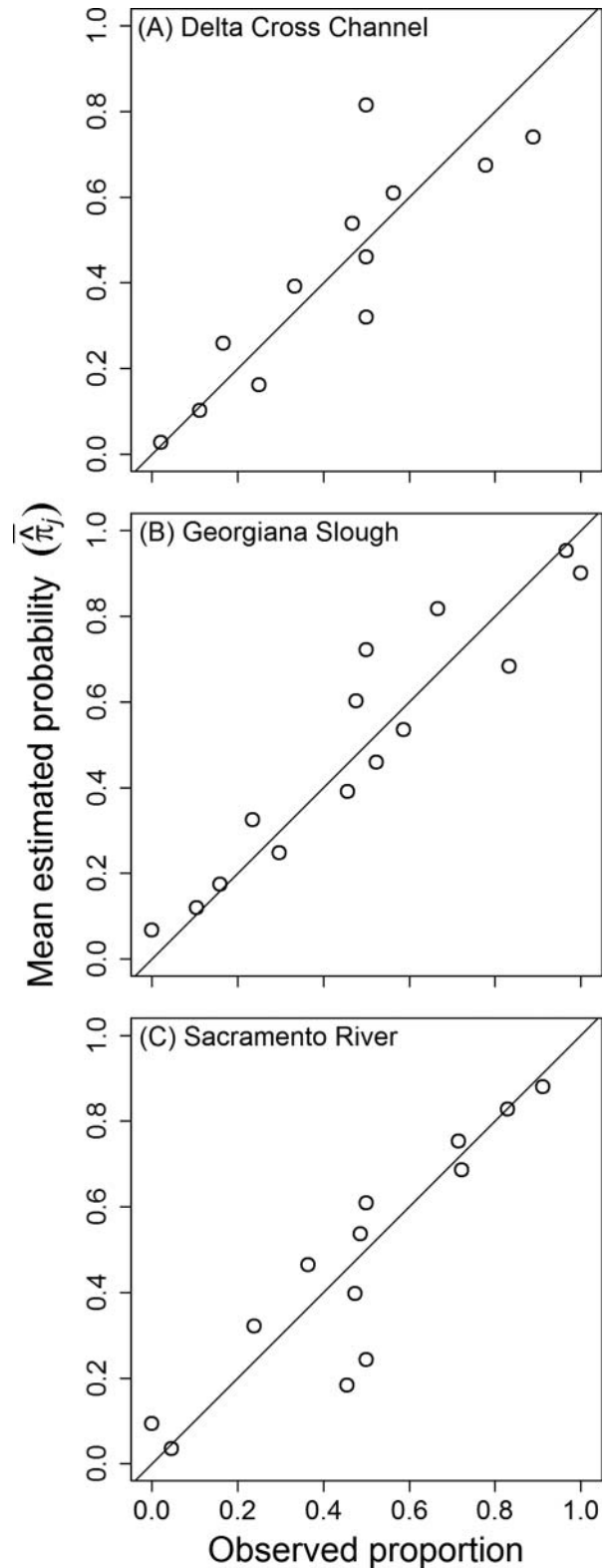

FIGURE 2. Observed proportions of juvenile Chinook Salmon entering **(A)** the Delta Cross Channel, **(B)** Georgiana Slough, and **(C)** the Sacramento River compared with the mean predicted probability of fish entry into each route. Groups were formed by discretizing the predicted probabilities into 14 intervals of equal-probability width.

Hydraulic variables.—We hypothesized that entrainment probabilities for each channel could be explained by the hydraulic conditions that were present when fish were detected as entering a given river channel. River discharge in each channel (Q_j) was the primary variable used to explain variation in entrainment probabilities (where $j = S$ for the Sacramento River, D for the Delta Cross Channel, or G for Georgiana Slough). U.S. Geological Survey gauging stations were located just downstream of the entrance to the Delta Cross Channel (station number 11336600), Georgiana Slough (station number 11447903), and the Sacramento River (station number 11447905; Figure 1). Total discharge entering the river junction was measured by a gauging station situated just upstream of the junction (Q_{inflow} in Figure 1; station number 11447890). These gauging stations recorded discharge and water velocity every 15 min, providing detailed information about the hydraulic conditions experienced by tagged fish when they migrated through the river junction.

The effect of tidal fluctuations on hydraulic conditions at the river junction was captured by two variables. First, an indicator variable (U) was set to 1.0 when flood tides caused river flow in the Sacramento River to be reversed (i.e., $U = 1$ when $Q_S < 0$; $U = 0$ otherwise). Second, the rate of change in discharge of the Sacramento River was measured as $\Delta Q_S(t) = Q_S(t + 1) - Q_S(t)$, where t is measured in units of 15 min. This variable accounted for hydraulic conditions that may be quite different on a flood-to-ebb transition compared with an ebb-to-flood transition, even though total discharge may be similar during each transition. When ΔQ_S was negative, discharge was decreasing, typical of the transition from an ebb tide to a flood tide. In contrast, when ΔQ_S was positive, discharge was increasing, as typical of the transition from a flood tide to an ebb tide.

