

DIEL ACTIVITY PATTERNS OF JUVENILE LATE FALL-RUN CHINOOK SALMON WITH IMPLICATIONS FOR OPERATION OF A GATED WATER DIVERSION IN THE SACRAMENTO–SAN JOAQUIN RIVER DELTA

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ABSTRACT

In the Sacramento–San Joaquin River Delta, California, tidal forces that reverse river flows increase the proportion of water and juvenile late fall-run Chinook salmon diverted into a network of channels that were constructed to support agriculture and human consumption. This area is known as the interior delta, and it has been associated with poor fish survival. Under the rationale that the fish will be diverted in proportion to the amount of water that is diverted, the Delta Cross Channel (DCC) has been prescriptively closed during the winter out-migration to reduce fish entrainment and mortality into the interior delta. The fish are thought to migrate mostly at night, and so daytime operation of the DCC may allow for water diversion that minimizes fish entrainment and mortality. To assess this, the DCC gate was experimentally opened and closed while we released 2983 of the fish with acoustic transmitters upstream of the DCC to monitor their arrival and entrainment into the DCC. We used logistic regression to model night-time arrival and entrainment probabilities with covariates that included the proportion of each diel period with upstream flow, flow, rate of change in flow and water temperature. The proportion of time with upstream flow was the most important driver of night-time arrival probability, yet river flow had the largest effect on fish entrainment into the DCC. Modelling results suggest opening the DCC during daytime while keeping the DCC closed during night-time may allow for water diversion that minimizes fish entrainment into the interior delta. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: fish entrainment; diel fish movement; gate operations; water withdrawal

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INTRODUCTION

How juvenile salmon distribute across space and time during downriver migration can influence their survival to the sea. In the Sacramento–San Joaquin River Delta, California, USA (hereafter referred to as the Delta), water diversions route juvenile salmon from the Sacramento River to the interior Delta where survival is low (Perry *et al.*, 2010; Figure 1). Likewise, management actions that reduce fish entrainment into the interior Delta should increase population survival by shifting fish to routes with higher survival (Perry *et al.*, 2013a). For example, under the rationale that fish distribute among routes in proportion to the mean discharge that enters a migration route (Low *et al.*, 2006), one such diversion, the Delta Cross Channel (DCC), has been prescriptively closed from mid-December through the remainder (March) of the migration season each year (NMFS, 1997; NOAA, 2008). However, the relationship between the proportion of fish that enter a diversion and proportion of flow that enter a diversion

is not well understood. Recent observations from studies using acoustic telemetry technology demonstrated that the proportion of fish entering a route can deviate markedly from the proportion of flow to that route (Perry, 2010). A better understanding of the mechanisms that affect fish distribution in association with water diversions from the Sacramento River could provide a basis for management actions that may allow for water diversion while minimizing juvenile Chinook salmon entrainment and mortality.

Fish behaviour in response to the river environment affects the spatial distribution of fish in the channel cross section and likely influences the probability of entrainment into the interior Delta. In particular, the influence of river flows on juvenile Chinook salmon behaviour can change between day and night periods and varies because of diel trade-offs between metabolic requirements, food availability and predation risk (Lima and Dill, 1990). In the Sacramento River, late fall-run Chinook salmon migrate mostly at night-time (Chapman *et al.*, 2012). Juvenile Chinook salmon in the Columbia River have varied their migration depths over the 24-h diel cycle (Beeman and Maule, 2001, 2006), which has been linked to daytime passage delays and the night-time entrainment of juvenile Chinook salmon into turbine

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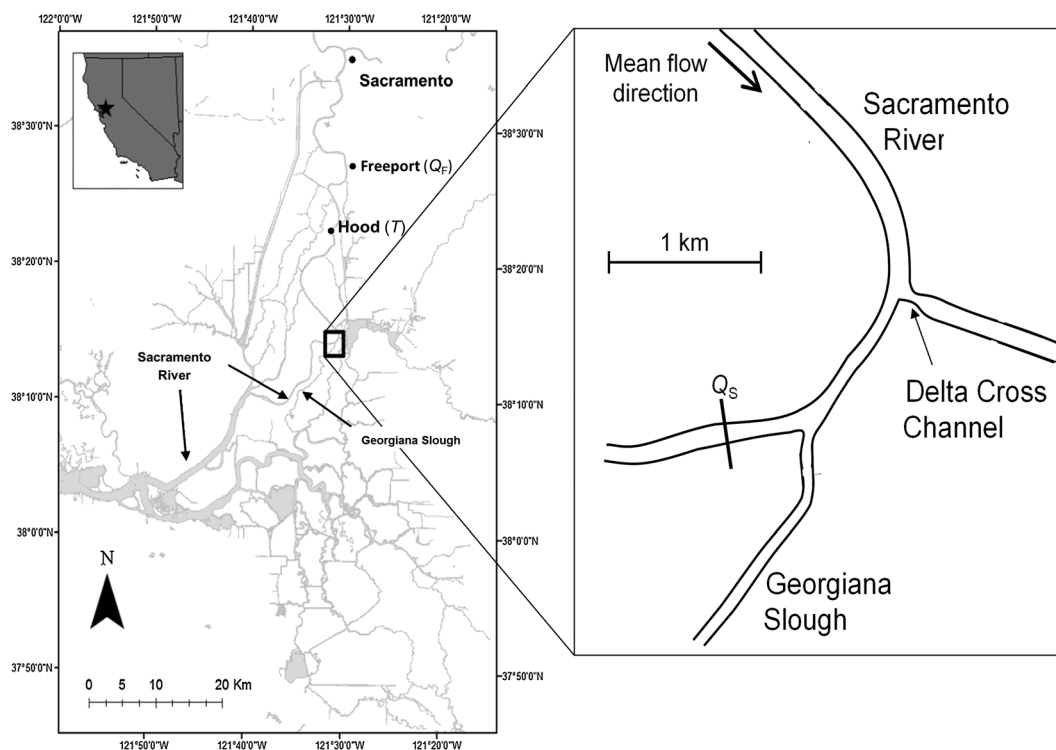


Figure 1. Map of the Sacramento–San Joaquin River Delta, California, USA, and a characterization of the junction of the Sacramento River with the Delta Cross Channel and Georgiana Slough. Also shown are the locations of the Sacramento River gauging stations that provided mean daily water temperatures at Hood (T), mean daily river flows at Freeport (Q_F) and 15-min river flows measured just downstream of the Delta Cross Channel (Q_S)

intakes at dams (Brege *et al.*, 1996; Evans *et al.*, 2008). Should these juvenile Chinook salmon tend to migrate at a particular time of day, then an important assumption behind estimates of their mortality from entrainment into water pumping stations may not hold (Kimmerer, 2008).

