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Authors
Hance, Dalton J.
Perry, Russell W.
Burau, Jon R.
et al.

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RESEARCH

Combining Models of the Critical Streakline and the Cross-Sectional Distribution of Juvenile Salmon to Predict Fish Routing at River Junctions

Dalton J. Hance*[1], Russell W. Perry[1], Jon R. Burau[2], Aaron Blake[2], Paul Stumpner[2], Xiaochung Wang[3], Adam Pope[1]

ABSTRACT

Because fish that enter the interior Delta have poorer survival than those emigrating via the Sacramento River, understanding the mechanisms that drive entrainment rates at side channel junctions is critically important for the management of imperiled juvenile salmon. Here, we implement a previously proposed process-based conceptual model to study entrainment rates based on three linked elements: the entrainment zone, critical streakline, and cross-sectional distribution of fish. The critical streakline is the location along a channel cross-section immediately upstream of a junction that forms the spatial divide between parcels of water that enter a side channel or remain in the main channel. The critical streakline therefore divides the main channel into entrainment zones within which fish would likely enter each channel. Combined with information about the cross-sectional distribution of fish upstream of a junction, this conceptual model provides a means to predict fish entrainment into each channel. To apply this conceptual model, we combined statistical models of the critical streakline, the cross-sectional distribution of acoustic tagged juvenile Chinook salmon, and their probability of entrainment into Georgiana Slough. We fit joint beta regression and logistic regression models to acoustic telemetry data gathered in 2011 and 2012 to estimate the cross-sectional distribution of fish upstream of the junction, and to estimate the probability of entrainment for fish on either side of the critical streakline. We show that entrainment rates can be predicted by understanding how the combination of critical streakline position and cross-sectional distribution of fish co-vary as a function of environmental covariates. By integrating over individual positions and entrainment fates to arrive at population-level entrain probability in relation to environmental covariates, our model offers managers a simple but powerful tool to evaluate how alternative actions affect migrating fish.

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* Corresponding author: *dhance@usgs.gov*

1 Western Fisheries Research Center
US Geological Survey
Cook, WA 98605 USA

2 California Water Science Center
US Geological Survey
Sacramento, CA 95819 USA

3 Bay–Delta Office
California Department of Water Resources
Sacramento, CA 95819 USA

KEY WORDS

Chinook Salmon, entrainment rates, Georgiana Slough, critical streakline, telemetry, Bayesian data analysis

INTRODUCTION

Juvenile anadromous fish emigrating from natal rivers must navigate a variety of riverine environments, both natural and anthropogenic. Variation in such environments may result in differential survival, depending on the migratory pathway emigrating fish select. For example, alternative passage routes at hydroelectric facilities typically expose fish to different survival rates (Skalski et al. 2009), leading fisheries managers to develop techniques to guide fish away from low-survival routes (Coutant 2001). In the Sacramento–San Joaquin River Delta, fish migrating through the southern Delta have been shown to have lower survival than those emigrating via the Sacramento River (Buchanan et al. 2013; Perry et al. 2010, 2013). Thus, the ability to predict which migratory pathway fish will select in response to environmental conditions would be a powerful management tool to evaluate how alternative actions affect migrating fish.

Before large-scale fish-tracking studies in the Sacramento River using acoustic telemetry tags, the working hypothesis was that migrating fish became entrained in side channels in direct proportion to the relative volume of water entering the side channel (Perry et al. 2016), where 'entrainment' simply means entering and remaining within a given side channel. The use of telemetry provided a better understanding of behavioral heterogeneity among individuals in a migrating population of juvenile salmon that leads to variable entrainment probabilities. As a result of this behavioral heterogeneity and as demonstrated by telemetry studies, entrainment rates differ from the proportion of flow that enters the side channel. For example, Perry et al. (2014) found that a fish's location in the river channel's cross-sectional profile immediately upstream of a river junction was an important determinant of its eventual fate, with fish located closer to the side-channel side of the river being more likely to enter the side channel. Similarly, Sridharan et al. (2018) used a bifurcating streamline model to better predict Delta Smelt salvage at the federal Central Valley Project (a water export facility that pumps water from the Delta) than similar estimates based on the proportion of flow that enters each channel. Thus, insights into behavioral and environmental complexity have demonstrated to be inadequate the working hypothesis that entrainment rates are directly proportional to discharge.

The observation that entrainment rates are not necessarily directly proportional to discharge led to the development of a conceptual model that involves the interaction of three components: the entrainment zone, the critical streakline, and the cross-sectional distribution of fish positions (see Box 3 in Perry et al. 2016, p. 16-17). The entrainment zone refers to the continuous parcel of water just upstream of a river junction which will enter the side channel. Passive particles suspended in this volume of water have a high probability of being transported into the side channel and thus becoming entrained. The critical streakline refers to the spatial divide between the parcel of water that enters the side channel and the parcel that remains in the main channel. Thus, the critical streakline defines the boundary of the entrainment zone. The cross-sectional distribution of fish refers to a probability distribution that describes the likelihood of observing a fish at a given cross-stream position in the cross-section of the river just upstream of the junction. For example, possible cross-sectional distributions include a unimodal distribution where fish are most likely to be in the center of the channel, with less probability of being near either bank; or alternatively, a U-shaped distribution where fish are more likely to hug either bank than to be in the center of channel.

Conceptually, the entrainment zone, critical streakline, and cross-sectional distribution of fish interact to determine entrainment rates. Fish within the entrainment zone are expected to have a high probability of entrainment and a low probability of remaining in the main channel. The probability that a fish is within the entrainment zone can be determined by the total probability mass of the cross-sectional distribution that is to the left (or the right, if the side channel exits to river right) of the critical streakline. This conceptual model illustrates some of the reasons why entrainment rates may not be directly proportional to the fraction of flow that enters the side channel. First, only by assuming uniform cross-sectional water velocities and uniform depth can the location of the critical streakline be directly calculated from the ratio of flow that enters the side channel. For a non-uniform distribution of water velocities, the location of the critical streakline is found by integrating velocity vectors over the channel cross-section until the accumulated discharge equals the discharge that enters the side channel (Perry et al. 2016). Second, only a uniform cross-sectional distribution of fish upstream of the channel, with no further lateral movement, would result in fish entering the side channel in direct proportion to the percentage of the channel that is within the entrainment zone. For a non-uniform cross-sectional distribution of fish, the proportion of fish within the entrainment zone is determined by total probability mass to the left of the critical streakline, which can be estimated by fitting an appropriate probability distribution to observations of cross-stream fish positions. A final reason why entrainment rates can differ from the ratio of flow is that migrating fish are not passive particles. Even fish within the entrainment zone may avoid entrainment as a result of individual fish behavior (e.g., volitional movements) and, similarly, fish outside the entrainment zone may eventually become entrained. Thus, while the critical streakline and cross-sectional distribution of fish will influence the likelihood a given fish is entrained, any model for the process of entrainment must be stochastic.

