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USING A NON-PHYSICAL BEHAVIOURAL BARRIER TO ALTER MIGRATION ROUTING OF JUVENILE CHINOOK SALMON IN THE SACRAMENTO–SAN JOAQUIN RIVER DELTA

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ABSTRACT

Anthropogenic alterations to river systems, such as irrigation and hydroelectric development, can negatively affect fish populations by reducing survival when fish are routed through potentially dangerous locations. Non-physical barriers using behavioural stimuli are one means of guiding fish away from such locations without obstructing water flow. In the Sacramento–San Joaquin River Delta, we evaluated a bio-acoustic fish fence (BAFF) composed of strobe lights, sound and a bubble curtain, which was intended to divert juvenile Chinook salmon (*Oncorhynchus tshawytscha*) away from Georgiana Slough, a low-survival migration route that branches off the Sacramento River. To quantify fish response to the BAFF, we estimated individual entrainment probabilities from two-dimensional movement paths of juvenile salmon implanted with acoustic transmitters. Overall, 7.7% of the fish were entrained into Georgiana Slough when the BAFF was on, and 22.3% were entrained when the BAFF was off, but a number of other factors influenced the performance of the BAFF. The effectiveness of the BAFF declined with increasing river discharge, likely because increased water velocities reduced the ability of fish to avoid being swept across the BAFF into Georgiana Slough. The BAFF reduced entrainment probability by up to 40 percentage points near the critical streakline, which defined the streamwise division of flow vectors entering each channel. However, the effect of the BAFF declined moving in either direction away from the critical streakline. Our study shows how fish behaviour and the environment interacted to influence the performance of a non-physical behavioural barrier in an applied setting. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: acoustic telemetry; Chinook salmon; non-physical barrier; migration; strobe lights; bubble curtain; sound

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INTRODUCTION

Rivers have long been harnessed to provide critical human services, such as hydroelectricity, irrigation and domestic water. These developments often affect fish populations by impeding fish migrations or by causing mortality at structures such as turbine intakes and irrigation diversions. To reduce these negative effects, guidance systems can be used to attract migrating fishes toward favourable locations or repel them from dangerous ones (Coutant, 2001a). Physical barriers such as screens and louver systems are measures commonly used to prevent fish from entering irrigation diversions or turbine intakes (Odeh, 1999, 2000). Although effective, these types of engineering solutions are costly and may also cause mortality when fish become impinged on these structures. Non-physical, behavioural barriers are an attractive alternative to physical barriers because they can deter fish without injury and without altering water flow (Noatch and Suski, 2012).

Non-physical barriers use behavioural stimuli such as sound, bubble curtains and strobe lights to deter fish from entering a potentially dangerous location. Laboratory studies have documented systematic avoidance responses of many fish species to behavioural stimuli, but field applications have met with mixed success because the environment may modify (e.g., water temperature) or override (e.g., water velocity) a fish's behavioural response (Popper and Carlson, 1998). For example, strobe lights were deployed at Cowlitz Falls Dam, Washington, to reduce entrainment of juvenile steelhead, *Oncorhynchus mykiss*, into turbine intakes. However, operation of strobe lights increased turbine entrainment, contrary to their intended purpose (Kock *et al*., 2009). The authors posited that fish were disoriented by the strobe lights, allowing them to be pulled into turbine intakes (see Flamarique *et al*., 2006). This example illustrates that non-physical barriers can have unintended effects on fish behaviour, but also highlights the need to carefully consider site-specific implementation of behavioural stimuli and to quantify fish response relative to the background

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environment. Recently, a barrier consisting of multiple behavioural stimuli forming a curtain of sound, bubbles and lights has been used to deter fish. Coined as the bio-acoustic fish fence (BAFF), this non-physical barrier has been shown to successfully divert a high proportion of juvenile Atlantic salmon (*Salmo salar*) from one river channel into another (Welton *et al*., 2002).

The Sacramento–San Joaquin River Delta (hereafter, the Delta) is a complex network of channels that has been highly altered to direct water toward large pumping stations in the interior Delta (Nichols *et al*., 1986; Figure 1). Threatened