Understanding juvenile Chinook salmon entrainment into the DCC is complicated by tidal forcing that causes the Sacramento River to reverse direction during flood tides. An analysis of flow and fish entrainment at the DCC revealed the presence of a tidal-flow threshold on entrainment into the interior Delta (Perry, 2010). When flows in the Sacramento River upstream of the DCC were below about $340 \text{ m}^3 \text{ s}^{-1}$ (or $12\,000 \text{ ft}^3 \text{ s}^{-1}$), flood tides caused the lower portions of the Sacramento River to reverse direction, but above this threshold, the river ceases to reverse direction during flood tides. In turn, reverse-flow flood tides increased the amount of flow entering the DCC and the probability of fish being entrained into the interior Delta via the DCC. Because daytime flood tides are often stronger than night-time flood tides during the winter out-migration period (Cloern and Nichols, 1985), the likelihood of fish entrainment into the interior Delta may largely depend on the time of day that fish arrive at the DCC. A better understanding of how river discharge and tidal stage interact with diel activity patterns of the fish may allow identification of alternative gate

operations that can better balance fish entrainment and survival with water diversion into the interior Delta.

Our objective was to describe entrainment of juvenile late fall-run Chinook salmon into the DCC as a function of time of day, river discharge and tidal stage. We used acoustic telemetry to determine arrival times and entrainment of fish at the DCC in relation to the diel period, temperature, flow, change in flow and the proportion of negative flows measured just downstream of the DCC. Simulation of night-time closures showed that fish entrainment may be reduced while still allowing some water to be diverted (Perry, 2010). Based on this modelling, the DCC was opened during the day and night during the 2008–2009 winter out-migration for juvenile salmon, to assess the probability of fish arrival and entrainment into the DCC in relation to arrival times over the 24-h diel cycle. The operation of both open and closed gate operations is not typical, and so this study provides a unique opportunity to measure fish arrival and entrainment into the DCC at different gate operations that may help to inform resource managers about different DCC operations when both water and fish resources must be considered. The goals of this study were to quantify the following: (1) the probability of night-time arrival by the tagged fish at the DCC junction (irrespective of gate position) and (2) the probability of entrainment into the DCC (given that the

gates were open). Our approach to attaining these goals was to first estimate the effects of diel cycle, river flow and tidal stage on the arrival and entrainment probabilities of the fish using logistic regression analysis. We then used observed environmental data and parameter estimates from the logistic regressions to project probabilities of night-time fish arrival and entrainment into the DCC over an entire migration season. Our results provide insight into alternative DCC gate operations that might reduce the average seasonal entrainment of juvenile Chinook salmon into the interior Delta while still allowing water diversion into the DCC.

MATERIALS AND METHODS

Study area

The Delta is one of the most managed river systems in the world (Figure 1; Cohen and Carlton, 1998) and is roughly delineated as the complex network of inter-connected channels between the main stem Sacramento and San Joaquin Rivers. The interior Delta supplies water for >25 million residents and supports a billion-dollar agricultural industry. Although, from an aerial perspective, the Delta appears complex, the individual channels are simple and homogeneous and lack natural river features such as deep areas on the outsides of bends and point bars on the insides of bends. The DCC is one of three man-made channels that directly connect the mainstem Sacramento River with the interior Delta. The DCC junction is located along an outside bend of the river, which is an ideal location to divert water (and fish) from the Sacramento River into the interior Delta. Sacramento River flows are largely dictated by the release of water from upstream storage reservoirs, and the distribution of water is determined by pumping stations in the southern delta that can export up to 50% of the total flow (Nichols *et al.*, 1986). In contrast, the DCC passively diverts water from the Sacramento River into the interior Delta. Natural processes such as winter precipitation and springtime snowmelt also determine Sacramento River flows, and in the lower portions of the river (including the DCC), tidal cycles that vary on diel, biweekly and annual timescales also determine the magnitude and direction of the Sacramento River.

Fish and tagging

Juvenile late fall-run Chinook salmon were obtained from the Coleman National Fish Hatchery and transported to the tagging and release sites at Tower Bridge (M Street) in Sacramento, California. Fish were transported in 265-L insulated tanks at a density of <20 g of fish per litre of water and supplied with bottled oxygen at 80–130% saturation. At the tagging site, transport tanks were supplied with

circulated fresh river water for 18–36 h prior to tagging. Fish were considered suitable for tagging if they were free of major injuries, were <20% descaled and had no other apparent abnormalities. To keep tag burden at <5%, only fish of >29.5 g were surgically implanted with a tag that weighed 1.6 g in air (Perry *et al.*, 2013b) and had a 12-day expected battery life (Hydroacoustic Technology Incorporated, Model 795-E, Seattle, Washington, USA). Transmitters were implanted according to the procedures of Adams *et al.* (1998a, b) and Liedtke and Rub (2012). Release groups ranged from 164 to 191 fish [mean = 179, standard deviation (SD) = 6.6], and releases were conducted every 2–3 days from 14 November 2008 to 17 January 2009. A primary objective of this study was to understand how fish distribute themselves in time and arrive at the DCC; therefore, we intentionally stratified the release schedule of the tagged fish to be evenly distributed over the 24-h day (Figure 2).

Modelling fish arrival and entrainment into the Delta Cross Channel

Telemetry stations were established just upstream, within and downstream of the DCC to monitor the arrival of tagged fish in the vicinity of the DCC and fish entrainment into the DCC. Each telemetry station consisted of multiple hydrophones (Hydroacoustic Technology Incorporated) that identified individual fish based on pulse rate from the acoustic transmitters. Acoustic detections of the tagged juvenile salmon were processed to eliminate false-positive detections and detections of fish that were likely consumed by a predator (Perry *et al.*, 2010; Romine *et al.*, 2014).