While elements of this conceptual model have been presented before (Perry et al. 2016), it has not yet been applied to build a predictive model for entrainment at a junction. Thus, the objective of this work is to formalize the conceptual model of the entrainment zone into a statistical model applied to observed field data of migrating juvenile salmon. We conduct the analysis in three parts by:

1. Developing a relationship to predict the location of the critical streakline based on the proportion of flow between two channels;

2. Quantifying the cross-sectional distribution of fish over a range of environmental conditions;

3. Estimating entrainment probability based on environmental covariates and whether or not a fish is in the entrainment zone.

Ultimately, we synthesize the results of these three elements to develop a predictive model of fish entrainment based on the physical relationship for critical streakline and the stochastic elements of cross-sectional fish distribution and entrainment probability. The data for this work come from two separate studies: (1) an acoustic Doppler current profile (ADCP) evaluation of the Sacramento River and Georgiana Slough junction conducted in 2014, and (2) a fish telemetry data study conducted in 2011 and 2012 to test the effectiveness of a non-physical barrier known as a Bio-Acoustic Fish Fence (BAFF) installed at the entrance of Georgiana Slough (Perry et al. 2014; CDWR 2012, 2015). We used the ADCP data to estimate the critical streakline based on integrating velocity vectors over the channel cross-section, and to predict the critical streakline position based on the proportion of flow that enters Georgiana Slough. We used the telemetry data to model the cross-sectional distribution of fish and the probability of entrainment, while accounting for BAFF operations in addition to environmental conditions of discharge and time of day. By quantifying the effects of environmental conditions on both entrainment probability and the cross-sectional distribution of fish, our ultimate goal was to determine whether the entrainment zone conceptual model could be translated into a quantitative model that is firmly rooted in the first principles thought to drive fish routing at important river junctions in the Sacramento–San Joaquin River Delta.

METHODS

Study Area

The general study area was the Sacramento–San Joaquin River Delta (the Delta) near Sacramento, California, where Georgiana Slough branches off the mainstem Sacramento River. The Delta is a complex network of natural and man-made channels through which threatened populations of juvenile salmonids must migrate to reach the Pacific Ocean. Migrating fish that enter the interior Delta, a network of channels to the south and west of the mainstem Sacramento River that include large state and federal water pumping stations, survive at lower rates than fish that remain in the Sacramento River (Perry et al. 2010). Georgiana Slough is one of two channels that diverge from the mainstem Sacramento River to the interior Delta, and is the focus of this case study. In particular, we used a cross-stream transect 102.4 meters wide located approximately 250 meters upstream of the far northeast corner of Andrus Island as a reference point to estimate the location of the critical streakline and fish locations as they approach Georgina Slough (Figure 1).

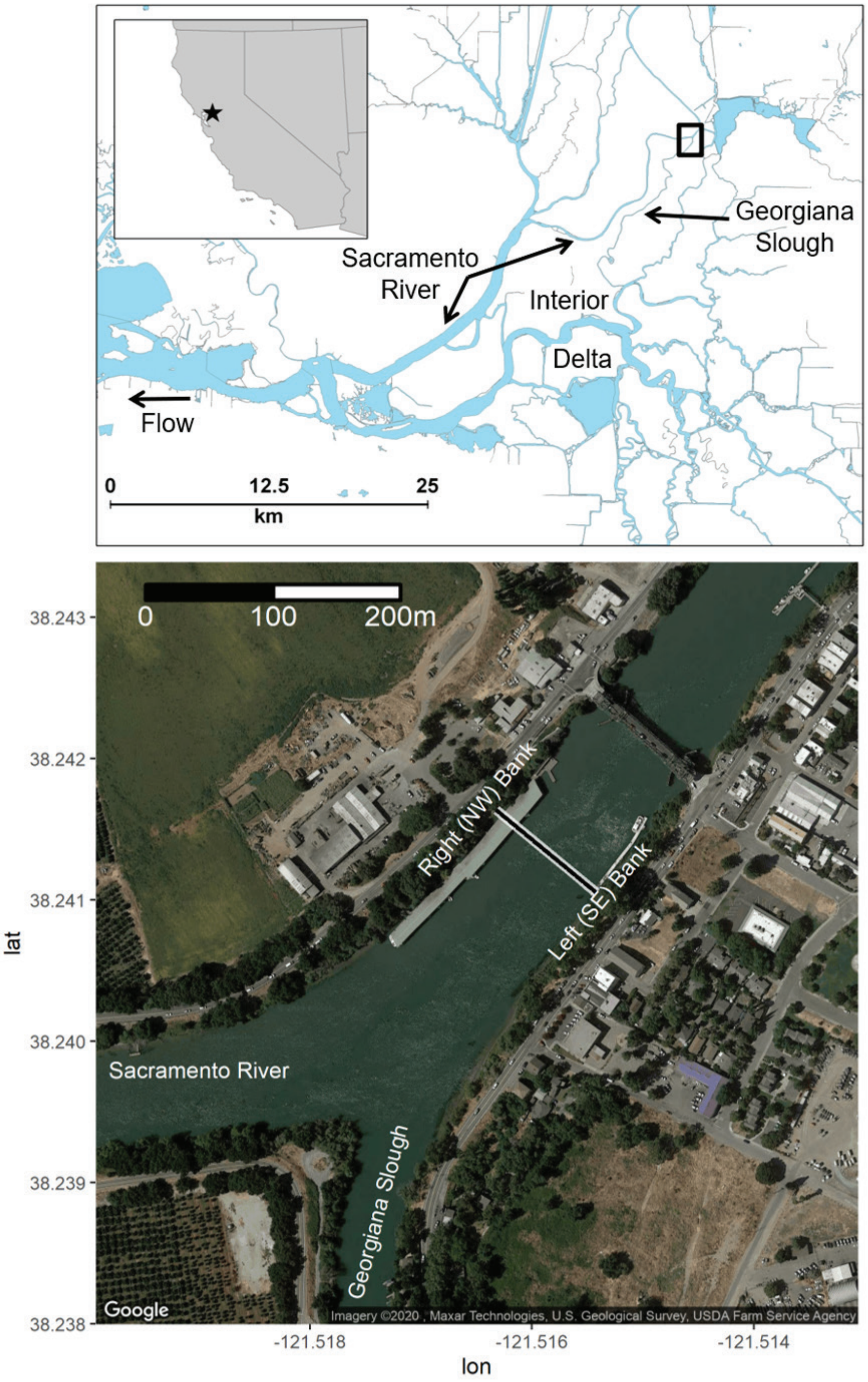

Figure 1 Map of study area focusing on the transect where the critical streakline was estimated based on ADCP data (*black line*). The wider white-shaded box around the black line represents the area where fish positions obtained from acoustic telemetry were retained to estimate fish cross-sectional distribution along the same transect for which acoustic Doppler profiler current (ADCP) data was collected.