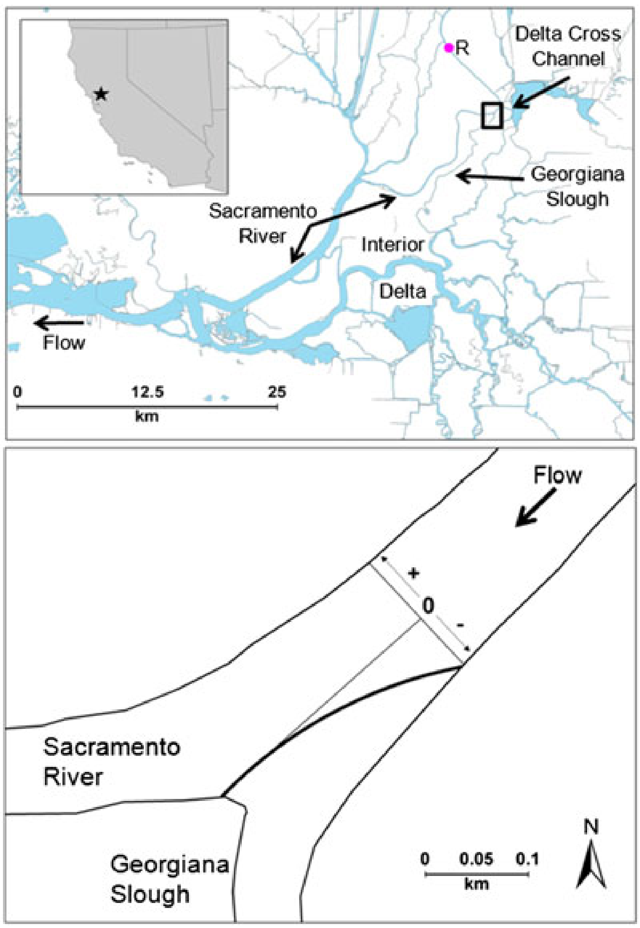

Figure 1. Map of the Sacramento–San Joaquin River Delta (top panel) showing the release location (denoted by "R") and the study area of the BAFF experiment (denoted by the inset box) detailed in the bottom panel. The Delta Cross Channel branches off the Sacramento River just upstream of the study area. In the bottom panel, the heavy solid line shows the location of the BAFF in the river junction, and thin lines show the streamwise (parallel to mean velocity vectors) and cross-stream (perpendicular to mean velocity vectors) co-ordinate system. Zero indicates the origin, with positive cross-stream co-ordinates indicating locations to the Sacramento River side of the BAFF and negative cross-stream co-ordinates to the Georgiana Slough side of the BAFF. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

populations of juvenile salmonids emigrating from the Sacramento River distribute among these channels and use multiple migration routes on their seaward journey (Perry *et al*., 2010). Migration routes vary in size and length, as well as in biotic and abiotic factors, all of which influence the survival of juvenile salmon. For instance, fish that migrate through the interior Delta survive at lower rates than fish that migrate within the Sacramento River, likely due to high predation rates, longer migration times and entrainment at pumping stations (Newman and Brandes, 2010; Perry *et al*., 2010, in press). Because survival in the interior Delta is lower than in other routes, population-level survival decreases as the fraction of the population entering the interior Delta increases (Perry *et al*., in press).

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) enter the interior Delta via two channels that diverge from the Sacramento River (Figure 1). Fish first pass the Delta Cross Channel, a man-made gated channel used to divert water into the interior Delta to reduce salinities at the pumping stations (Figure 1). Fish remaining in the Sacramento River then pass Georgiana Slough, a natural channel located 1 km downstream from the entrance to the Delta Cross Channel (Figure 1). These two channels may entrain up to 50% of fish into the interior Delta, exposing a substantial fraction of the population to low survival probabilities (Perry, 2010). Due to high entrainment into the interior Delta, managers are investigating whether a non-physical behavioural barrier can be used to divert fish away from the entrance of Georgiana Slough, and into the Sacramento River where survival is higher. Thus, the goals of our study were to (1) estimate the effect of a BAFF on entrainment probabilities into Georgiana Slough and (2) quantify the effects of behavioural and physical factors on the performance of a BAFF.

A number of physical factors driven by river flow may influence whether a fish enters a particular river channel at a river junction and the potential effectiveness of a non-physical barrier such as the BAFF. Both the relative distribution of flow among river channels and the spatial distribution of fish approaching a river junction will influence the probability of fish entering a given river channel. Intuitively, fish migrating close to one shore will likely remain in the channel along that shore, whereas fish along the opposite shore will tend to enter the opposite channel. The streamwise division of flow vectors entering each channel (defined as the critical streakline) relative to the spatial distribution of fish in the channel cross-section will influence the proportion of fish entering each channel, as well as the fraction of fish that interact with the BAFF. For example, fish located on the Georgiana Slough side of the critical streakline are more likely to enter Georgiana Slough than fish located on the opposite side of the critical streakline. Other factors affecting response of fish to the

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BAFF include water velocity and turbidity. We used acoustic telemetry techniques to obtain two-dimensional tracks of juvenile salmon under varying levels of river discharge. These data allowed us to quantify how physical processes interacted with the operation of a BAFF to affect the proportion of fish entering each river channel.