To estimate the probability of fish arriving at the DCC during the night (and day), we first defined night-time as being between mean sunrise (06:52:06 PST) and sunset (16:17:49 PST) times over the study period (i.e. 11 November 2008 to 3 February 2009). If a fish's acoustic signal was detected between sunset and sunrise, it was classified as a night-time arrival, and the event was coded as 1; otherwise, the fish arrived during daytime and was coded as 0. We used a logistic regression to quantify factors affecting night-time arrival ($\hat{\pi}_{\text{night}}$) and entrainment ($\hat{\pi}_{\text{entrain}}$) probabilities (McCullagh and Nelder, 1989; Agresti, 1996). We express our full logistic regression model for $\hat{\pi}_{\text{night}}$ with all potential predictors as

$$\hat{\pi}_{\text{night}} = \text{logit}^{-1} \left(\hat{\beta}_0 + \hat{\beta}_1 P_{\text{rev}} + \hat{\beta}_2 Q_{\text{F}} + \hat{\beta}_3 T \right) \quad (1)$$

where the $\hat{\beta}$'s are the estimated coefficients that correspond to the following: (1) the proportion of the diel period that the Sacramento River flow was reversing (P_{rev}), (2) the daily discharge of the Sacramento River at Freeport (Q_{F} ; $\text{m}^3 \text{s}^{-1}$; U.S. Geological Survey gauge 11447890) on the date the fish arrived at the DCC and (3) the mean water temperature (T ; °C) of the Sacramento River (California Department of

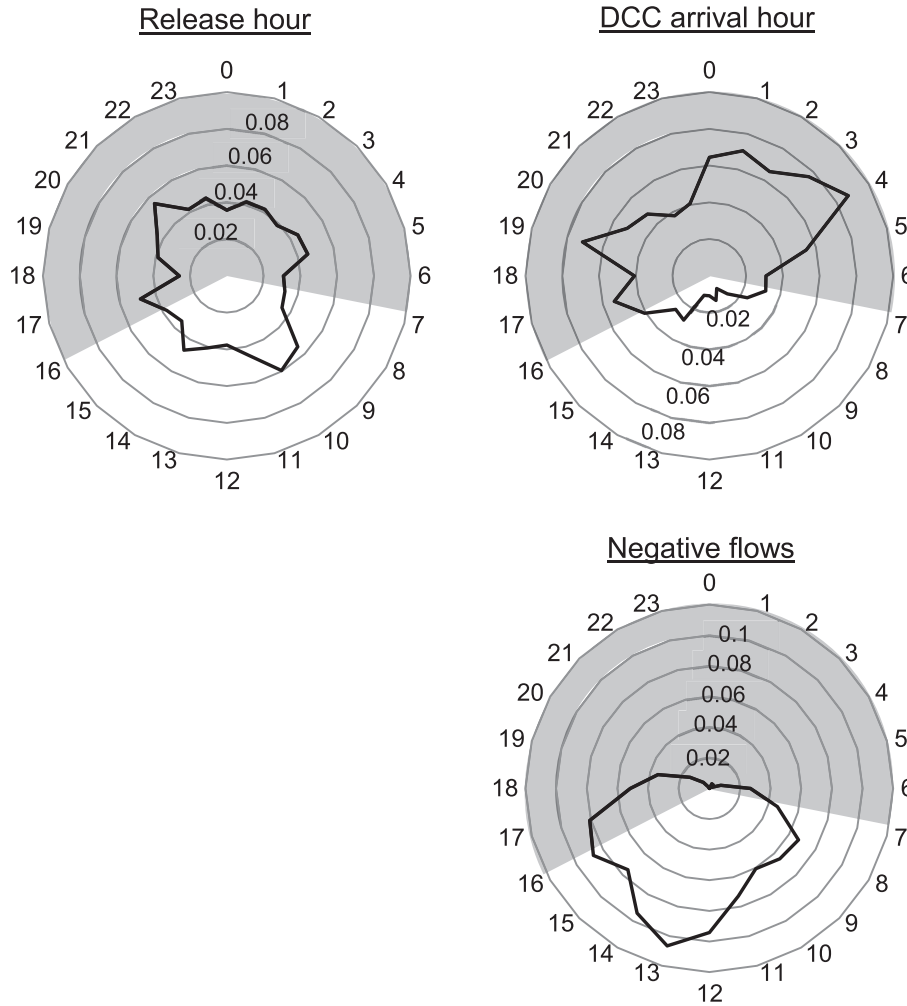


Figure 2. Circular histograms presented as a 24-h clock (midnight=0) showing the proportions of acoustic-tagged subyearling late fall-run Chinook salmon that were released (upper left) and subsequently arrived at the Delta Cross Channel (DCC) (upper right). Also shown are the proportions of negative flows at the DCC junction over the 24-h diel cycle (lower right). Shaded areas represent night-time hours

Natural Resources gauge—Sacramento River at Hook (SRH)) during the diel period that the fish arrived at the DCC. Rapid changes in flow direction and magnitude may determine fish arrival timing at the DCC. Water temperature has also been experimentally shown to affect fish travel rates and the predisposition to migrate (Muir *et al.*, 1994), which may influence fish arrival times at the DCC.

Similarly, we subset the telemetry data to include only those fish that arrived at the DCC junction when the DCC was open and fit the following full logistic regression model for $\hat{\pi}_{\text{entrain}}$ that we express as

$$\hat{\pi}_{\text{entrain}} = \text{logit}^{-1}(\hat{\theta}_0 + \hat{\theta}_1 Q_S + \hat{\theta}_2 \Delta Q_S + \hat{\theta}_3 P_{\text{diel}}) \quad (2)$$

the $\hat{\theta}$'s are the estimated coefficients that correspond to the following: (1) the Sacramento River discharge (Q_S ; $\text{m}^3 \text{s}^{-1}$; U.S. Geological Survey gauge 1147905) just downriver of

the Sacramento–DCC junction in the Sacramento River at the time the fish was detected entering the DCC (interpolated between 15-min flow measurements), (2) the change in river flow (ΔQ_S) between 15-min flow measurements ($t_{+1} - t$) when the fish was detected entering the DCC and (3) the diel period (P_{diel}) during which the fish was detected entering the DCC.

Flow data were obtained from the California Data Exchange Center's website: <http://cdec.water.ca.gov/>. Except for P_{rev} , which ranges from 0 to 1, all continuous predictors in the model were standardized by subtracting the mean and dividing by the standard deviation. The mean $Q_F = 249.1 \text{ m}^3 \text{ s}^{-1}$ (SD ± 30.03 ; range = 181.0–392.8), and the mean $T = 10.2 \text{ }^\circ\text{C}$ (SD ± 1.60 ; range = 7.2–14.9) during our study. The mean $Q_S = 109.04 \text{ m}^3 \text{ s}^{-1}$ (SD ± 128.95 ; range = -216.7 to 261.2), and mean $\Delta Q_S = -3.57 \text{ m}^3 \text{ s}^{-1}$ (SD ± 14.86 ; range = -54.71 to 42.61).

Model fit and selection

We first assessed the fit of the full models for night-time arrival ($\hat{\pi}_{\text{night}}$; Equation 1) and fish entrainment into the DCC ($\hat{\pi}_{\text{enrain}}$; Equation 2). The numbers of fish that had arrived or were entrained into the DCC were assumed to follow a binomial distribution. Overdispersion was assessed using a bootstrapped goodness-of-fit test to test whether the model adequately described variation in the data (Faraway, 2006).