ADCP and the Critical Streakline

We developed an entrainment zone model by: (1) using ADCP data to empirically estimate the location of the critical streakline, and (2) relating the location of the critical streakline to tidally- varying river flow. We collected ADCP data along the cross-section of the Sacramento River upstream of the Georgiana Slough junction over a wide range of flows and tidal conditions during 2014, including reversing flows where the incoming

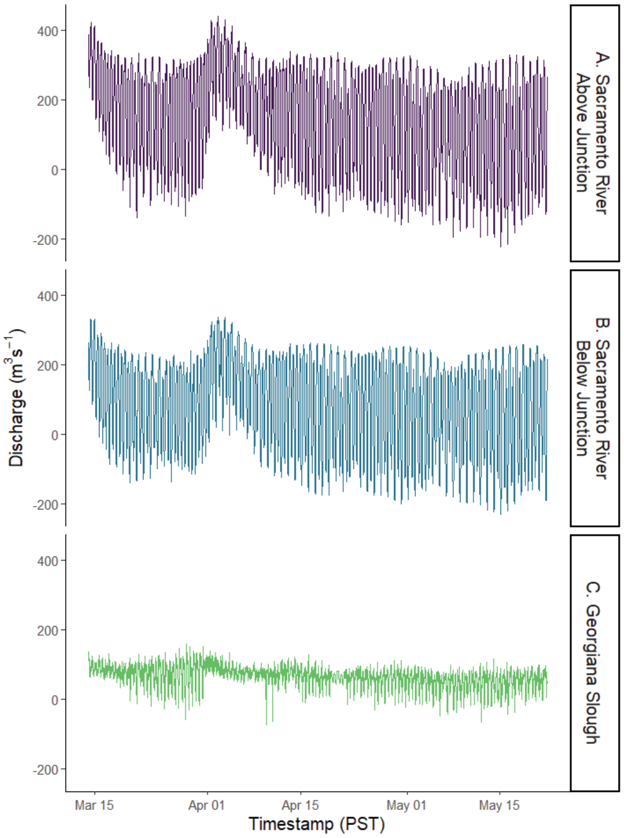

Figure 2 Sacramento River and Georgiana Slough discharge during collection of acoustic Doppler profiler current (ADCP) data used to estimate the critical streakline location in 2014

tide results in a net inland flow (Figure 2). We processed ADCP data to produce depth-averaged water velocities at 15-minute intervals. For each time-series observation, we calculated the location of the critical streakline by integrating velocity vectors for depth over the channel cross-section, starting on the left (eastern) bank, until the accumulated discharge equaled the discharge entering Georgina Slough. The resulting location was normalized to a (0, 1) interval by dividing the distance of the streakline from the left bank by the width of the channel (102.4 meters). Further details of ADCP data collection and critical streakline calculation are in CDWR (2015).

To predict the location of the critical streakline during the BAFF study in 2011 and 2012, we used linear regression to establish a relationship between the 2014 ADCP-derived integral-calculated streakline and a simpler ratio-calculated streakline based on the actual flows observed during the study. We refer to this number as the modeled integral-calculated streakline (S_I). The ratio-calculated critical streakline (S_R) is an approximation of the streakline location based on the ratio of discharge entering the side channel (Q_G) to the sum of discharge entering the side channel and that remaining in the main channel (Q_B):

$$S_R = \frac{Q_G}{Q_G + Q_B} \tag{1}$$

This approximation assumes uniform water velocity across the channel cross-section. To correct for non-uniformity of the channel, we determined a relationship between the integral-calculated and the ratio-calculated critical streakline in the 2014 data using linear regression methods on the logit-transformed values of critical streakline (Figure 3). We chose to use a logit transformation for streakline calculation because this resulted in a linear relationship while preserving the constraint on values between 0 and 1 upon back transformation. Although flow conditions during ADCP collection in 2014 were lower than those observed during the 2011 and 2012 (range 2014: –222 to 440 m^3s^{-1}; range 2011–2012: –10 to 1427 m^3s^{-1}), the location of the integral-calculated critical streakline stabilized around a mean = 0.36 (range: 0.33 to 0.4) as flows exceeded 400 m^3s^{-1}. We excluded reversing flows from 2014 from the regression because reversing flows were only rarely observed in 2011 and 2012 during the BAFF study.

Acoustic Telemetry

We assessed fish behavior in the study area using acoustic telemetry techniques to obtain spatially explicit two-dimensional (2-D) estimates of fish position. We briefly describe details of the acoustic telemetry data that are necessary to characterize fish cross-stream distribution and entrainment fate. A more detailed description of the acoustic telemetry equipment and fish tagging and release procedures can be found in Perry et al. 2014, CDWR 2012, and CDWR

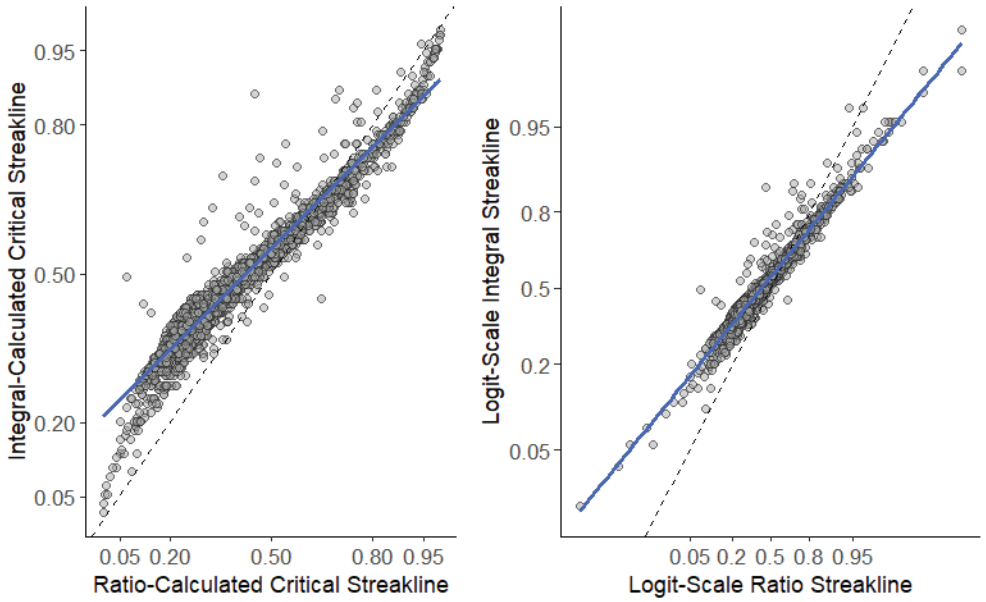

Figure 3 The location of the critical streakline calculated using two methods: the ratio of discharge between the junctions and the integration of velocity vectors on the normalized and the logit-scale. Under normalization, 0 indicates the left (SE) bank and 1 the right (NW) bank of the Sacramento River. The *dashed line* indicates the 1:1 line; the *solid line* represents the linear regression fit to the raw and transformed data. The non-linear shape of the untransformed data is a result of steepening of river bed slope near the banks.