Diel variation in the spatial distribution of juvenile salmon in the river's cross section could also influence entrainment probabilities. For example, if fish are distributed close to shore during the day but near the center of the channel at night, then this type of diel variation could influence entrainment probabilities. To assess whether entrainment probabilities varied between day and night, we included time of day as a binary covariate in the model (time of day = 1 for fish detected during the day; time of day = 0 for fish detected at night). Day and night were defined based on daily times of sunrise and sunset. Lastly, all continuous covariates were standardized by subtracting the mean from each observation and then dividing by the SD (Table 2).

Model selection and goodness of fit.—To identify the variables that best described the entrainment probabilities, stepwise deletion procedures were used. The full model included all possible explanatory variables for both π_D and π_G; the exception was Q_D, which was excluded from this model because it was highly correlated with Q_S ($r = -0.84$). Variables with the largest P-values were then dropped one at a time from $g(\pi_D)$ and $g(\pi_G)$, and the model was refitted. This process was

TABLE 2. Summary of river discharge (Q_j; m³/s) experienced by juvenile Chinook Salmon that were detected at the junction of the Sacramento River ($j = S$) with the Delta Cross Channel ($j = D$) and Georgiana Slough ($j = G$). Discharge at Freeport is the mean daily discharge of the Sacramento River upstream of the Delta on dates during which fish were detected at the river junction; Q_{inflow} is the total discharge just upstream of the river junction; and ΔQ_S is the change in Q_S from time t to time $t + 1$.

Flow variable	Mean	SD	Range
Q at Freeport	390.8	183.6	192.6 to 1,152.5
Q_{inflow}	293.1	126.9	−61.4 to +798.5
Q_S	177.1	139.3	−173.3 to +577.5
Q_G	86.2	32.4	30.3 to 228.6
Q_D	31.2	63.6	−38.8 to +258.8
ΔQ_S	−2.1	13.5	−47.0 to +38.5

repeated until no further variables could be dropped at $\alpha = 0.05$. Two-way interactions were then formed from the variables remaining in the reduced model and were re-examined using the same stepwise deletion procedures. Tests of significance were based on likelihood ratio tests, but for comparison we also present Akaike's information criterion for each model (Burnham and Anderson 2002).

Goodness of fit was assessed using the Hosmer–Lemeshow test by grouping the observed data into discrete classes and comparing observed and predicted probabilities of occurrence (Hosmer and Lemeshow 2000). The area under the receiver operating curve (AUC) was used to quantify the overall predictive performance of the selected model. The receiver operating curve plots the true-positive rate against the false-positive rate for all possible cutoff values that are used to classify the predicted probability into binary outcomes. An AUC of 0.5 indicates no prediction ability, and a value of 1.0 indicates perfect prediction ability. In practice, AUC values between 0.7 and 0.8 are considered "acceptable," and values between 0.8 and 0.9 are considered "excellent" (Hosmer and Lemeshow 2000).

Simulation of alternative gate operations.—To illustrate how the entrainment model can be used to evaluate the potential effects of water management actions on fish entrainment into the interior Delta, we simulated entrainment probabilities under two management scenarios: (1) a historical scenario in which the Delta Cross Channel gates were open until December 15 and closed thereafter; and (2) an alternative scenario wherein the Delta Cross Channel gates were open during the day but closed at night for the entire simulation period. The premise of this latter management action is that most of the water enters the interior Delta during large, daytime flood tides, whereas most of the late-fall Chinook Salmon smolts migrate at night (Chapman et al. 2013). The rationale is that closing the gates at night will minimize the risk of entrainment for most of the fish population, while opening the gates during the day still allows for substantial water diversion to the interior Delta.

To implement the simulation, we used the Delta Simulation Model II (DSM2; CH2MHILL 2009; CADWR 2013) to simulate river flows at a 15-min time step. The DSM2 is a hydrographic model for simulating one-dimensional, unsteady, open-channel flow in the Delta in response to river inflows, tidal forcing, and water management actions. We used historical simulations of Delta hydrodynamics from November 1, 2006, to January 31, 2007, a period during which the Delta Cross Channel gates were open until December 15, 2006, and closed thereafter. We focused on this period because historically, 45 d of discretionary gate closures were allowed for fisheries protection, thereby providing flexibility to managers in operating the Delta Cross Channel (SWRCB 1995). Our alternative management scenario was the same as the historical simulation except that the Delta Cross Channel gates were opened at sunrise and closed at sunset for the entire simulation period (hereafter, the "closed-at-night" operation). Hence, for the period November 1–December 15, 2006, simulated gate operations were switched from open 24 h/d (historical) to closed at night (alternative); and for the period December 15, 2006, to January 31, 2007, gate operations were switched from closed 24 h/d (historical) to closed at night (alternative).