METHODS

Study area and BAFF

The study area was located near Sacramento, California, where Georgiana Slough branches off the mainstem Sacramento River (Figure 1). The average water depth within the study area was 6.3 m and the width of the river channel was 144.8 m. The BAFF is a patented structure that incorporates air bubbles, sound and light to deter fish (Fish Guidance Systems, Ltd.). The BAFF was 192 m long (Figure 1) and composed of sixteen 12-m-long frames (for detailed engineering drawings, see California Department of Water Resources, 2012). The junction of adjacent frames was able to pivot and, where needed, was supported with a piling or support column and pier block. The top of the frame sections was positioned to be at least 2.4 m from the average low tide water surface elevation. The alignment of the frames relative to the direction of river flow was adjusted to ensure that flow vectors met the barrier at an angle such that fish needed to make relatively small angular adjustments in swimming direction to be guided along the face of the barrier (Rainey, 1985; Turnpenny and O'Keefe, 2005). On the basis of the sustained swimming speed for Chinook salmon (Swanson *et al*., 2004), the size of the fish used in the study and the expected maximum water velocity in the river, the BAFF was aligned such that its angle relative to the flow never exceeded 24°. This alignment resulted in a calculated maximum approach velocity perpendicular to the barrier of $0.25\,\mathrm{m\ s^{-1}}$.

A curtain of air bubbles was created along the length of the BAFF by passing compressed air into a perforated hose at a rate of approximately $2.0\,\mathrm{L\ s^{-1}}$ per 1 m length of hose. The primary function of the bubbles was to contain, or trap, the sound generated by the sound projectors. Using this approach, we were able to produce a behavioural deterrent consisting of a precise linear wall of sound that was typically only a small percentage of its peak level within 2 to 3 m of the source. The sound projectors, 96 in total over the length of the BAFF, consisted of electromechanical transducers (model FGS MkIII 30–600) that produced sound in the frequency range of 5 to 600 Hz at 146 to 159 dB re 1 μPa (mean = 152 dB re 1 μPa). The sound projectors were synchronized with intense lights flashing at a rate of 3 Hz to provide a combined stimulus that maximized the potential effect on fish behaviour. The light was generated along the length of the BAFF by light-emitting, diode-powered light bars that projected white light at a minimum output of 847.44 lx at 1 m from the source. The lights were flashed on and off rapidly and were aimed at the rising air bubbles as they were emitted from the perforated hose. This alignment resulted in a wall of light that reflected off of the bubbles, and was intended to improve the visibility of the bubble curtain to approaching fish.

Acoustic telemetry monitoring equipment

The acoustic telemetry monitoring system consisted of transmitters, hydrophones and receivers that operated at 307 kHz (Hydroacoustic Technology Inc., Seattle, Washington). The transmitters (hereafter referred to as tags) were 6.5 mm in diameter, 16.3 mm in length, averaged 0.67 g in air and had a typical battery life of 15 days (HTI Model 795Lm). Each tag emitted a unique acoustic signal composed of a primary and secondary acoustic pulse, allowing simultaneous monitoring of multiple tags by a single hydrophone (Ehrenberg and Steig, 2003). The pulse rate of tags ranged from 2.003 to 3.474 s, and the pulse length of the transmitted signal was 0.003 s.

Twenty hydrophones (HTI, Model 590) were installed in the Sacramento River immediately upstream, downstream and adjacent to the BAFF to monitor tagged fish as they encountered and responded to the barrier. Hydrophones were capable of detecting tagged fish in a 330° radius and were installed on the bottom of the river or near the surface. The position of the hydrophones relative to one another, often referred to as the geometry of the array, was designed to gather three-dimensional positions of tagged fish as they moved through the array. To obtain accurate three-dimensional positions, a tagged fish must have been detected on at least four hydrophones that were in different vertical planes, and within direct line of sight of the tagged fish. As a tagged fish passed through the area monitored by the four hydrophones, the difference in the arrival time of each pulse emitted by the tag was used to triangulate the exact location of the signal. Successive estimates of the tag's position were used to generate fish tracks as they swam through the array, thereby providing detailed information about their behaviour as they approached and interacted with the BAFF.

The hydrophones were connected via cable to receivers (HTI Model 290 Acoustic Tag Receivers) located on shore. For this study, two receivers, each linked to a personal computer, were used to collect and store the acoustic data for the 20 hydrophones in the array. The two receivers were synchronized with an internal GPS. Filters in the receivers were set to identify the acoustic signal emitted by the tag and discriminate it from ambient background noise. A detailed description of the procedures used to process the data can be found in California Department of Water

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Resources (2012). In short, data were processed using the vendor's software to acquire, store and identify the acoustic signal.

Fish tagging and release

Fish used in the study were juvenile, late fall–run Chinook salmon obtained from the Coleman National Fish Hatchery operated by the US Fish and Wildlife Service. Hatchery conditions and ration levels were maintained to produce fish ranging in size from 110 to 140 mm fork length. Fish were selected for tagging so that transmitter burden (weight of the tag relative to the weight of the fish) did not exceed 5%. Fish were transported daily from the hatchery to the tagging and release site located 8.9 km upstream of the study site. Fish rations were withheld 24 h before transport to reduce stress from transport, handling and tagging. Fish were held in flow-through holding containers within the Sacramento River for 18 to 24 h before tagging and 24 h after tagging.