2015. Fish used in the study were juvenile, late fall-run, hatchery-origin Chinook salmon from Coleman National Fish Hatchery. We implanted fish with an acoustic transmitter and released them 8.9 kilometers upstream of the study site. Tagged fish were monitored using 20 hydrophones installed upstream, downstream, and adjacent to the Georgiana Slough junction. Two-dimensional positions of the fish (Easting–Northing) were estimated from acoustic signals detected by the hydrophones as fish migrated through the study area. Successive position data were assembled into continuous fish tracks, which provided detailed information on fish behavior as they moved through the study area. Potential predation was identified using the methods of Romine et al. (2014), and these tags were removed from subsequent analyses.

For this analysis, the track data served two purposes. First, the cross-stream position of each fish was measured where each track intersected the transect where the critical streakline was measured. Second, the fish tracks were used to identify the entrainment fate of each fish (Georgiana Slough or Sacramento River). To determine each fish's cross-stream position, we retained detections from each fish's 2-D acoustic telemetry track that occurred within 3 meters upstream or downstream of the cross-section where the critical streakline was measured (see Figure 1). For fish with multiple detections within this window, only the last detection was retained to ensure that the cross-stream position used for each fish best represented its location as it approached Georgiana Slough. For this final position, cross-stream position for each fish was measured as the relative distance from the left bank (y; $0<y<1$). Based on the time-stamp of the retained detection, six covariates were assigned to each fish: operation of the BAFF (B; on = 1, off = 0), time of day (D; day = 0, night = 1), and discharge of the Sacramento River above (Q_A; m^3s^{-1}) and below (Q_B; m^3s^{-1}) the junction discharge of Georgiana Slough (Q_G; m^3s^{-1}), and whether the fish's cross-stream position was within the Georgiana Slough entrainment zone ($E = 1$ if $y < S_I$; 0 otherwise). The estimate of E was based on the location of the modeled integral-calculated critical streakline at the time fish passed the cross-section (S_I; $0 < S_I < 1$). Fish exiting the study area via Georgiana Slough were assigned the fate $F = 1$. Fish exiting the study area via the Sacramento River were assigned $F = 0$.

DATA ANALYSIS

Overview

We used two statistical models to describe the processes that affect fish entrainment into Georgiana Slough. First, we used beta regression to characterize the cross-stream distribution of fish in the cross-section upstream of the BAFF. Second, we used logistic regression to determine the probability of entrainment based, in part, on whether a fish's cross-stream position placed it in the Georgiana Slough entrainment zone—that is, on the Georgiana Slough side of the critical streakline. We then combined these two models to estimate the probability of entrainment as a function of covariates. We fit the combined models using the Stan probabilistic programming language (Carpenter et al. 2017) through the RStan interface in the R statistical computing platform.

Fish Cross-Stream Distribution

Beta regression models a continuous response variable that is restricted to the interval (0, 1) as a function of covariates that affect the shape of the beta distribution from which the response is drawn (Ferrari and Cribari–Neto 2004). The beta distribution can take a variety of shapes depending on the value of the parameters, including unimodal symmetric and asymmetric shapes, a uniform shape, and "U" shapes where most of the probability mass lies on either tail. Thus, it is particularly well-suited to describe the cross-stream distribution of fish that must necessarily be restricted to the river channel. We base our regression on the parameterization of Ferrari and Cribari–Neto (2004) in terms of the mean (μ), and the precision (ϕ):

$$f\left(y;\mu,\phi\right)=\frac{\Gamma\left(\phi\right)}{\Gamma\left(\mu\phi\right)\Gamma\left(\left(1-\mu\right)\phi\right)}y^{\mu\phi-1}\left(1-y\right)^{\left(1-\mu\right)\phi-1} \quad (2)$$

$$\textbf{for } 0<y<1$$

where and $0<\mu<1$ and $\phi>0$.

We modeled the mean cross-stream position for the i^{th} fish as a function of k covariates (X_i) using the logit link such that:

$$\mu_i=\frac{e^{X_i'\beta}}{1+e^{X_i'\beta}} \quad (3)$$

where $X'_i = (1, x_{1i}, \ldots, x_{ki})$ and $\beta = (\beta_0, \ldots, \beta_k)'$. We modeled the precision of the cross-stream distribution for the i^{th} fish—a measure of whether fish are diffusely or compactly distributed around the mean cross-stream position—as a function of j covariates (Z_i) using the log-link such that:

$$\phi_i = e^{Z_i'\gamma} \quad (4)$$

where $Z'_i = (1, z_{1i}, \ldots, z_{ji})$ and $\gamma = (\gamma_0, \ldots, \gamma_j)'$. Both link functions are commonly used for beta regression to maintain the constraints on the parameter space.

For all regression parameters, we used the weakly informative priors recommended by Gelman et al. (2008, 2014). Specifically, for the intercept terms (β_0, γ_0), we used Student's t-distribution with mean 0, standard deviation of 10, and 4 degrees of freedom. For all other terms, we used Student's t-distribution with mean 0, standard deviation of 2.5, and 4 degrees of freedom.

We selected the best model to describe cross-stream position by fitting a set of candidate models to the data, and evaluating the support for each model, given the data. We used Watanabe–Akaike information criterion (WAIC) to rank models based on their pointwise out-of-sample prediction accuracy (Watanabe 2010; Vehtari et al. 2017). To identify the final model used to describe fish cross-stream distribution, we first fit a series of models to select the best model for the precision term of the beta regression, holding the covariate model for the mean term constant. We fixed the mean term to the fullest possible model, which included the covariates for discharge upstream of the junction (Q_A), time of day (D), BAFF operation (B), and all possible interactions. After selecting the model for the precision term, we selected the best model for the mean term, holding the model for the precision term fixed to terms selected in the previous step. We assessed the fit of the final selected model using a posterior predictive check (Gelman et al. 2014). We considered posterior p-values below 0.05 or 0.95 to be evidence of lack of fit.