Given the flow data simulated under these scenarios, we used our entrainment model to predict entrainment probabilities for each 15-min flow observation. To assess the effect of different diel activity patterns, we calculated the mean daily probability of fish entry into the interior Delta,

$$\overline{\pi}_{ID,d} = A_{Day}\overline{\pi}_{ID,d,Day} + (1 - A_{Day})\overline{\pi}_{ID,d,Night},$$

where A_{Day} is the probability of fish arrival at the junction during daylight hours; $\overline{\pi}_{ID,d,Day}$ is the mean probability of fish entry into the interior Delta during daylight hours on day d; and $\overline{\pi}_{ID,d,Night}$ is the mean probability of fish entry into the interior Delta during the night. The probability of entering the interior Delta is the sum of the probabilities of entering the Delta Cross Channel and Georgiana Slough. We compared daily entrainment probabilities between alternative gate operations for two scenarios of diel activity: (1) nocturnal migration behavior, wherein 85% of fish arrived at night; and (2) a uniform diel distribution, in which fish displayed no bias toward nocturnal or diurnal migration. These scenarios were chosen to bracket the range of diel activity patterns observed in our study, as the percentage of fish arriving at night varied from 55% to 86% among release groups.

RESULTS

Model Selection and Goodness of Fit

Although the full model consisted of 16 parameters, many variables failed to improve model fit (Table 3), thus yielding a final model comprising seven parameters and four explanatory variables (Table 4). Time of day was eliminated from the model because likelihood ratio tests showed that it did not significantly improve model fit. Upstream flow in the Sacramento River (U) and Q_G did not affect entrainment probability for the Delta Cross Channel (π_D), whereas the ΔQ_S did not influence the probability of fish entry into Georgiana Slough (π_G; Table 3). None of the remaining variables could be eliminated without significantly increasing the negative log-likelihood ($\chi_1^2 \geq 10$, $P \leq 0.002$), and none of the two-way interactions among the remaining variables was significant (Table 3).

We found little evidence of systematic departures of predicted values from observed values. The Hosmer–Lemeshow goodness-of-fit tests ($\hat{C}$) were not significant (π_D: $\hat{C} = 4.84$, $P = 0.775$; π_G: $\hat{C} = 5.19$, $P = 0.737$). Plots of observed

TABLE 3. Model selection results for the effects of hydraulic variables on the probability of late-fall Chinook Salmon entering Georgiana Slough (π_G) and the Delta Cross Channel (π_D). Shown are the likelihood ratio (LR) test and associated statistics for the model with the given variable dropped relative to the preceding model with one additional variable (AIC = Akaike's information criterion; NLL = negative log-likelihood).

Variable dropped[a]	Response	Number of parameters	AIC	NLL	LR	P-value
None (full model)		12	794.7	385.3		
Time of day	π_G	11	792.7	385.4	0.03	0.863
U	π_D	10	790.8	385.4	0.10	0.752
Time of day	π_D	9	789.1	385.6	0.30	0.584
Q_G	π_D	8	787.6	385.8	0.54	0.462
ΔQ_S	π_G	7	787.6	386.8	1.98	0.159
None (all interactions)		11	790.3	384.2		
$Q_S \times U$	π_G	10	788.3	384.4	0.03	0.863
$Q_S \times Q_G$	π_G	9	786.9	384.5	0.57	0.450
$Q_G \times U$	π_G	8	786.5	385.3	1.63	0.202
$Q_S \times \Delta Q_S$	π_D	7	787.6	386.8	3.08	0.079

[a] Q_j = standardized discharge of channel j (j = S for the Sacramento River or G for Georgiana Slough); ΔQ_S = change in Q_S from time t to time $t + 1$; and U = indicator of reverse flow in the Sacramento River ($U = 1$ for $Q_S < 0$; $U = 0$ otherwise). Time of day is coded as 1 for daytime and 0 for nighttime.

TABLE 4. Maximum likelihood parameter estimates for the best-fit model relating the probabilities of juvenile Chinook Salmon entrainment into Georgiana Slough (π_G) and the Delta Cross Channel (π_D) to hydraulic variables (Q_S = standardized discharge of the Sacramento River; Q_G = standardized discharge of Georgiana Slough; ΔQ_S = change in Q_S from time t to time $t + 1$; U = indicator of reverse flow in the Sacramento River).