After assessing the fit of the full models, we used Akaike’s information criterion (AIC) to determine if a better parsimonious model could be determined relative to the full model (Burnham and Anderson, 2002). We compared single-term deletions of the main effects from each of the respective full models (Equations 1 and 2). A variable was dropped from a full model if there was little change or a decline in the AIC value relative to the full model.

For the parsimonious models for fish arrival and entrainment into the DCC, we then calculated a receiver operating curve (Hosmer and Lemeshow, 2000) to determine the true-positive versus false-positive rate of classification, and the area under the curve (AUC) to provide a measure of the given model’s classification ability. An AUC of 0.5 indicates a model that has no ability to predict the fish’s arrival or entrainment, whereas AUC=1 indicates perfect classification ability. In practice, an AUC between 0.7 and 0.8 is considered ‘acceptable’, and that between 0.8 and 0.9 is considered ‘excellent’ (Hosmer and Lemeshow, 2000).

Estimating fish arrival and entrainment into the Delta Cross Channel

To demonstrate the joint consequence of fish arrival timing on entrainment into the DCC, we used the observed environmental conditions to project a time series of probabilities for night-time and daytime arriving fish (13 November 2008 to 31 March 2009). To do this, we used the AIC best model and calculated (1) $\hat{\pi}_{\text{night}}$ and conversely (2) $\hat{\pi}_{\text{day}} = (1 - \hat{\pi}_{\text{night}})$. We also used our AIC best model for fish entrainment into the DCC to calculate $\hat{\pi}_{\text{enrain}}$ for each 15-min (*i*th) observation over the number of night-time ($n_{\text{night},d}$) and daytime ($n_{\text{day},d}$) observations in the environmental dataset. We then calculated the average $\hat{\pi}_{\text{enrain}}$ over the daily number of night-time and daytime observations in the environmental dataset to provide conditional probabilities of entrainment given that the fish arrived during the night ($\bar{\pi}_{\text{enrain}|\text{night}}$) or during the day ($\bar{\pi}_{\text{enrain}|\text{day}}$). How these probabilities relate to the overall entrainment ($\bar{\pi}_{\text{enrain},d}$) of fish arriving on day *d* can be expressed as

$$\bar{\pi}_{\text{enrain},d} = [\hat{\pi}_{\text{night},d} \cdot \bar{\pi}_{\text{enrain}|\text{night},d}] + [\hat{\pi}_{\text{day},d} \cdot \bar{\pi}_{\text{enrain}|\text{day},d}] \quad (3)$$

The two summands for night-time and daytime observations on the right side of Equation 3 represent the *joint* probabilities of arriving *and* being entrained into the DCC during the night ($\bar{\pi}_{\text{night enrain},d}$) or during the day ($\bar{\pi}_{\text{day enrain},d}$).

RESULTS

Fish release and arrival at the Delta Cross Channel

A total of 2983 fish were implanted with acoustic transmitters and released upstream of the DCC. Of the juvenile salmon released, 33% (1008 of 2983) were subsequently detected in the vicinity of the DCC from 15 November 2008 to 31 January 2009. We determined that 13% (154 of 1162) of the fish detected in the vicinity of the DCC were predators that had consumed a tagged fish, and so these fish were removed from the following analyses.

Although fish were released evenly over a 24-h cycle, most fish arrived at the DCC during night-time (Figure 2). The proportion of fish arriving at the DCC during the night (83%, 840 of 1008) was greater than the percentage of fish

Table I. Model selection among models of night-time arrival and Delta Cross Channel (DCC) entrainment probabilities for acoustic-tagged juvenile late fall-run Chinook salmon, showing the model, number of parameters (*K*), Akaike’s information criterion (AIC), the change in AIC from the lowest AIC value (Δ AIC), the likelihood of the model given the data (LM) and Akaike’s weights (*w*) for each candidate model

Model	<i>K</i>	AIC	Δ AIC	LM	<i>w</i>
Night-time arrival models					
(Full) $P_{\text{rev}} + Q_{\text{F}} + T$	4	740.3	0.0	1.00	0.96
$P_{\text{rev}} + T$	3	746.6	6.3	0.04	0.04
$P_{\text{rev}} + Q_{\text{F}}$	3	756.2	15.9	0.00	0.00
P_{rev}	2	762.1	21.8	0.00	0.00
$T + Q_{\text{F}}$	3	973.3	233.0	0.00	0.00
T	2	974.0	233.7	0.00	0.00
(Null)	1	977.8	237.5	0.00	0.00
Q_{F}	2	978.2	237.9	0.00	0.00
DCC entrainment models					
$Q_{\text{S}} + \Delta Q_{\text{S}}$	3	106.2	0.0	1.00	0.40
Q_{S}	2	106.6	0.5	0.80	0.32
(Full) $Q_{\text{S}} + \Delta Q_{\text{S}} + P_{\text{diel}}$	4	108.1	2.0	0.37	0.15
$\Delta Q_{\text{S}} + P_{\text{diel}}$	3	108.5	2.3	0.32	0.13
P_{diel}	2	144.9	38.7	0.00	0.00
$\Delta Q_{\text{S}} + P_{\text{diel}}$	3	145.4	39.2	0.00	0.00
ΔQ_{S}	2	146.1	40.0	0.00	0.00
(Null)	1	146.2	40.0	0.00	0.00

The modelled effects are the proportion of negative flows within the diel period (P_{rev}), the mean daily Sacramento River flow at Freeport (standardized, Q_{F}), the mean temperature during the diel period the fish arrived at the DCC (standardized, T), the Sacramento River flows just downstream of the DCC (standardized, Q_{S}), the change in Sacramento River flow (standardized, ΔQ_{S}) and the diel period when fish entered the DCC (P_{diel}).

released during night (61%, 608 of 1008) and the percentage of night-time hours (63%, 15 of 24h).

Factors affecting fish arrival at the Delta Cross Channel

The full model used to estimate night-time arrival probabilities fit the data well. A bootstrapped goodness-of-fit test indicated no lack of fit ($p=0.55$), and the AUC (0.77) showed acceptable predictive performance when classifying night-time arrival of the fish relative to chance.

Among the potential candidate models, the full model was the most parsimonious model for juvenile Chinook salmon night-time arrival probabilities at the DCC (Table I). Based on the relative differences in the Δ AIC values from the full mode, however, P_{rev} was the more important driver of $\hat{\pi}_{\text{night}}$. When P_{rev} exceeded ~ 0.4 , $\hat{\pi}_{\text{night}}$ approached zero, but when $P_{\text{rev}}=0$, $\hat{\pi}_{\text{night}} = 0.937$ (Standard Error (SE) = 0.008), such that when negative flows were greater than about 20% of the diel period, then the probability of night-time arrival declined rapidly (Table II and Figure 3).