Entrainment Probability

We used logistic regression to estimate the probability that a fish will be entrained in Georgiana Slough as a function of whether or not the fish is in the entrainment zone. We modelled fish fate, F, as a Bernoulli random variable, and estimated entrainment probability, π_i, as a function of individual covariates. While our primary interest is in whether the entrainment zone is an adequate predictor of entrainment probability, we recognize that other factors may influence entrainment, especially BAFF operation. Therefore, we compared the support in the data for a set of alternative models. The covariates used included the indicator variable for whether the fish was in the entrainment zone as it passed the upstream cross-section (E), time of day (D), BAFF operation (B), and discharge (Q_A). The fullest model we considered included all two-way interactions between the covariates. We fit this set of models by including all models simpler than the fullest model, and then systematically excluding one or more terms. Models were selected as described previously.

Combined Predictive Model

Ultimately, we combined these two models to determine whether entrainment probability can be predicted independent of an individual fish's cross-stream position. The goal of this exercise was to derive a predictive relationship between covariates of flow, time of day, BAFF operations, and marginal entrainment probability. The marginal probability of entrainment can be thought of as the probability of entrainment after integrating out the influence of an individual fish's cross-stream position. Thus, the marginal probability of entrainment directly links environmental conditions and barrier operations to entrainment while accounting for the range of expected fish positions through the beta regression.

We constructed the predictive model by summing the probabilities of entrainment conditional on whether a fish was in or not in the entrainment zone. For each fish, we ignored the observed cross-stream position, and instead used the beta regression model to predict the posterior probability that the fish would be in the entrainment zone. We predicted this probability by using the cumulative distribution function of the beta distribution, conditional on observed covariates for each individual fish: $\Pr(E_i = 1 | D_i, B_i, Q_{Ai}) = \Pr(y_i < S_I | D_i, B_i, Q_{Ai})$. We next used the results of the logistic regression model to predict the probability of entrainment for each fish conditional only on the observed covariates at the time it passed the critical streakline transect. First, we calculated the probability of entrainment conditional on the fish being in the entrainment zone and all other observed covariates $\Pr(F_i = 1 | E = 1, D_i, B_i, Q_{Ai})$. Second, we calculated the complementary probability of entrainment conditional on the fish not being in the entrainment zone $\Pr(F_i = 1 | E = 0, D_i, B_i, Q_{Ai})$. We then combined these three elements to calculate the total posterior probability of entrainment for each fish:

$$p_{ei} = \Pr(F_i = 1 | E = 1, D_i, B_i, Q_{Ai}) \Pr(E = 1) + \Pr(F_i = 1 | E = 0, D_i, B_i, Q_{Ai}) \Pr(E = 0) \tag{5}$$

By summing the total posterior probability of entrainment over all fish, we calculated the expected number of fish entrained. We compared the expected number of fish entrained to the observed number of fish entrained as a final assessment of this predictive model based only on covariates.

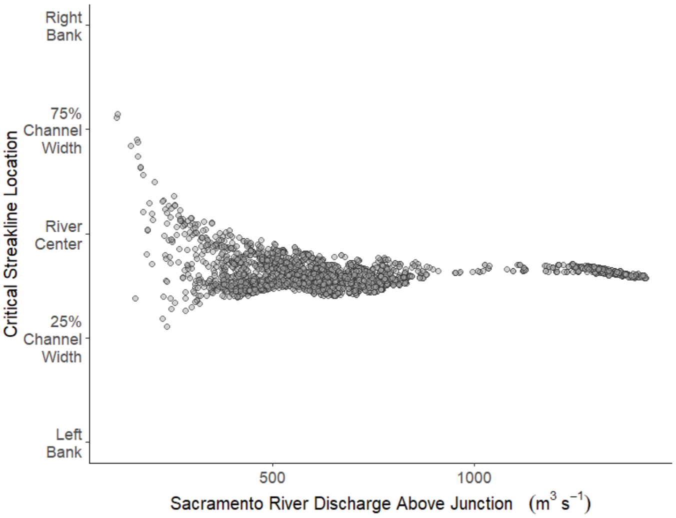

Figure 4 Location of critical streakline and river discharge each fish experienced as it passed the critical streakline transect

RESULTS

ADCP and the Critical Streakline

The simple logit-linear regression revealed that the ratio-calculated streakline was a good predictor of integral-calculated streakline (Figure 3, $R^2 = 0.96$). Applying this regression to the data, we identified the location of the critical streakline as relatively stable at higher flows, with more variation at lower flows. On average, the critical streakline was located at 40% of the channel width (approximately 41 meters from the southeastern bank). The location of the streakline at low flows varied from approximately 25% to 80% of the channel width (Figure 4).

Acoustic Telemetry Data

After applying the predation filter, a total of 2,525 fish were detected passing the critical streakline transect. Slightly more than half of these fish were from the 2011 study (1,385). Conditions were balanced across the data set, with approximately equal numbers of fish passing during the night and day, and when the BAFF was on and off (Table 1). Between one-quarter and one-third of fish passed the critical streakline transect on the Georgiana Slough side of the critical streakline (i.e., in the entrainment zone). Although the number of fish entrained differed between time of day and BAFF operations, a greater proportion of fish in the entrainment zone were entrained into Georgiana Slough relative to fish *not* in the entrainment zone (Table 1).

Fish Cross-Stream Distribution

Model selection statistics for the beta regression resulted in a model where increasing discharge (Q_A) was associated with decreasing precision, while the mean cross-stream position changed as an additive function of discharge, time of day (D), and BAFF operations (B). We found no evidence for lack of fit of the selected beta regression model to the data (Bayesian P-value = 0.51). The negative coefficient estimate for the effect of discharge on precision indicates that the cross-stream distribution of fish becomes more diffuse as discharge increases (Table 2). For the mean term of the beta regression, the use of logit-link means that a value of zero indicates the mean location to be exactly at mid-channel, with negative values corresponding to the Georgiana

Table 1 Number of fish entrained out of the number passing the critical streakline and cross-sectional distribution transect during bio-acoustic fish fence (BAFF) operations, during the night and the day, and on either side of the critical streakline in 2011 and 2012

BAFF	Time	Side of streakline	Number of fish	Number entrained	Percent entrained
BAFF: Off	Day	Sacramento River	461	55	0.12
BAFF: Off	Day	Georgiana Slough	189	81	0.43
BAFF: Off	Night	Sacramento River	434	46	0.11
BAFF: Off	Night	Georgiana Slough	191	116	0.61
BAFF: On	Day	Sacramento River	467	16	0.03
BAFF: On	Day	Georgiana Slough	178	31	0.17
BAFF: On	Night	Sacramento River	455	18	0.04
BAFF: On	Night	Georgiana Slough	150	53	0.35

Table 2 Parameter estimates for beta regression model that describes fish cross-sectional distribution, logit-scale for mean terms, and log-scale for precision terms. Covariates are centered and scaled Sacramento River discharge above Georgiana Slough junction (*Q*), an indicator variable for day or night (*D*), and an indicator variable for BAFF off or on (*B*).