Response	Variable	Parameter estimate	SE
π_G	Intercept	−0.900	0.106
	Q_S	−1.163	0.154
	Q_G	0.852	0.107
	U	1.595	0.512
π_D	Intercept	−2.337	0.391
	Q_S	−2.694	0.337
	ΔQ_S	−0.474	0.158

proportions versus mean predicted probabilities supported the statistical tests, showing no evidence of systematic deviations (Figure 2). We found that AUC was 0.785 for $\hat{\pi}_{iG}$, 0.873 for $\hat{\pi}_{iD}$, and 0.841 for $\hat{\pi}_{iS}$, indicating that the model had an excellent ability to predict the ultimate fates of fish. Taken together, the goodness-of-fit measures suggested little evidence of lack of fit, a close agreement between predicted and observed values, and a good ability to predict the likelihood of fish entering migration routes in response to hydraulic dynamics.

Under the best-fit model, Q_S, Q_G, and U significantly affected π_G, whereas Q_S and ΔQ_S affected π_D (Table 4). Parameter estimates indicated both the direction and magnitude of these variables' effects on entrainment probabilities when the remaining variables were held constant. For π_G, the slope parameter for Q_S was negative, indicating that increases in Q_S produced decreases in π_G. In contrast, the positive slope estimate for Q_G indicated that π_G increased with Q_G. Slope estimates for Q_G and Q_S were of similar magnitude, showing that a 1-SD change in either variable affected π_G by a similar magnitude but in opposite directions. The positive parameter estimate for U indicated that water flowing upstream from the Sacramento River into the river junction increased π_G over and above the effect of Q_G and Q_S. For the Delta Cross Channel, decreases in both Q_S and ΔQ_S generated increases in π_D, but the slope estimate for Q_S was five times that for ΔQ_S, indicating that Q_S was the dominant factor driving the probability of entrainment into the Delta Cross Channel (Table 4).

Response of Entrainment Probabilities to Fluctuating River Flows

At the mean river flows observed during our study (Table 2), flood tides caused the Sacramento River to reverse direction twice daily (Figures 3A, 4A). Under these conditions, Q_S varied substantially from −142 m³/s during the full flood tide to 283 m³/s during the full ebb tide only a few hours later. Flow into the Delta Cross Channel was inversely related to Q_S, increasing rapidly during the transition from ebb tide to

flood tide as Q_S decreased (i.e., when $\Delta Q_S < 0$). Relative to Q_S and Q_D, Q_G exhibited much less variability regardless of whether the Delta Cross Channel gates were open or closed.

In response to fluctuating river flows driven by the tides, entrainment probabilities varied substantially throughout the day. For the Delta Cross Channel, π_D closely tracked Q_D and was inversely related to Q_S (Figure 3B). Thus, π_D was close to zero during the full ebb tide, when the Sacramento River flow was at its maximum and when cross channel flow was minimal. As the tide transitioned from ebb to flood, Q_S decreased and π_D increased to a maximum of about 75% just as the Sacramento River reached full flood tide. The value of π_D was nearly always less than the fraction of total discharge entering the Delta Cross Channel. After the peak of the flood tide, however, π_D declined despite the fact that the proportion of flow entering the cross channel remained relatively constant through the flood tide. This pattern was driven by the relative contributions of Q_S and ΔQ_S in the equation for π_D (Table 4). The negative slope for ΔQ_S indicated that π_D increased when Q_S declined during ebb-to-flood transitions, whereas π_D
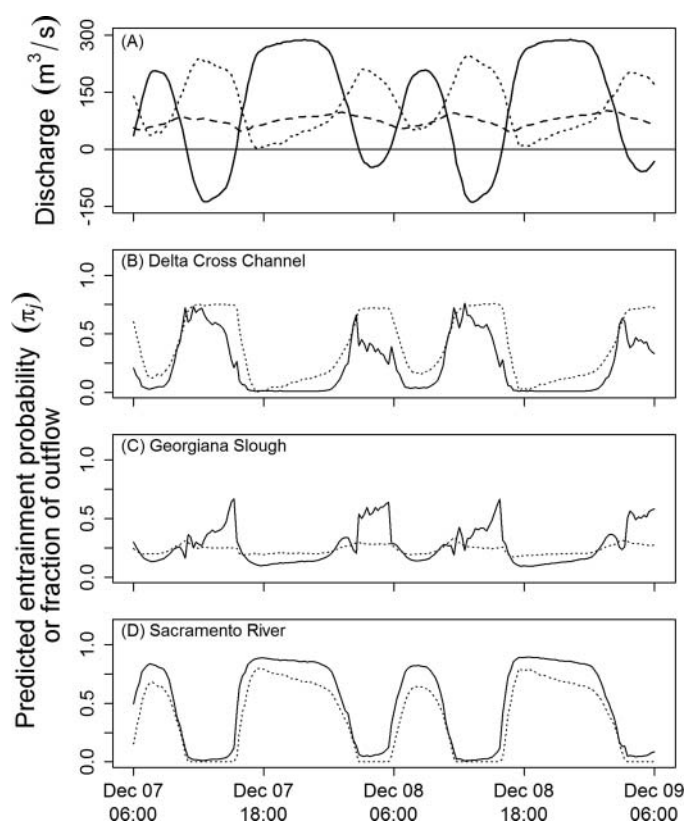