Fish handling and surgical implantation procedures were based on Liedtke and Wargo-Rub (2012). Fish were anesthetized using buffered tricaine methanesulfonate (MS-222) until loss of equilibrium, and were then weighed, measured and placed ventral side-up on a surgical platform for 5 min or until non-responsive. Irrigation with a light dose (20 mg L^{-1} MS-222) was provided during the brief (2–3 min) surgical procedure. A small incision was made anterior to the pelvic girdle and a disinfected transmitter was placed within the body cavity. The incision was then closed using two interrupted sutures with Vicryl + 5-0 absorbable suture material. After surgery, fish were transferred to a recovery container and monitored until they regained equilibrium. Groups of four to five fish, representing a release group, were held together in flow-through containers until release. Tagging operations were conducted twice daily to reduce variability in post-tagging holding times, and tagged fish were released every 3 h ($N = 1500$ tagged fish) during two release periods (16 March–28 March 2011 and 15 April–15 May 2011).

Data analysis

We used logistic regression to quantify factors affecting the migration routes used by acoustically tagged juvenile salmon. Specifically, we modelled the fate of each fish, F_i, as a Bernoulli random variable where $F_i = 1$ for fish entering Georgiana Slough and $F_i = 0$ for fish remaining in the Sacramento River. Migration routes used by each fish were determined based on whether two-dimensional tracks exited the study area via the Sacramento River or Georgiana Slough. The probability of entrainment into Georgiana Slough, $\pi_{G,i}$, was modelled as a function of individual covariates using generalized linear models in the R statistical platform (R Development Core Team, 2011). We used the logit link function, which models $\ln(\pi_{G,i} / (1 - \pi_{G,i}))$ as a linear function of covariates. Entrainment probability for each individual was then expressed as a function of covariates using the inverse logit function:

$$\pi_{G,i} = \frac{\exp\left(\beta_0 + \beta_1 Y_{1,i}, \cdots, \beta_n Y_{n,i}\right)}{1 + \exp\left(\beta_0 + \beta_1 Y_{1,i}, \cdots, \beta_n Y_{n,i}\right)} \quad (1)$$

where $Y_{1,i}, \ldots, Y_{n,i}$ are the values of n covariates for the ith fish, β_0 is the intercept and $\beta_1, \ldots, \beta_n$ are slope coefficients for the n covariates.

We considered five covariates for inclusion in candidate models: operation of the BAFF (B; on = 1, off = 0), time of day (D; day = 1, night = 0), discharge entering the river junction (Q, $m^3\,s^{-1}$), cross-stream position (X) of tagged fish and location of the critical streakline (S). Turbidity and water velocity upstream of the BAFF were also considered, but both were highly correlated with discharge ($r = 0.89$ for turbidity; $r = 0.97$ for velocity) and were therefore excluded from the analysis. Values of individual covariates were assigned based on the time at which fish were closest to the BAFF.

Cross-stream position measures the fish's location in the cross-section upstream of the BAFF, whereas the streakline position indicates whether fish were located within water parcels likely to enter one channel or another. Cross-stream position was measured using each fish's nearest two-dimensional position to a cross-section aligned with the upstream end of the BAFF (Figure 1). The critical streakline estimates the cross-stream location that divides the river channel into water parcels entering either the Georgiana Slough or the Sacramento River:

$$S = W\left(\frac{Q_G}{Q_S + Q_G}\right) - 37.5 \quad (2)$$

where W is the width of the channel (144.8 m) and Q_G and Q_S is discharge of Georgiana Slough and the Sacramento River, respectively, measured downstream of the river junction. This equation makes the simplifying assumption of a rectangular channel and uniform velocity distribution. Both S and X were offset by 37.5 m to set the origin to the outermost position of the BAFF (Figure 1). Thus, for $X < 0$, fish were located to the Georgiana Slough side of the BAFF in the river channel just upstream of the junction and for $X > 0$, fish were located toward the Sacramento River side of the BAFF in the river channel just upstream of the junction. Likewise, for $S < 0$, the critical streakline intersects the BAFF, but for $S > 0$, the streakline extends into the Sacramento River beyond the BAFF. Similarly, $X < S$ indicates that fish were located in the parcel of water likely

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to enter Georgiana Slough, whereas $X > S$ indicates that fish were more likely to remain in the Sacramento River.

The model selection process consisted of fitting alternative models to the data, ranking the models based on an information criterion, and then using the best fit model for inference. We used the Bayesian information criterion (BIC) for model selection (Schwarz, 1978), which is calculated as $2 \times \text{NLL} + k \times \ln(n)$, where NLL is the minimized negative log-likelihood, k is the number of parameters and n is the sample size. This information criterion seeks to identify the most parsimonious model by trading off goodness-of-fit, measured by the maximized log-likelihood of a given model, with a penalty term based on the number of parameters used to fit the model. Models with lower BIC are considered more parsimonious models. We interpret differences of less than 3 BIC units between models (ΔBIC) as models that explain the data equally well.