We measured a positive effect of temperature on $\hat{\pi}_{\text{night}}$. Over the range in temperatures of this study, $\hat{\pi}_{\text{night}}$ was about 0.734 at 7.2 °C, but $\hat{\pi}_{\text{night}}$ was about 0.971 at 14.9 °C (Table II). In contrast to temperature, the effect of average daily river flows as measured at Freeport had a negative effect on $\hat{\pi}_{\text{night}}$. For example, at a low flow of about $206 \text{ m}^3 \text{ s}^{-1}$, $\hat{\pi}_{\text{night}} = 0.912$, and at a high flow of about $392 \text{ m}^3 \text{ s}^{-1}$, $\hat{\pi}_{\text{night}} = 0.778$. Although temperatures and river flows influenced $\hat{\pi}_{\text{night}}$, the fraction of negative flows over the diel period had a larger effect on $\hat{\pi}_{\text{night}}$.

Factors affecting fish entrainment into the Delta Cross Channel

The DCC was opened and closed for water diversion during the day and night from 13 November 2008 to 3 February 2009, gate operations during the study were the result of deliberations that weighed concerns about fish protections and water use. In total, the DCC was open for water

Table II. Summary statistics for Akaike's information criterion best logistic regression model of night-time arrival probabilities at the Delta Cross Channel and entrainment probabilities into the Delta Cross Channel by acoustic-tagged juvenile late fall-run Chinook salmon

Coefficients	Estimate	SE
β_0 – intercept	2.714	0.148
β_1 – P_{rev}	-11.614	0.900
β_2 – Q_{F}	-0.289	0.097
β_3 – T	0.409	0.102
θ_0 – intercept	-1.893	0.305
θ_1 – Q_{S}	-1.409	0.252
θ_2 – ΔQ_{S}	0.336	0.219

diversion into the interior Delta for about 24 days (29%; between 13 November and 12 December 2008) over the 83-day study. Of the fish that arrived at the DCC, 13% (143 of 1008) arrived when the DCC was open. Given these 143 fish, 20% (20 of 100) that arrived at night were entrained into the DCC, and 21% (9 of 43) that arrived during the day were entrained into the DCC, suggesting there was similar fish entrainment into the DCC between day and night.

Model diagnostics indicated a good fit of the full model to the entrainment data. A bootstrapped goodness-of-fit test supported a good fit ($p=0.57$). Model selection indicated that the effect of diel period (P_{diel} ; Δ AIC > 38.7) should be removed from the full model, which corroborates our previous observation that entrainment proportions were similar between day and night (Table I). The model that included just Q_{S} and ΔQ_{S} was the favoured model for $\hat{\pi}_{\text{entrain}}$ (AIC=106.2). This reduced model performed well at classifying entrainment relative to chance, yielding an AUC=0.847 and suggesting excellent predictive performance. The effect of higher Sacramento River flow on DCC entrainment was to reduce entrainment, resulting in $\hat{\pi}_{\text{entrain}} = 0.715$ at the lowest $Q_{\text{S}} = -160 \text{ m}^3 \text{ s}^{-1}$, but $\hat{\pi}_{\text{entrain}}$ was < 0.01 when $Q_{\text{S}} > 240 \text{ m}^3 \text{ s}^{-1}$ (Table II and Figure 4). The effect of higher changes in river flow was to increase fish entrainment, resulting in $\hat{\pi}_{\text{entrain}} = 0.07$ at $\Delta Q_{\text{S}} = -31.8 \text{ m}^3 \text{ s}^{-1}$, but $\hat{\pi}_{\text{entrain}} = 0.23$ at $\Delta Q_{\text{S}} = 25.8 \text{ m}^3 \text{ s}^{-1}$.

Fish arrival and entrainment into the Delta Cross Channel

Using the observed conditions over our study to produce estimates of arrival and entrainment probabilities showed the potential consequences of arriving at night versus the day over the winter out-migration period (November–March; Figure 5). Modelled estimates of night-time arrival probabilities (mean=0.81) were much higher than daytime arrival probabilities (mean=0.16; Figure 5a), and because negative flows were predominant during daytime (Figure 5d), the probabilities of entrainment for fish that arrived during the day was slightly higher (mean=0.25) than for those that arrived during the night (mean=0.17; Figure 5b). Likewise, $\bar{\pi}_{\text{night entrain}}$ (mean=0.14) was much higher than $\bar{\pi}_{\text{day entrain}}$ (mean=0.06; Figure 5c), and so entrainment into the DCC was dictated by both the fraction of night-time arriving fish and the proportion of time the diel period had negative river flows (Figure 5d). These model estimates suggest that had the DCC been hypothetically open the entire season, then the average proportional difference between night-time ($\bar{\pi}_{\text{night entrain}}$) and daytime arriving fish ($\bar{\pi}_{\text{day entrain}}$) was 58% (i.e. $[\bar{\pi}_{\text{night entrain}} - \bar{\pi}_{\text{day entrain}}] / \bar{\pi}_{\text{night entrain}}$). This hypothetical scenario serves to illustrate how opening the DCC during the day (and closing the DCC at night) may be the best option

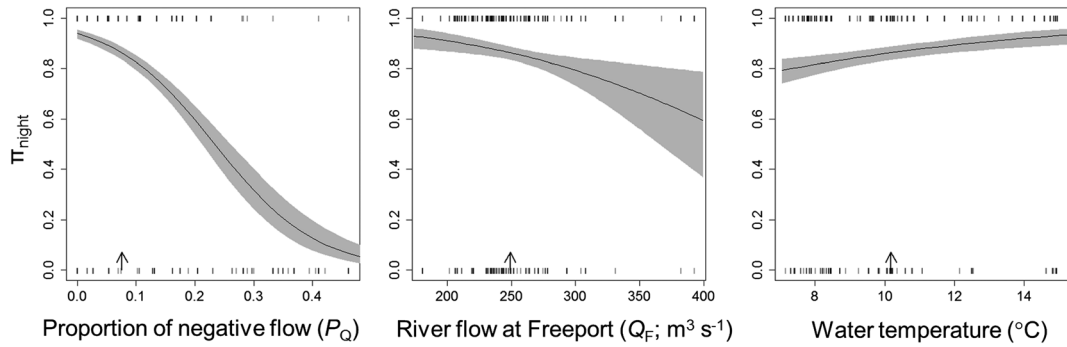


Figure 3. The primary effects from Akaike’s information criterion best models of night-time arrival probabilities for acoustic-tagged juvenile late fall-run Chinook salmon at the junction of the Sacramento River and the Delta Cross Channel (DCC). Solid lines are the expected effects for the proportion of time the diel period had negative river flows at the DCC (P_{rev}), the mean daily discharge at Freeport (Q_F) and the mean daily water temperature (T). The shaded areas are the regions encompassed by the 95% confidence intervals. Also shown are rug plots of the observed 0’s and 1’s over the range of the predictors, while the arrows depict the observed mean of the predictor. Other factors in the model that are not plotted are held constant at the observed mean

for allowing for water diversion, while minimizing fish entrainment into the DCC.