FIGURE 3. Predicted probability of juvenile Chinook Salmon entrainment into route j as a function of river flow entering each channel for 2 d in December 2007 under average flow conditions, with the Delta Cross Channel gates open. Panel **(A)** shows discharge just downstream of the river junction in the Sacramento River (Q_S; solid line), the Delta Cross Channel (Q_D; dotted line), and Georgiana Slough (Q_G; dashed line). Panels **(B)**–**(D)** show the predicted probability of fish entry into each channel (π_j; solid line) and the fraction of total outflow entering each channel (dotted line).

decreased when Q_S increased during flood-to-ebb transitions (Figure 3B).

The Q_G was relatively constant throughout the tidal cycle, yet π_G varied substantially over the day (Figures 3C, 4B). When the Delta Cross Channel gates were open and Q_S was positive, π_G tended to track the fraction of discharge entering Georgiana Slough (Figures 3C, 4C). However, during reverse-flow flood tides, π_G considerably exceeded the fraction of discharge entering Georgiana Slough (Figure 3C). In contrast, when the Delta Cross Channel gates were closed, the fraction of discharge entering Georgiana Slough varied between 20% and 100% as Q_S cycled between negative and positive flows about a relatively constant Q_G (Figure 4C). Therefore, when the Delta Cross Channel was closed, π_G closely tracked the fraction of flow entering Georgiana Slough, ranging from approximately 0.10 during the full ebb tide to 0.95 during the flood tide. During flood tides, π_G was higher when the cross channel gates were closed than when the gates were open

(Figures 3C, 4C), illustrating that closure of the gates increased the probability of fish entry into Georgiana Slough.

Since π_G increased when the cross channel gates were closed, thereby entraining fish that would have otherwise entered the Delta Cross Channel, entrainment probability for the Sacramento River (π_S) followed a similar pattern regardless of the whether the cross channel gates were open or closed (Figures 3D, 4D). In general, π_S followed a step function, switching quickly from a high probability that fish would remain in the Sacramento River during an ebb tide to a very low probability during a flood tide (Figures 3D, 4C). During the full ebb tide, π_S remained at about 0.90 regardless of cross channel gate position. However, when the cross channel gates were open during a flood tide, π_S was near zero, indicating that fish migrating through the river junction during this tidal stage would almost certainly enter either the Delta Cross Channel or Georgiana Slough (Figure 3D). When the cross channel gates were closed, although π_S remained low during flood tides, the fish still had a 5–10% chance of remaining in the Sacramento River (Figure 4D).

Simulation of Alternative Gate Operations

Relative to the historical gate operations, closure of the Delta Cross Channel at night had a large influence on the fraction of discharge entering the interior Delta but exerted much less of an effect on the expected daily entrainment into the interior Delta (Figure 5). Sensitivity to gate closure was much lower for daily entrainment probabilities than for the fraction of discharge entering the interior Delta because the instantaneous probability of entrainment in Georgiana Slough increased when the cross channel gates were closed (Figures 3C, 4C). When the Delta Cross Channel was open 24 h/d (i.e., prior to December 15), switching to the closed-at-night operation reduced the fraction of discharge entering the interior Delta by an average of 15 percentage points (Figure 5). However, daily entrainment probabilities decreased by only 5 percentage points on average for a uniform diel arrival distribution and decreased by 7 percentage points if 85% of fish arrived at night. When the gates were closed for 24 h/d (i.e., after December 15), switching to the closed-at-night operation increased the interior Delta flow proportion by 11 percentage points on average. In this case, daily entrainment probabilities increased by 3.0 percentage points on average for the uniform arrival distribution and by 1.3 percentage points for the scenario in which 85% of fish arrived at night. Thus, relative to a fully closed gate position, opening the gates during the day was expected to have little effect on entrainment, particularly if most of the migration occurred at night. Regardless of diel activity pattern, however, the change in daily entrainment probabilities was considerably less than the change in the fraction of discharge because closure of the Delta Cross Channel increased π_G. These findings illustrate how our entrainment model can be used to understand the
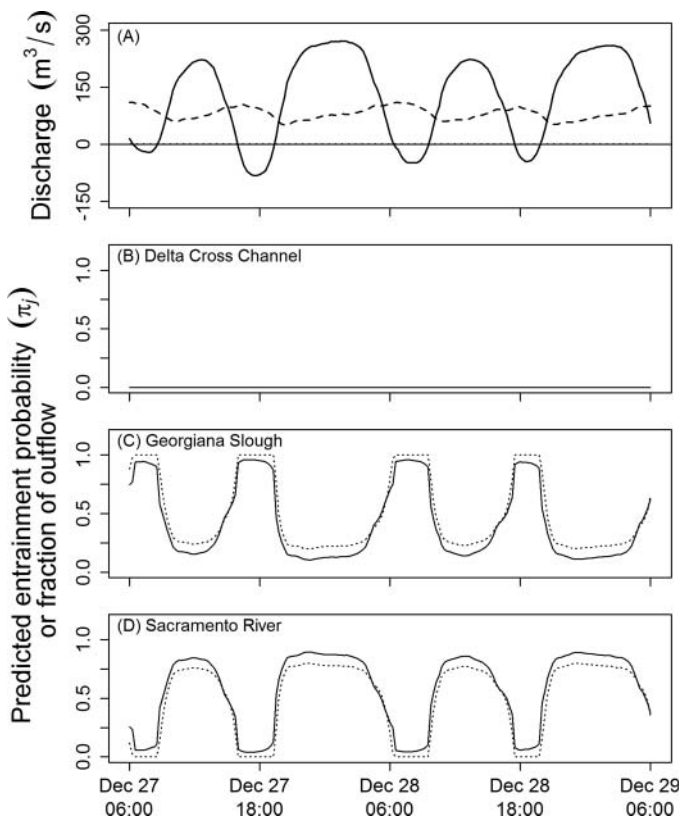