To identify the best model, we fit a series of main-effects models and added two-way interactions (i.e. products of variables) to the best-fit main effects model. We fit all possible main-effects models formed using the five predictor variables, resulting in 32 models. We then added biologically reasonable two-way interactions to the main-effects model that was selected on the basis of ΔBIC. Interaction terms assessed whether the effectiveness of the BAFF varied with time of day (D), cross-stream location of fish (X) and discharge (Q). The model with the lowest BIC value in the set of models was then selected as the best-fit model explaining variation in migration routing of juvenile salmon. To assess the relative importance of each variable, we also calculated the difference in BIC of each model (ΔBIC) relative to the lowest-BIC model within groups of models of similar complexity.

We assessed model fit to the data using both quantitative and descriptive techniques. To check for systematic deviations of predicted from observed values, we performed the Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2000). We also calculated the area under the receiver operating curve (AUC) to quantify how well the model predicts the fates of fish (Hosmer and Lemeshow, 2000). The AUC is calculated as follows: if estimated probabilities of $\pi_{G,i}$ are greater than an arbitrary cutoff value of π_G, then the ith fish is assigned to Georgiana Slough. For a particular cutoff value, the actual route used by each fish is compared with the predicted route, and the false-positive and true-positive rate calculated. The receiver operating curve plots the true-positive rate versus the false-positive rate for all possible cutoff values and AUC is the area under this curve. An AUC of 0.5 indicates the model has no ability to predict the fish's migration route, whereas $\text{AUC} = 1$ indicates perfect classification ability. In practice, models with AUC between 0.8 and 0.9 are considered to have "excellent" discrimination ability and $\text{AUC} > 0.9$ is considered "outstanding" (Hosmer and Lemeshow, 2000).

We present results from the best-fit model in three ways. First, the parameter estimates (i.e. the slope coefficients) indicate whether each variable positively or negatively influenced entrainment into Georgiana Slough. To illustrate the effect of each variable on entrainment probability, we plot the relationship between $\pi_{G,i}$ and each covariate while holding all other covariates constant. Second, to examine how covariates interacted to affect entrainment probabilities, we divided the data set into day and night, BAFF on and BAFF off, and high- and low-flow periods (i.e. before and after 5 April 2011; see Figure 2), resulting in eight strata. We then examined the relationship between predicted entrainment probabilities and mean values of covariates within each stratum. Last, the observed fraction of fish entrained into Georgiana Slough arises as a function of individual entrainment probabilities integrated across the conditions experienced by each fish as it passed through the river junction. Given estimated individual entrainment probabilities from the best fit model, we estimated the fraction of fish entering Georgiana Slough as the mean of individual entrainment probabilities during each stratum. We then compared mean estimated entrainment probabilities to the observed fraction of fish entering Georgiana Slough to assess how well the best-fit model predicted entrainment at the population level.

RESULTS

River conditions and BAFF operation

During the course of the study between 16 March and 15 May 2011, discharge entering the river junction receded from approximately 1450 to 566 $m^3 \cdot s^{-1}$ (Figure 2). To assess the effect of the BAFF over a range of discharges, the

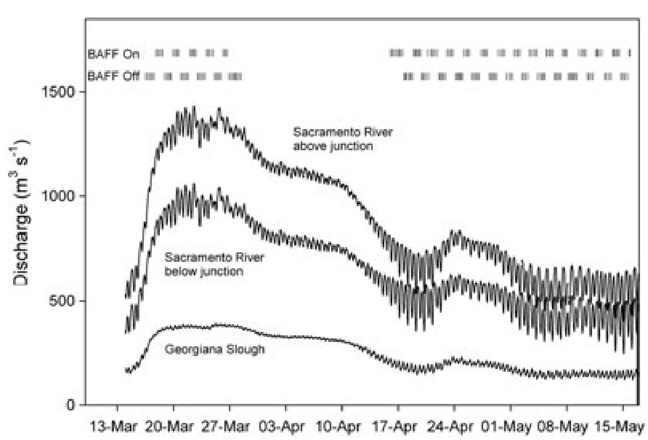

Figure 2. River discharge and BAFF treatment when each fish was detected in the acoustic array at the river junction of the Sacramento River and Georgiana Slough

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experiment was postponed in late March until flows had receded (Figure 2). Of the 1500 fish released, 86 fish were excluded from the analysis because they never arrived in the study area or were classified as having been predated within the acoustic array, leaving 1414 fish available for analysis. During the course of the experiment, 7.7% of the fish were entrained into Georgiana Slough when the BAFF was on, whereas 22.3% entered Georgiana Slough when the BAFF was off, suggesting that operation of the BAFF reduced entrainment in Georgiana Slough.