DISCUSSION

Interactions between behavioural and physical processes can alter the diel activity patterns of fish, and in turn, their entrainment into the DCC. Others have also evaluated the diel movements of acoustic-tagged juvenile Chinook salmon in the Sacramento River (Chapman *et al.*, 2012), yet this study adds to past research by evaluating the diel arrival of acoustic-tagged fish at a single river junction in relation to tidal forcing and DCC gate operations.

This and past research shows that tidal flows determine in part the arrival and entrainment of juvenile Chinook salmon

into the DCC (Perry *et al.*, 2010, 2013a; Cavallo *et al.*, 2012). High river flows reduce the proportion of the time with negative flows, but above a threshold of about $340\text{ m}^3\text{ s}^{-1}$, negative flows are eliminated, and having both Q_F and P_{rev} in the model helped to capture the different components of variation in probability of $\hat{\pi}_{night}$ with changing flows and tides. A majority of fish (83%, $SE = 1.12$) arrived during the night when negative flows were less frequent relative to daytime (27%; 254 of 934 negative flow observations; Figure 2). Selective tidal-stream transport (STST) is a hypothesis that might explain nocturnal movements by juvenile salmon (Moore *et al.*, 1998; IRP, 2012). This hypothesis suggests that juvenile Chinook salmon may tend to move to high-velocity areas near the centre of the river and outmigrate on outgoing ebb tides, while moving to near-shore, low-velocity areas during incoming flood tides. As the

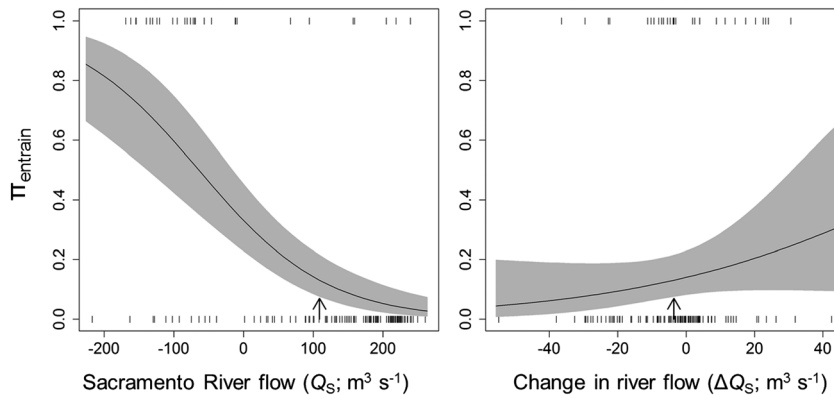


Figure 4. The primary effects from Akaike’s information criterion best model of entrainment probabilities for acoustic-tagged juvenile late fall-run Chinook salmon into the Delta Cross Channel. Solid lines are the expected effects for Sacramento River discharge (Q_s) and the rate of change in Sacramento River discharge (ΔQ_s), and shaded areas are the regions encompassed by the 95% confidence intervals. Also shown are rug plots of the observed 0’s and 1’s over the range of the predictors, while arrows depict the observed mean of the predictor. Other factors in the model that are not plotted are held constant at the observed mean