FIGURE 4. Predicted probability of juvenile Chinook Salmon entrainment into route j as a function of river flow entering each channel for 2 d in December 2007 under average flow conditions, with the Delta Cross Channel gates closed. Panel (**A**) shows discharge just downstream of the river junction in the Sacramento River (Q_S; solid line), the Delta Cross Channel (Q_D; dotted line), and Georgiana Slough (Q_G; dashed line). Panels (**B**)–(**D**) show the predicted probability of fish entry into each channel (π_j; solid line) and the fraction of total outflow entering each channel (dotted line).
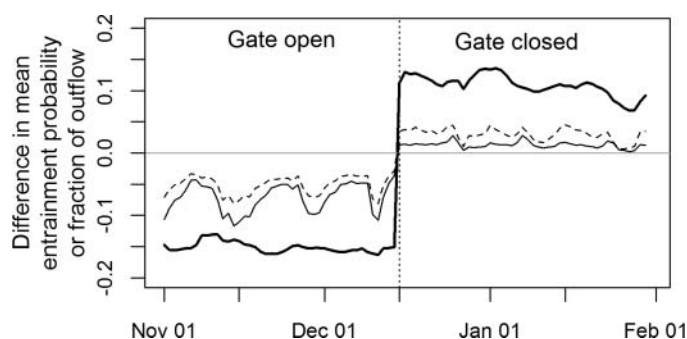
FIGURE 5. Mean daily difference between gate operation scenarios for fraction of discharge and juvenile Chinook Salmon entrainment into the interior Sacramento–San Joaquin River Delta. The vertical dotted line indicates the historical gate operations scenario in which the Delta Cross Channel gates were open until December 15, 2006, and closed thereafter. For the alternative scenario, the Delta Cross Channel gates were closed at night but open during the day for the entire simulation period. The bold solid line shows the difference in the fraction of junction inflow entering the interior Delta (closed-at-night scenario minus historical operations scenario). Also shown is the difference in mean daily fish entrainment probability between scenarios assuming either a uniform diel arrival of fish at the junction (dashed line) or 85% of fish arriving at night (thin solid line).

effect of management actions on the routing of fish in the Delta.

DISCUSSION

Prior to this study, fisheries managers had little mechanistic information with which to guide water management actions for minimizing fish entrainment into the interior Delta. Uncertainty about the driving mechanisms has forced fisheries managers to act in a precautionary manner, implementing actions that are least likely to harm endangered populations but at the expense of consumptive water use. Tagging studies have indicated that juvenile salmon entering the interior Delta via the Delta Cross Channel and Georgiana Slough survive at a lower rate than fish migrating within the Sacramento River (Newman and Brandes 2010; Perry et al. 2010, 2013). Consequently, the Delta Cross Channel has been prescriptively closed after December 15 each year under the rationale that fish distribution among the alternative migration routes is proportional to discharge (Low et al. 2006). However, our analysis suggests that the mechanisms governing route selection are more complex, and this relationship needs to be considered in managing water resources for the benefit of both fish and human use.