Model selection

Model selection results suggested that cross-stream position (X), followed by BAFF operation (B), had the largest influence on entrainment into Georgiana Slough; however, all variables affected migration routing to some extent. Among single-variable models, cross-stream location of fish (X) had the lowest BIC, followed by BAFF operation (B), streakline (S), discharge (Q) and time of day (D; Table I). The second-ranked univariate model had a within-group $\Delta\text{BIC} > 300$, indicating that the location of fish in the cross-section was the primary factor driving migration routing. Among two-variable models, the lowest BIC model included both X and B, supporting the hypothesis that the BAFF affected migration routing (Table I). For the more complex models, the BIC rankings followed the ranking of simpler models. For example, among three-variable models, X appeared in the top six models and B appeared in the top three models. Among all main-effects models, the lowest

Table I. Model selection results for logistic regression expressing the probability of fish entering Georgiana Slough as a function of covariates

Model	Group	No. variables	NLL	BIC	Group ΔBIC	Overall ΔBIC
$D+B+S+Q+X+Q\times X+B\times Q$	1	7	321.8	701.7	5.2	5.2
$D+B+S+Q+X+Q\times X$		6	322.9	696.5	0.0	0.0
$D+B+S+Q+X+Q\times B$			337.7	726.2	29.7	29.7
$D+B+S+Q+X+D\times B$			340.4	731.5	35.0	35.0
$D+B+S+Q+X+B\times X$			342.1	734.9	38.4	38.4
$D+B+S+Q+X$	2	5	342.1	727.8	2.3	31.2
$B+S+Q+X$		4	344.6	725.5	0.0	28.9
$D+B+Q+X$			348.2	732.8	7.3	36.2
$D+B+S+X$			352.7	741.8	16.3	45.2
$D+S+Q+X$			372.8	781.8	56.3	85.3
$D+B+S+Q$			552.4	1141.0	415.5	444.5
$B+Q+X$	3	3	353.8	736.6	0.0	40.1
$B+S+X$			354.7	738.5	1.9	42.0
$D+B+X$			363.0	755.1	18.5	58.6
$S+Q+X$			375.4	779.9	43.2	83.3
$D+Q+X$			380.5	790.0	53.4	93.5
$D+S+X$			385.3	799.5	62.9	103.0
$B+S+Q$			552.4	1133.8	397.2	437.3
$D+B+S$			556.3	1141.6	405.0	445.1
$D+B+Q$			560.2	1149.5	412.8	452.9
$D+S+Q$			582.7	1194.4	457.8	497.9
$B+X$	4	2	368.8	759.3	0.0	62.7
$Q+X$			386.7	795.2	35.9	98.7
$S+X$			387.3	796.3	37.1	99.8
$D+X$			397.9	817.5	58.2	120.9
$B+S$			556.3	1134.4	375.2	437.9
$B+Q$			561.0	1143.8	384.5	447.3
$D+B$			567.6	1157.0	397.8	460.5
$S+Q$			582.7	1187.2	428.0	490.7
$D+S$			588.1	1198.1	438.8	501.5
$D+Q$			592.1	1206.0	446.7	509.5
X	5	1	403.9	822.3	0.0	125.8
B			568.7	1151.9	329.6	455.4
S			588.1	1190.8	368.5	494.3
Q			592.9	1200.3	378.0	503.7
D			601.7	1217.9	395.6	521.4
Intercept only		0	602.7	1212.7	390.4	516.2

NLL, negative log-likelihood; BIC, Bayesian information criterion; ΔBIC, the difference in BIC of each model relative to the lowest BIC model (either within groups of models or over all models).

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BIC model included X, B, Q and S, followed closely by the model with all five variables (ΔBIC = 2.3; Table I). Although time of day (D) was excluded from the most parsimonious main effects model, we chose to retain D in the model to evaluate interaction terms involving D.

Among models with interaction terms, a $Q \times X$ interaction was strongly supported, having a BIC that was 31.2 units lower than the five-variable main effects model, whereas adding a $B \times Q$ interaction slightly reduced BIC relative to the main effects model (ΔBIC = 1.6). Neither a $B \times D$ interaction nor a $B \times X$ interaction was supported, as evidenced by BIC for these models being larger than the BIC for the five-variable main effects model (Table I). Given these findings, we also assessed a model that included both $Q \times X$ and $B \times Q$, but the BIC of this model was 5.2 units greater than the model with only the $Q \times X$ interaction. On the basis of these findings, the model with all five covariates and a $Q \times X$ interaction, which had the lowest BIC over all models, was selected for inference (Table I).

Goodness-of-fit diagnostics showed no evidence of lack-of-fit and indicated that the model predicted the fates of individuals well. The Hosmer–Lemeshow goodness-of-fit test was not significant ($\hat{C}$ = 13.0, $df = 17$, $p = 0.734$) and the area under the AUC was 0.928, indicating that the model had excellent ability to predict the fates of individuals. For example, a cutoff of $\pi_G > 0.2$ correctly predicted 82% of the fish that entered Georgiana Slough (true positive rate) and incorrectly assigned only 11% of fish with a Sacramento River fate to Georgiana Slough (false positive rate).

Effects of covariates on entrainment probability

Parameter estimates indicate the effect of the covariates on the probability of fish entering Georgiana Slough. The negative coefficient for D, where $D = 1$ is day, showed that $\pi_{G,i}$ was lower during the day (Table II). However, differences in entrainment probability between day and night were relatively small compared with the effect of other covariates (Figure 3A). The negative coefficient for B, where $B = 1$ is BAFF on, indicated that operation of the BAFF reduced the probability of fish entering Georgiana Slough (Table II). The slope estimate for streakline (S) was positive, indicating that as the streakline moved in a positive direction (i.e. toward the Sacramento side of the river channel), the probability of fish entering Georgiana Slough increased (Table II; Figure 3B).