	Posterior mean	Posterior standard deviation	Posterior 5th percentile	Posterior 95th percentile
Mean: Intercept (day, off)	−0.21	0.04	−0.28	−0.15
Mean: Q	0.10	0.02	0.06	0.14
Mean: D	0.08	0.02	0.04	0.12
Mean: B	0.06	0.03	0.02	0.10
Precision: Intercept	2.50	0.06	2.39	2.60
Precision: Q	−0.27	0.04	−0.34	−0.19

Slough side of the channel (river left), and positive values corresponding to the Sacramento River side of the channel (river right). Thus, the negative estimate for the intercept of the mean parameter indicates that the cross-stream distribution of fish is biased to the Georgiana Slough side of the channel at very low flows during the day and when the BAFF is off. Increasing flows, night, and operation of the BAFF all result in the center of mass of the fish cross-stream distribution moving toward the Sacramento River side of the channel.

Figure 5 demonstrates the effect of flow on the cross-stream distribution of fish for two representative conditions. At low flows (approximately 175 m^3s^{-1}) during the day with the BAFF off, the posterior distribution of fish cross-stream position has a center of mass toward the river left, and more mass concentrated about this center. At high flows (approximately 1375 m^3s^{-1}), the center of mass is to the right of the river center, but the distribution is more diffuse.

Entrainment Probability

Model selection statistics for logistic regression of fish fate resulted in a model that related increasing discharge (Q_A) to decreased probability of entrainment for fish on the Sacramento River side of the critical streakline, and increased probability of entrainment on the Georgiana Slough side. Time of day (*D*) and BAFF operations (*B*) modified this relationship, with the conditional probability of entrainment being lower overall when the BAFF was on

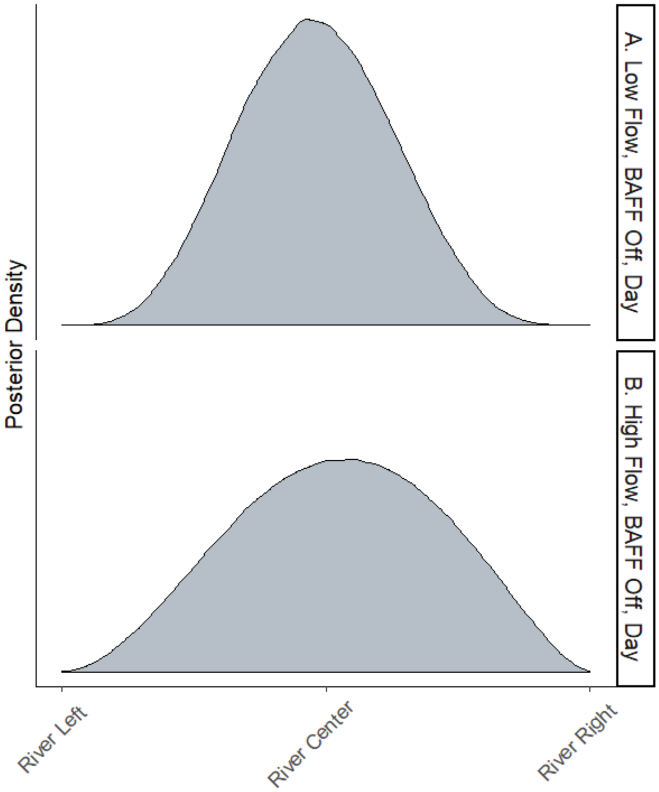

Figure 5 Posterior density for fish cross-stream position at representative conditions. (**Top panel**) low flow (approximately 175 m^3s^{-1}) during the day, when the BAFF is off. (**Bottom panel**) high flow (approximately 1375 m^3s^{-1}) during the day, when the BAFF is off. Posterior distributions are of a fish's position in the channel based on 10,000 Markov Chain Monte Carlo (MCMC) iterations.

and during the day. In selecting the logistic regression model for fish fate, the top model contained all variables plus all interactions, except the interaction between time of day and BAFF operation; however, 15 other models were only slightly lower. All 16 models contained all main-effects terms as well as the interaction of time of day and relative fish position, and the interaction of discharge and relative fish position. A direct comparison of the top model (estimated effective number of parameters = 7.7) to the model that contained all singular terms and just the two interactions (estimated effective number of parameters = 6.7) resulted in a difference of WAIC of 1.4 with a standard error of 2.8, indicating that these two models were indistinguishable in terms of predictive error. Therefore, we selected the simpler model of the two.

While the conditional probability of entrainment was generally higher for fish in the Georgiana Slough entrainment zone compared to fish on the Sacramento River side of the streakline, this difference increased with increasing flow (Figure 6). At the highest observed flows, the difference between probability of entrainment on the Georgiana Slough and Sacramento River sides of the streakline ranged from 0.85 when the BAFF was off and during the night, to 0.52 when the BAFF was on and during the day. Only at the lowest flows observed in the data was there little difference in the probability of entrainment on either side of the streakline.

Combined Predictive Model

The posterior probability of being in the entrainment zone (Figure 7) displayed a similar pattern to the critical streakline location (Figure 4). However, the posterior probability of being in the entrainment zone took on a greater range of values, especially at low flows. This reflects the relatively compact distribution of fish cross-stream position at low flows compared to the more diffuse cross-stream distribution at high flows.

The marginal probability of entrainment for each fish was relatively constant over the range of flows and conditions observed in 2011 and 2012 (Figure 8). When the BAFF was not operating, the mean marginal probability of entrainment was 0.27 at night (range: [0.19, 0.37]) and 0.21 during the day (range: [0.17, 0.28]). When the BAFF was operating, the mean marginal probability of entrainment was 0.12 at night (range: [0.07, 0.2]) and 0.08 during the day (range: [0.06, 0.15]).