Our analysis revealed the strong influence of tidal forcing on the probability of fish entrainment into the interior Delta. The probability of entrainment into both Georgiana Slough and the Delta Cross Channel was highest during reverse-flow flood tides, and the probability of fish remaining in the Sacramento River was near zero during flow reversals. The magnitude and duration of reverse flows at this river junction decrease as inflow of the Sacramento River increases, ceasing

at inflows greater than about 566 m³/s at Freeport ($Q_{inflow} \approx$ 360 m³/s). Consequently, reduced Sacramento River inflow increases the frequency of reverse flows at this junction, thereby increasing the proportion of fish that are entrained into the interior Delta, where mortality is high (Perry 2010). In the future, Sacramento River inflows may decrease through climate change (Hayhoe et al. 2004; Maurer 2007; Cloern et al. 2011) or through water management actions that reduce discharge of the Sacramento River (BDCP 2013).

Owing to hourly variation in river flows driven by tidal forcing, migration routing among channels in the Delta will be strongly dependent on fish arrival timing at river junctions. If fish actively migrate during both day and night, we would expect the mean daily entrainment into the interior Delta to be proportional to the mean fraction of discharge entering the interior Delta. However, diel activity patterns that shift migration toward nocturnal, diurnal, or crepuscular migration may decouple the mean entrainment probabilities from the mean fraction of discharge entering a particular route, shifting entrainment more toward the time-specific conditions experienced by the bulk of the population. Under these circumstances, the realized outcome of management actions based on distribution of mean flow may deviate considerably from expectations. Since diel activity patterns are observed in many fish species (Reebs 2002), our study highlights the need for understanding fish behavior in the context of water management actions. We have shown how detailed information about the response of individuals to hydraulic conditions can inform models that allow managers to develop management actions to minimize impacts on fish populations while maximizing human benefits. Our simulation analysis demonstrated how operation of the cross channel at hourly time scales (nighttime gate closures) allowed water to be diverted for human uses while having little effect on entrainment into a low-survival migration route, particularly if most of the fish migration occurred at night.

Factors that drive the diel movement patterns of juvenile salmon in the Delta are poorly understood but may vary with season, environment, life stage, and life history strategy. In our study, the proportion of juvenile Chinook Salmon that were detected at night averaged 75% even though nighttime comprised about 60% of the 24-h period. More importantly, nighttime arrival varied from 55% to 86% among release groups, ranging from diel arrival that was proportional to the availability of daylight hours to substantial nocturnal migration. Chapman et al. (2013) also found considerable variation in diel activity patterns of juvenile salmonids (Chinook Salmon and steelhead *O. mykiss*) in the Sacramento River and San Francisco Bay. Such variation is unsurprising given that diel activity patterns can switch from day to night in response to trade-offs among predation risk, physiological state, and environmental cues (Metcalfe et al. 1998, 1999). For example, an increase in nighttime activity with decreasing temperature is hypothesized as a behavioral response to lower metabolic

requirements, reducing the need for juvenile salmon to feed during the day, when predation risk is high. In our study, some preference for nocturnal migration was expected given that the study occurred during winter at water temperatures ranging from 6°C to 12°C. Evidence suggests that at higher temperatures, juvenile salmon in the Delta migrate preferentially during the day (Wilder and Ingram 2006). Although we have illustrated how gate operations can be managed to minimize entrainment by accounting for the behavior of hatchery-origin late-fall Chinook Salmon, management actions must also account for variation in behavior among species, life history strategies, life stages, and environmental conditions.

Our modeling approach may be applied more broadly both within and outside of the Delta. Within the Delta, a suite of management actions known as the Bay Delta Conservation Plan (BDCP) is currently being considered for implementation. Specifically, one BDCP scenario proposes to divert up to 255 m^3/s from the Sacramento River upstream of the Delta and convey this water through tunnels to pumping stations in the southern Delta (BDCP 2013). Similar to our simulation example, our entrainment model could be coupled with hydrodynamic simulations to quantify the effect of this management action on the proportion of the population entrained into the interior Delta. Although the Delta and related management issues are somewhat unique, our analytical approach may also be applicable to other systems. For example, hydroelectric dams typically have alternative routes of fish passage, some of which cause higher mortality (e.g., turbines) than others (e.g., spillways; Bickford and Skalski 2000). Our analytical approach could be used to understand how dam operations influence routing probabilities and, ultimately, total dam passage survival. Moreover, because we were able to link fine-scale variation in the river environment with the fates of individual fish, our modeling approach provides a basis for understanding the underlying mechanisms that give rise to population-level outcomes of management actions. Tools such as this are critically needed to help inform management actions that are intended to recover endangered fish populations while maintaining ecosystem services for human benefit.

ACKNOWLEDGMENTS

REFERENCES

Agresti, A. 2002. Categorical data analysis. Wiley, Hoboken, New Jersey.