Table II. Parameter estimates for the best-fit model

Variable	Parameter estimate	SE	95% Confidence interval
Intercept (night, off)	−2.104	0.361	−2.812, −1.397
D	−0.531	0.215	−0.951, −0.110
B	−1.700	0.232	−2.150, −1.242
S	0.082	0.024	0.035, 0.129
Q	0.240	0.044	0.153, 0.327
X	0.045	0.028	−0.010, 0.101
$Q \times X$	−0.020	0.004	−0.028, −0.013

Variables defined as follows: D, time of day (day, 1; night, 0), B, BAFF operation (on, 1; off, 0); S, critical streakline; Q, discharge; and X, cross-stream position of fish. The reference group for the intercept is D (night) and B (off).

Due to the interaction between Q and X, the effect of cross-stream position on $\pi_{G,i}$ depended on discharge. The slope for cross-stream position is negative at all values of discharge, indicating that $\pi_{G,i}$ decreased, moving from the Georgiana Slough side of the river channel to the Sacramento River side of the channel (Figure 3C). However, the magnitude of the slope for X increases (i.e. becomes more negative) with flow, indicating that higher flows increased the gradient of $\pi_{G,i}$ across the river channel. For example, at high flows, $\pi_{G,i}$ transitioned sharply from near zero at $X = 20$ m to near one at $X = -20$ m, whereas this transition was more gradual at lower flows (Figure 3C). Likewise, the slope for Q decreases as X increases, but switches from positive to negative at about $X = 10$ m (Figure 3D). Therefore, $\pi_{G,i}$ increased with flow for fish located on the Georgiana Slough side of the channel, but decreased with flow for fish located toward the Sacramento River side of the channel (Figure 3D).

Entrainment probabilities during low-flow and high-flow periods

Because covariates other than discharge differed between high- and low-flow periods (Table III), examining the predicted entrainment probability for different strata takes into account the simultaneous effect of covariates. First, regardless of the effect of any covariate, fish on the Sacramento River side of the channel had a low probability of entering Georgiana Slough (Figure 4A). For example, the probability of entrainment into Georgiana Slough was less than 0.20 for $X > 10$ m for all groups (Figure 4A). Given the cross-stream distribution of fish approaching the river junction (Figure 4C), more than 60% of the fish were located at $X > 10$ m, indicating that the majority of fish were unlikely to enter Georgiana Slough. These findings also suggest that the BAFF had little influence on fish located at $X > 10$ m. For example, for $X > 10$ m, the difference in predicted entrainment probability between BAFF on and BAFF off was less than 0.10 (Figure 4B).

In contrast, for fish distributed toward the Georgiana Slough side of the river channel ($X < 10$ m), $\pi_{G,i}$ increased rapidly approaching Georgiana Slough and depended on discharge and BAFF operation. As cross-stream position decreased (i.e. moving toward Georgiana Slough), entrainment for the high-flow period increased more rapidly than for low flow, approaching unity at $X < -15$ m (Figure 4A).

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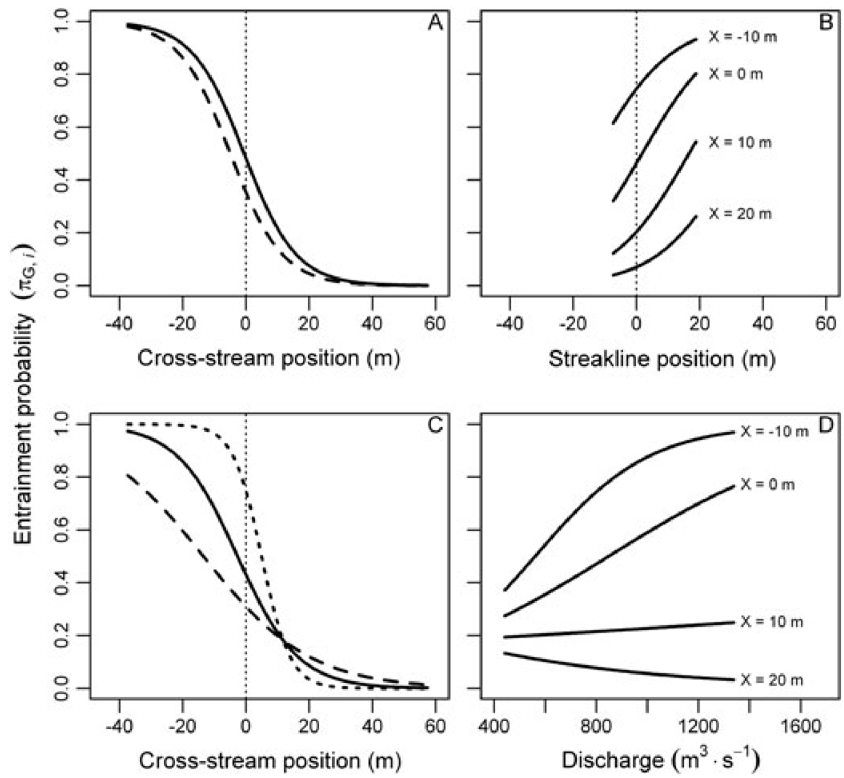