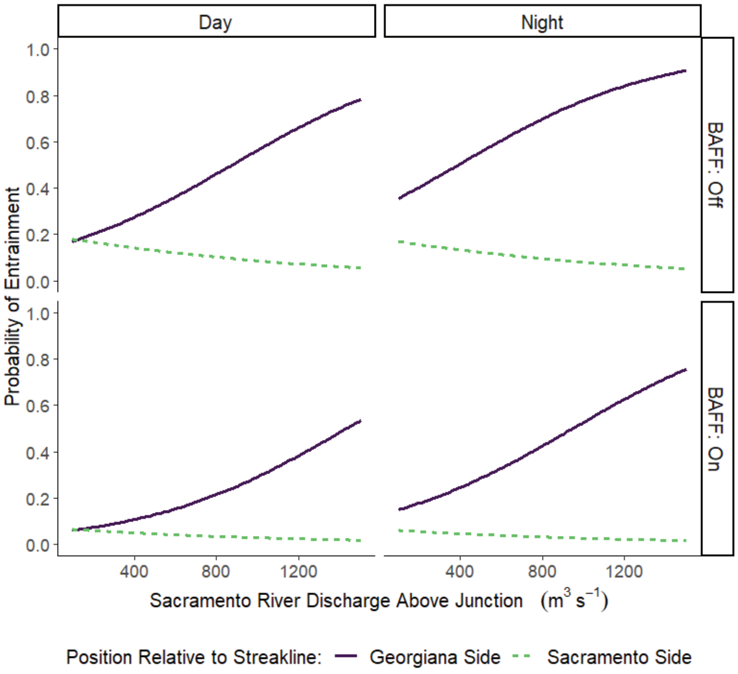

Figure 6 Probability of entrainment in Georgiana Slough based on a fish's position relative to the critical streakline, BAFF operations, and night/day across the conditions observed in 2011–2012. The Georgiana slough side of the critical streakline is considered to be the entrainment zone.

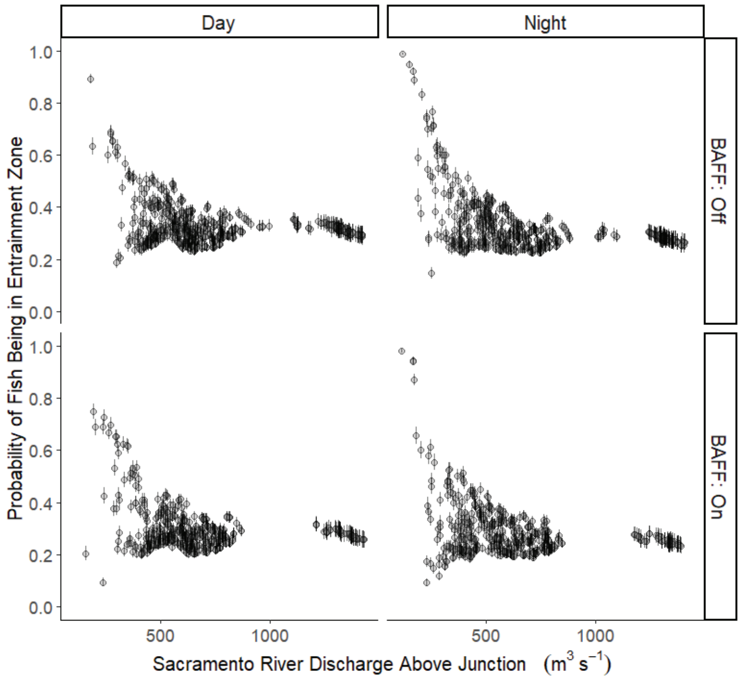

Figure 7 Posterior probability of being in entrainment zone for each fish based on critical streakline location and cross-sectional distribution as determined by the beta regression model. Error bars represent the 90% posterior interval.

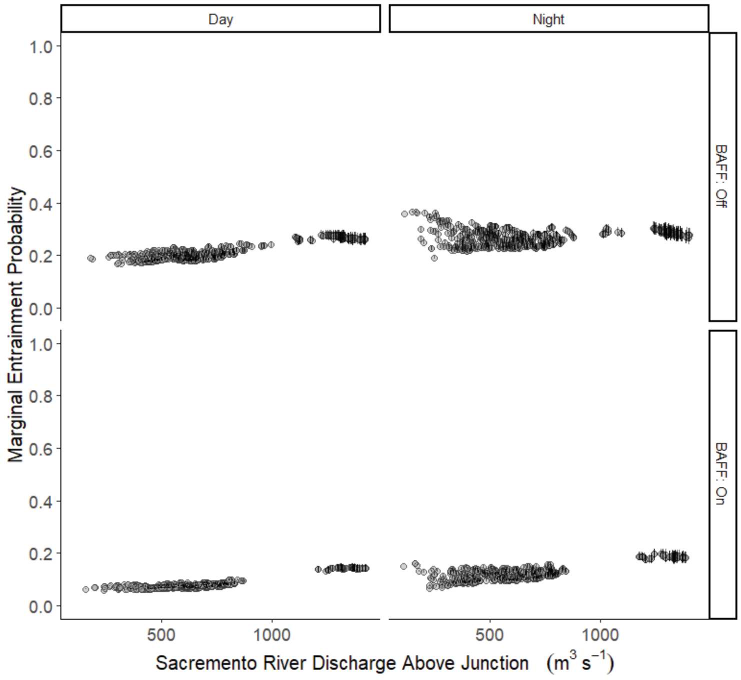

Figure 8 The marginal probability of being in the entrained in Georgiana Slough for each fish, conditioned on observed covariates of Sacramento River discharge, BAFF operating status, and day or night at the time of arrival at the cross-stream transect upstream of Georgiana Slough. Note: for this part of the analysis, we ignore each fish's observed cross-stream position and observed entrainment fate.

Table 3 Expected number entrained versus observed number entrained

Expected number entrained (posterior mean)	Posterior 5th percentile	Posterior 95th percentile	Observed number entrained
428.6	417.6	439.8	416

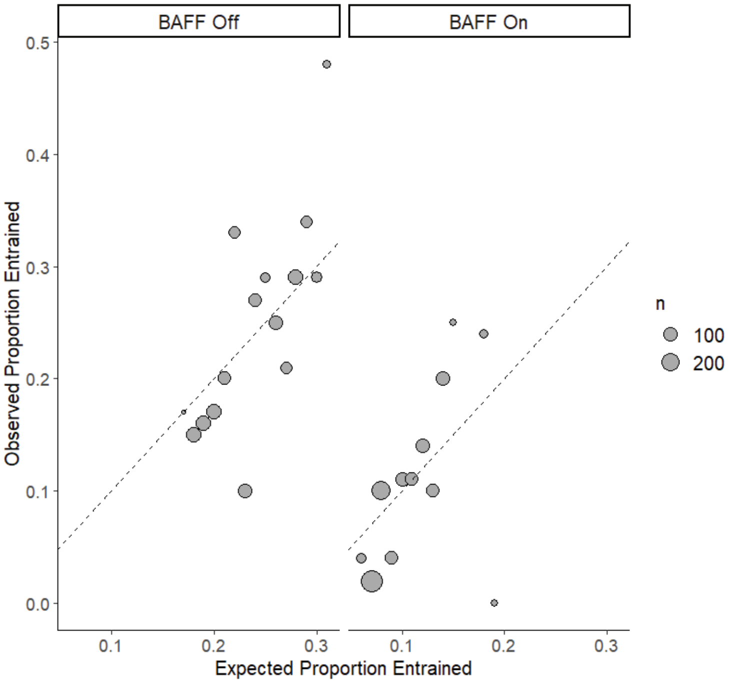

Figure 9 Observed proportion of juvenile Chinook Salmon entering Georgiana Slough compared with expected proportion as predicted by the combined cross-sectional distribution and entrainment probability model. Group were formed by binning all fish with predicted entrainment probabilities into 0.01 units. The size of the dot indicates the number of the fish in each bin.