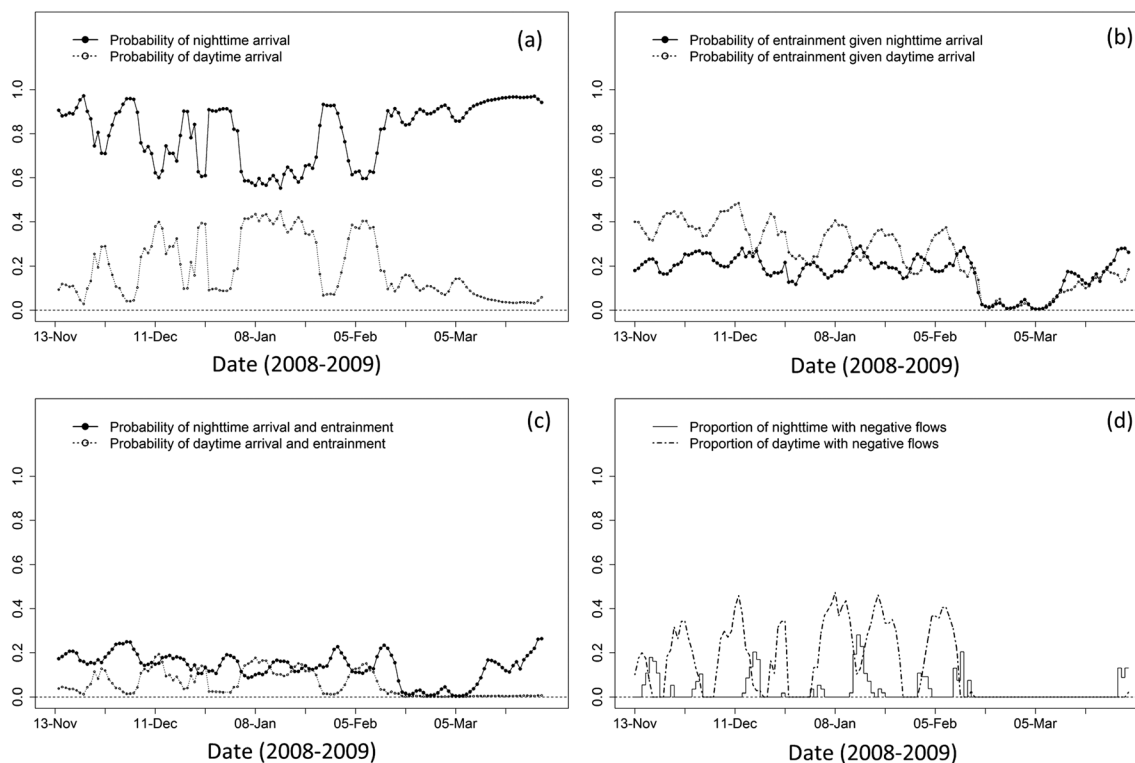


Figure 5. Time series of fish arrival and entrainment into the Delta Cross Channel (DCC) based on modelled estimates for (a) night-time ($\hat{\pi}_{\text{night}}$) or daytime ($\hat{\pi}_{\text{day}}$) arrival probabilities, (b) conditional probabilities of fish entrainment given night-time ($\hat{\pi}_{\text{entrain|night}}$) or daytime ($\hat{\pi}_{\text{entrain|day}}$) fish arrival at the DCC, (c) probabilities of fish arriving at night ($\hat{\pi}_{\text{night entrain}}$) or day ($\hat{\pi}_{\text{day entrain}}$) and being entrained into the DCC and (d) the proportion of negative flows during the day or night. Estimates were obtained from the observed conditions and Akaike's information criterion best logistic regression models that were fit to data on acoustic-tagged fish arriving at the DCC junction

proportion of the night having negative flows increased beyond $P_{\text{rev}} = 0.5$, then $\hat{\pi}_{\text{night}}$ approaches 0 rapidly, indicating that fish were unlikely to arrive at the DCC (from upstream) at night when flood tides encompassed a majority of the diel period. The STST hypothesis is supported by the vertical migrations of fish and phytoplankton over the tidal cycle required to remain in the Delta (Bennett *et al.*, 2002; Kimmerer, 2008) and by multiple species that also exhibit behaviours consistent with the STST hypothesis (Gibson, 2003). Our findings show similar support for the STST hypothesis as reported by Hering *et al.* (2010) where subyearling Chinook salmon in relatively unaltered habitats demonstrated a general preference but not a strict selection for movement with tidal flows (Hering *et al.*, 2010).

Factors other than the tides also influence nocturnal movement by juvenile Chinook salmon. Chapman *et al.* (2012) documented greater prevalence of nocturnal movement (91%; range = 57–91%) by juvenile Chinook salmon in reaches of the Sacramento River that were far upriver of any tidal influence, indicating that factors other than the physical effect of upriver flows may also re-enforce the behaviour of night-time movement. The prevalence of night-time arrival by juvenile Chinook salmon (Figure 2)

could pose the lower risk and, thus, may represent a behavioural tactic that is selected because of the survival benefit that night-time travel provides. Night-time movement by juvenile Chinook salmon may be a strategy to reduce predation risk (Beeman and Maule, 2006; Olla and Davis, 1990). Even though upriver tidal flows may create obvious physical limitations on fish arrival at the DCC, factors such as predation risk may select for nocturnal movement by juvenile Chinook salmon independent of upstream flows from tides.

The diel activity patterns of fish have been shown to interact with temperature and predation risk (Metcalf *et al.*, 1998, 1999), and Chapman *et al.* (2012) also showed variable but general increases in night-time detections of acoustic-tagged juvenile late fall-run Chinook salmon in the Sacramento River with increasing temperatures. In our study, $\hat{\pi}_{\text{night}}$ was high and changed little over the temperature range (8–14 °C), and so nocturnal movement was prevalent regardless of temperature. One explanation for the change in $\hat{\pi}_{\text{night}}$ with temperature is that metabolic rates and activity of piscivores will increase at higher temperatures, and so juvenile Chinook salmon may favour less-risky night-time movements at higher temperatures. An alternative explanation is that

temperatures acted as a proxy for other unmeasured factors that also affected $\hat{\pi}_{\text{night}}$ and covaried with temperatures. Although the mechanisms that lead to higher $\hat{\pi}_{\text{night}}$ with higher temperatures are unclear, night-time movements by juvenile Chinook salmon are not solely the result of tidal forces and river flows.

In contrast to our findings for fish arrival at the DCC, day or night had little bearing on fish entrainment into the DCC with about 20% of fish entrained during day or night. This finding is important because our analysis depends on the assumption that fish entrainment is independent of time of day. However, because most fish arrive at night, time of day appears to be the single most important factor influencing fish entrainment into the DCC. Opening the DCC during daytime when few fish arrive at the DCC but closing the DCC at night when most fish arrive at the DCC may allow for water diversion while minimizing fish entrainment. However, this conclusion should be made cautiously because other fishes of concern (e.g. delta smelt, *Hypomesus transpacificus*) may respond differently than juvenile Chinook salmon, and fish can still arrive at the DCC from the downstream direction during daytime flood tides when river flows at the DCC can be reversed. However, the tagged fish that were entrained into the DCC after initially passing the DCC were included in our analysis (13%, 19 of 143), and so fish entrained into the DCC from the downstream direction are not likely to affect this study's general results and conclusions about juvenile Chinook salmon.

Using the logistic regression models to generate a time series of probabilities for fish arrival and entrainment into the DCC helped to illustrate the difference in fish entrainment between daytime and night-time arriving fish (Figure 5). If the DCC had been open during the entire study, then the average probability of entrainment for night-time arriving fish was 14%. In contrast, average probability of entrainment for daytime arriving fish was 6%, illustrating a rather large (57%) difference in the joint probability of arrival and entrainment between night-time and daytime gate operations. This finding makes sense given that this and other studies have shown that a majority (57–91%) of these fish and other salmonids tend towards nocturnal movements (Metcalf *et al.*, 1999; Chapman *et al.*, 2012). Given that water diversion into the DCC is best facilitated by flood tides that occur primarily during the day, this study demonstrates how differences in the temporal distribution of fish can lead to fish entrainment in disproportion to the amount water that is diverted.

The prevalence for night-time movement by the fish suggests that resource managers may be able to close the DCC during night to reduce fish entrainment into the interior Delta via the DCC and help to improve fish survival (Perry, 2010; Perry *et al.*, 2010, 2013a). Perhaps this study's greatest limitation is that it evaluates fish arrival and

entrainment at a single river junction for water diversion into the interior Delta. Just downstream of the DCC is Georgiana Slough, a natural channel that also diverts water and fish into the interior Delta (Figure 1; Perry *et al.*, 2010). As with the DCC, fish entering the slough are directed to the interior delta and so suffer high mortality. Resource managers should consider changes to both migration routing and fish survival when prescribing a particular operation for water diversion. If operation of the DCC affects the hydrodynamics or the routing of water that also inadvertently increases fish entrainment into the Georgiana Slough and subsequent mortality, then benefits gained by reducing fish entrainment into the DCC could be negated (Perry, 2010; Perry *et al.*, 2010, 2013a). Another concern is that the timing of the tides will shift with the passing of each decade, so that negative flows that currently prevail during the day (as in this study) will shift to primarily occur at night over the next several decades (Cloern and Nichols, 1985). Inasmuch as river flows determine fish arrival, any DCC operations based on time of day should be considered in relation to the timing of the tides. Despite these uncertainties, however, the DCC is a major junction that leads into the interior Delta where fish survival is very poor (Perry *et al.*, 2010). Given that tidal effects and night-time fish arrival will be high when river flows are low, night-time closure and daytime opening of the DCC during the winter months may represent one of the rare instances when operational changes may be used to minimize fish mortality and allow for water diversion.