BDCP (Bay Delta Conservation Plan). 2013. 2013 BDCP draft chapters available for review. Available: http://baydeltaconservationplan.com/Library/DocumentsLandingPage/BDCPDocuments.aspx. (November 2013).

Bickford, S. A., and J. R. Skalski. 2000. Reanalysis and interpretation of 25 years of Snake–Columbia river juvenile salmonid survival studies. North American Journal of Fisheries Management 20:52–68.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

CADWR (California Department of Water Resources). 2013. Delta simulation model II (DSM2). Available: http://baydeltaoffice.water.ca.gov/modeling/deltamodeling/dsm2usersgroup.cfm. (November 2013).

CH2MHILL. 2009. Delta simulation model II (DSM2) recalibration. Prepared for the California Department of Water Resources, Sacramento.

Chapman, E. D., A. R. Hearn, C. J. Michel, A. J. Ammann, S. T. Lindley, M. J. Thomas, P. T. Sandstrom, G. P. Singer, M. L. Peterson, R. B. MacFarlane, and A. P. Klimley. 2013. Diel movements of out-migrating Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. Environmental Biology of Fishes 96:273–286.

Cloern, J. E., N. Knowles, L. R. Brown, D. Cayan, M. D. Dettinger, T. L. Morgan, D. H. Schoellhamer, M. T. Stacey, M. van der Wegen, R. W. Wagner, and A. D. Jassby. 2011. Projected evolution of California's San Francisco Bay–Delta River system in a century of climate change. PLoS (Public Library of Science) ONE [online serial] 6(9):e24465.

Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emission pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences of the USA 101:12422–12427.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Wiley, New York.

Low, A. F., J. White, and E. Chappel. 2006. Relationship of Delta Cross Channel gate operations to loss of juvenile winter-run Chinook Salmon at the CVP/SWP delta facilities. California Department of Fish and Game. Available: http://science.calwater.ca.gov/pdf/ewa/EWA_delta_cross_channel_closures_06_111406.pdf. (November 2013).

Maurer, E. P. 2007. Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Climatic Change 82:309–325.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. Proceedings of the Royal Society of London B 265:1503–1507.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371–381.

Newman, K. B., and P. L. Brandes. 2010. Hierarchical modeling of juvenile Chinook Salmon survival as a function of Sacramento–San Joaquin Delta water exports. North American Journal of Fisheries Management 30:157–169.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. Science 4738:567–573.

Perry, R. W. 2010. Survival and migration dynamics of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Sacramento–San Joaquin River Delta. Doctoral dissertation. University of Washington, Seattle.

Perry, R. W., P. L. Brandes, J. R. Burau, A. P. Klimley, B. MacFarlane, C. Michel, and J. R. Skalski. 2013. Sensitivity of survival to migration routes

used by juvenile Chinook Salmon to negotiate the Sacramento–San Joaquin River Delta. Environmental Biology of Fishes 96:381–392.

Perry, R. W., P. L. Brandes, P. T. Sandstrom, A. Ammann, B. MacFarlane, A. P. Klimley, and J. R. Skalski. 2010. Estimating survival and migration route probabilities of juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta. North American Journal of Fisheries Management 30:142–156.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org/. (November 2013).

Reebs, S. G. 2002. Plasticity of diel and circadian activity rhythms in fishes. Reviews in Fish Biology and Fisheries 12:349–371.

Singer, G. P., A. R. Hearn, E. D. Chapman, M. L. Peterson, P. E. LaCivita, W. N. Brostoff, A. Bremner, and A. P. Klimley. 2013. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall-run Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Environmental Biology of Fishes 96: 363–379.

Steel, A. E., P. T. Sandstrom, P. L. Brandes, and A. P. Klimley. 2013. Migration route selection of juvenile Chinook Salmon at the Delta Cross Channel, and the role of water velocity and individual movement patterns. Environmental Biology of Fishes 96:215–224.

SWRCB (State Water Resources Control Board). 1995. Water quality control plan for the San Francisco Bay/Sacramento–San Joaquin Delta estuary. Available: http://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/wq_control_plans/1995wqcp/docs/1995wqcpb.pdf. (November 2013).

Vogel, D. A. 2008. Pilot study to evaluate acoustic-tagged juvenile Chinook Salmon smolt migration in the northern Sacramento–San Joaquin Delta 2006–2007. Prepared for the California Depart of Water Resources, Sacramento.

Wilder, R. M., and J. F. Ingram. 2006. Temporal patterns in catch rates of juvenile Chinook Salmon and trawl net efficiencies in the lower Sacramento River. IEP (Interagency Ecological Program) Newsletter 19(1): 18–28.

Williams, J. G. 2008. Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. Hydrobiologia 609:241–251.

Williams, R. N. 2006. Return to the river: restoring salmon to the Columbia River. Elsevier, San Diego, California.