The expected number of fish entrained, calculated by summing the probability of entrainment, slightly over-predicted the observed number of fish entrained overall. However, the lower bound of the 90% credible interval for total number of fish entrained was greater than the observed number by less than 2 (Table 3). Thus, the marginal probability of entrainment made by integrating out each individual fish's cross-stream position resulted in a reasonable prediction of aggregate individual fates.

DISCUSSION

The movement and survival of juvenile salmon populations in different channels of the Sacramento–San Joaquin Delta can be influenced by management actions that alter the quantity and distribution of water. Models to predict migration routing of juvenile salmon in response to water management actions span a spectrum from purely mechanistic to purely statistical models. The development of spatially explicit mechanistic fish movement models in response to environmental conditions was identified as an important step in improving water resource management in the Sacramento–San Joaquin Delta (Rose et al. 2011; Delta ISB 2015). Yet statistical models that summarize the relationship between migration routing and hydrodynamics have been instrumental in understanding how individual fish behavior gives rise to emergent patterns that water management actions ultimately influence (Cavallo et al. 2015; Perry et al. 2015, 2018). We view our model as a bridge between a purely mechanistic or purely statistical model because it provides a quantitative description of a conceptual model that is rooted in physical and biological principles. The model we constructed simultaneously describes the cross-stream position of fish and integrates over the range of possible positions to provide a single estimate of the probability of entrainment in relation to environmental conditions. Thus, we were able to directly link environmental conditions of streamflow, time of day, and barrier operations to entrainment probability with a model that accommodates animal behavior. Our model should prove useful in the development of more complex agent-based movement models, because such models should reproduce the emergent patterns our model described, such as the expected cross-stream fish distribution.

Perry et al. (2014) previously identified the BAFF as an effective management tool for reducing entrainment under a range of conditions at Georgiana Slough, but noted that additional factors were important determinants in entrainment probability as well. Cross-stream position was identified as the most important factor affecting migration routing—a finding which was an important motivation for this work. In the light of this previous work, one surprising finding from this new approach is that BAFF operations influenced the cross-stream position of fish approximately 150 meters upstream of the BAFF. However, because the spatial extent over which fish perceive and respond to the BAFF cannot be quantified from the available data, it remains an open question whether the shift in cross-stream positions associated with BAFF operations is causative or merely a correlation.

This work was motivated by the conceptual model of the critical streakline and entrainment zone, and we directly assessed the hypothesis that fish in the entrainment zone are much more likely to be entrained than fish on the main channel side of the critical streakline. The results of this work demonstrate the viability of this conceptual model, while also highlighting conditions under which fish within the Georgiana Slough entrainment zone were actually less likely than random chance to enter Georgiana Slough. Under all conditions observed in this study, fish in the Georgiana Slough entrainment zone were more likely to be entrained into Georgiana Slough than fish not in the entrainment zone. Under the highest flows, the entrainment probability on either side of the critical streakline exhibited the largest difference, with fish on the Georgiana Slough side of the streakline almost certain to be entrained, and fish on the Sacramento River side almost certain to avoid entrainment. However, under lower flows, the difference in entrainment between the two sides of the critical streakline was less apparent. This occurred both because fish on the Sacramento River side of the critical streakline were more likely to be entrained than under higher flows and because fish on the Georgiana Slough River side were less likely to be entrained. The simple conceptual model of the entrainment zone hypothesis assumes that fish travel along streamlines; that is, that a migrating fish maintains the same relative position in the cross-channel as it moves downstream. An explanation for the patterns observed in our analysis is that fish movement in the cross-stream direction (i.e., across streamlines) is a substantial component of the downstream migration process. Indeed, our results provide evidence that the interplay between downstream water velocity and lateral movement of fish dictate its fate, or the probability of fish in the entrainment zone being entrained into Georgiana Slough. As downstream water velocity decreases, lateral movement causes a fish's eventual position at some downstream location to become less predictable as distance increases. The availability of ADCP data used to estimate the critical streakline location determined our choice of the location to estimate the cross-sectional distribution of fish. If the cross-sectional distribution of fish and critical streakline were determined closer to the actual junction, we expect the resulting model to be more predictive of a fish's ultimate fate.

One novel aspect of this study was the prediction of the critical streakline location at all observed flows based on ADCP data. Using a simple data transformation, we were able to identify a robust relationship between the ratio-calculated and integral-calculated streakline locations. Such an approach can be readily replicated at other junctions in the Sacramento–San Joaquin Delta. The advantage of this approach is that observed data from a relatively brief field study can be used to produce reliable predictions of the critical streakline over a broad range of flows and hydrologic water years. This allows the critical streakline conceptual model to be more easily developed and applied at other river junctions.

River discharge during the time of this study encompassed only relatively high to moderate flows. In particular, reversing flow conditions from tidal forcing were largely absent during the 2011 and 2012 portion of the field study. This analysis does not include those conditions in the characterization of fish distributions and entrainment probabilities. However, Perry et al. (2015) estimated entrainment probability for Georgiana Slough based on telemetry data collected from 2007 to 2009, which encompassed time-periods of lower flow and reversing flows (mean discharge of Sacramento River upstream of junction: 293; range: –61 to 799 m^3s^{-1}). Given that this analysis found the cross-stream distribution of fish to be less meaningful at lower flow, particularly those less than approximately 200 m^3s^{-1}, the model of Perry et al. (2015) provides a suitable method of estimating entrainment at these lower flows.

In conclusion, spatially explicit water velocity and telemetry data allowed us to quantify the conceptual framework put forth by the critical streakline/entrainment zone hypothesis presented by Perry et al. (2016). We found that both the spatial distribution of fish in the channel cross-section and the location of the critical streakline varied with river flow and other factors, and both cross-sectional distribution and streakline location interact to determine entrainment probability. While the critical streakline/entrainment zone hypothesis forms a useful conceptual model for framing how fish behavior interacts with hydrodynamics to affect migration routing, we also found evidence that cross-stream movement behavior contributed to a lower probability of entrainment at lower flows when fish in the entrainment zone had sufficient time to swim across streamlines to exit the entrainment zone. Thus, our work provides a mechanistic framework to evaluate migratory fish routing at river junctions that could be incorporated into a variety of predictive tools and analyses. Correctly predicting the migratory pathway or fish in response to environmental conditions is a significant development toward a powerful management tool to evaluate the effects of alternative actions on migrating fish.

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