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REFERENCES

- Adams NA, Rondorf DW, Evans SD, Kelly JE, Perry RW. 1998a. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook salmon. *Transactions of the American Fisheries Society* **127**: 128–136.

- Adams NA, Rondorf DW, Evans SD, Kelly JE, Perry RW. 1998b. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 781–787.
- Agresti A. 1996. *An Introduction to Categorical Data Analysis*. Wiley, Hoboken, New Jersey.
- Beeman JW, Maule AG. 2001. Residence times and diel passage distributions of radio-tagged juvenile spring Chinook salmon and steelhead in a gatewell and fish collection channel of a Columbia River dam. *North American Journal of Fisheries Management* **21**: 455–463.
- Beeman JW, Maule JG. 2006. Migration depths of juvenile Chinook salmon and steelhead relative to total dissolved gas supersaturation in a Columbia River reservoir. *Transactions of the American Fisheries Society* **135**: 584–594.
- Bennett WA, Kimmerer WJ, Burau JR. 2002. Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. *Limnology and Oceanography* **47**: 1496–1507.
- Brege DA, Absolon RF, Graves RT. 1996. Seasonal and diel passage of juvenile salmonids at John Day Dam on the Columbia River. *North American Journal of Fisheries Management* **16**: 659–665.
- Burnham KP, Anderson DR. 2002. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- Cavallo B, Merz J, Setka J. 2012. Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. *Environmental Biology of Fishes*. DOI 10.1007/s10641-012-9993-5.
- Chapman ED, Hearn AR, Michel CJ, Ammann AJ, Lindley ST, Thomas MJ, Sandstrom PT, Singer GP, Peterson ML, MacFarlane RB, Klimley AP. 2012. 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 JE, Nichols JE. 1985. Time scales and mechanisms of estuarine variability, a synthesis from studies of San Francisco Bay. *Hydrobiologia* **129**: 229–237.
- Cohen A, Carlton J. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* **279**: 555–558.
- Evans SD, Adams NS, Rondorf DW, Plumb JM, Ebberts BD. 2008. Performance of a prototype surface collector for juvenile salmonids at Bonneville Dam's first powerhouse on the Columbia River, Oregon. *River Research and Applications* **24**: 960–974.
- Faraway JJ. 2006. *Extending the Linear Model With R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Chapman and Hall/CRC, Boca Raton, Florida.
- Gibson RN. 2003. Go with the flow: tidal migration in marine animals. *Hydrobiologia* **503**: 153–161.
- Hering DK, Bottom DL, Prentice EF, Jones KK, Flemming IA. 2010. Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 524–533.
- Hosmer DW, Lemeshow S. 2000. *Applied Logistic Regression*. John Wiley and Sons, New York, New York.
- IRP (Independent Review Panel). 2012. Report of the 2012 Delta science program independent review panel (IRP) on the long-term operations opinions (LOO) annual review. Delta Science Program, 1 December 2012.
- Kimmerer WJ. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* **6**: 1–27.
- Liedtke TL, Rub AMW. 2012. Techniques for telemetry transmitter attachment and evaluation of transmitter effects on fish performance. In *Telemetry Techniques: A User Guide for Fisheries Research*, N. S. Adams, J. W. Beeman, and J. H. Eiler (eds). American Fisheries Society: Bethesda, Maryland; 45–87.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**: 619–640.
- Low AF, White J, Chappel E. 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 (accessed February 2010).
- McCullagh P, Nelder JA. 1989. *Generalized Linear Models*, 2nd edition. Chapman and Hall, New York.
- Metcalf NB, Fraser NHC, Burns MD. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society of London* **265**: 1503–1507.
- Metcalf NB, Fraser NHC, Burns MD. 1999. Food availability and the nocturnal vs. diurnal foraging trade-offs in juvenile salmon. *Journal of Animal Ecology* **68**: 371–381.
- Moore A, Ives S, Mead TA, Talks L. 1998. The migratory behavior of wild Atlantic salmon (*Salmo salar* L) smolts in the River Test and Southampton water, southern England. *Hydrobiologia* **371**: 295–304.
- Muir WD, Zaugg WS, Giorgi AE, McCutcheon S. 1994. Accelerating smolt development and downstream movement in yearling Chinook salmon with advanced photoperiod and increased temperature. *Aquaculture* **123**: 387–399.
- Nichols FH, Cloern JE, Luoma SN, Peterson DH. 1986. The modification of an estuary. *Science* **4738**: 567–573.
- NMFS. 1997. *NMFS Proposed Recovery Plan for the Sacramento River Winter-run Chinook*. National Marine Fisheries Service, Southwest Regional Office: Long Beach, CA.
- NOAA. 2008. Fisheries off West Coast States and in the Western Pacific; West Coast salmon fisheries; 2008 management measures and a temporary rule. *Federal Register* **73**: 23971–23981.
- Olla BL, Davis MW. 1990. Behavioral responses of juvenile Pollock *Theragra chalcogramma* Pallas to light, thermoclines and food: possible role in vertical distribution. *Journal of Experimental Marine Biology and Ecology* **135**: 59–68.
- Perry RW. 2010. Survival and migration dynamics of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento–San Joaquin River Delta. Dissertation, University of Washington.
- Perry RW, Brandes PL, Sandstrom PT, Ammann A, MacFarlane B, Klimley AP, Skalski JR. 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.
- Perry RW, Brandes PL, Bureau JR, Klimley AP, MacFarlane B, Michel C, Skalski, JR. 2013a. 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 RW, Plumb JM, Fielding SD, Adams NS, Rondorf DW. 2013b. Comparing effects of transmitters within and among populations: application to swimming performance of juvenile Chinook salmon. *Transactions of the American Fisheries Society* **142**: 901–911.
- Romine JG, Perry RW, Johnston SV, Fitzer CW, Pagliughi SW, Blake AR. 2014. Identifying when tagged fishes have been consumed by piscivorous predators: application of multivariate mixture models to movement parameters of telemetered fishes. *Animal Biotelemetry* **2**: 3, DOI: 10.1186/2050-3385.