Figure 3. Effect of each covariate on probability of entrainment into Georgiana Slough at fixed values of other covariates with the BAFF off. Effect of day (dashed line) and night (solid line) plotted over the range of observed cross-stream positions (A). Effect of streakline position (*X*) at different cross-stream locations (B). Effect of cross-stream position (*X*) at the 5th (dashed line), 50th (solid line) and 95th (dotted line) percentiles of discharge (510, 730 and 1300 $m^3 \cdot s^{-1}$, respectively; C). Effect of discharge (*X*) at different cross-stream locations (D). Entrainment probabilities are plotted for night (B, C, and D only), at the mean discharge of 818 $m^3 \cdot s^{-1}$ (A and B only), and at the mean streakline position of 0.88 m (A, C, and D only)

These findings reveal that BAFF operation had little effect on entrainment probability at $X < -15$ m during high flows. However, during low-flow periods, $\pi_{G,i}$ for BAFF on remained considerably lower than for BAFF off over the range of $X < 10$ m (Figure 4A).

Our findings indicate that the spatial zone of influence of the BAFF varied with discharge at the river junction. Under both high and low flows, operation of the BAFF reduced the probability of fish being entrained into the Georgiana Slough by up to 40 percentage points (Figure 4B). However,

Table III. Summary of covariates used in logistic regression

Discharge level	Time of day	BAFF operation	Discharge (Q, $m^3 \cdot s^{-1} \cdot 100$)	Streakline (S, m)	Cross-stream position (X, m)	N	No. entering Georgiana Slough	Fraction entering Georgiana Slough	$\bar{\hat{\pi}}_G$
High	Day	On	12.6 (0.33)	3.0 (1.6)	19.9 (19.9)	71	15	0.211 (0.048)	0.149 (0.034)
		Off	12.2 (1.1)	3.6 (1.7)	13.5 (22.4)	105	31	0.295 (0.045)	0.322 (0.039)
	Night	On	12.6 (0.31)	3.6 (1.5)	22.9 (20.7)	71	9	0.127 (0.040)	0.150 (0.037)
		Off	12.3 (0.75)	3.9 (1.3)	21.4 (20.4)	119	29	0.244 (0.039)	0.262 (0.034)
Low	Day	On	6.88 (0.88)	−1.3 (3.8)	14.3 (16.4)	301	5	0.017 (0.007)	0.047 (0.005)
		Off	6.76 (0.91)	−1.0 (4.1)	12.9 (16.7)	290	56	0.193 (0.023)	0.167 (0.012)
	Night	On	6.62 (0.97)	1.2 (4.8)	17.8 (17.0)	243	21	0.086 (0.018)	0.060 (0.006)
		Off	6.45 (0.99)	1.5 (4.6)	14.2 (17.2)	214	49	0.229 (0.029)	0.241 (0.016)

The observed fraction of fish entering Georgiana Slough, and the mean predicted probability of entering Georgiana Slough ($\bar{\hat{\pi}}_G$) stratified into categories of high and low discharge level (before and after 5 April 2011, respectively), time of day and BAFF operation. Values represent the mean (SD) for Q, S and X, the mean (SE) for $\bar{\hat{\pi}}_G$ and the fraction entering Georgiana Slough. N is the total number of fish observed in each strata. For $\bar{\hat{\pi}}_G$, the standard error is based on variance in $\hat{\pi}_G$ among individual fish, whereas standard error is based on the binomial distribution for the observed fraction of fish entering the Georgiana Slough.

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during the low-flow period, the BAFF reduced the probability of entrainment by more than 10 percentage points for a 55-m section of the cross-channel (from about $X = -40$ m to $X = 15$ m; Figure 4B). In comparison, under high flows, this same reduction in $\pi_{G,i}$ occurred for a 30-m section of channel (from about $X = -15$ m to $X = 15$ m; Figure 4B).

Estimating entrainment into Georgiana Slough

The observed fraction of fish entering Georgiana Slough varied considerably among strata from 0.016 to 0.295 (Table III). Our analysis helps to explain the factors driving this variation. The mean estimated entrainment probability over individuals estimates the fraction of fish entering Georgiana Slough by integrating individual entrainment probabilities over the conditions experienced by each fish. We found that the mean probability of entrainment into Georgiana Slough closely matched the observed fraction of fish entering Georgiana Slough, indicating that our model captured the influence of covariates on entrainment at the population level (Figure 5; Table III). With the BAFF on, observed entrainment for the high-flow period was 8.4 and 11.7 percentage points lower than with the BAFF off (for day and night, respectively), whereas during the low-flow period, entrainment was 17.6 and 14.3 percentage points lower (Table III). These results are consistent with our finding that high flows increased

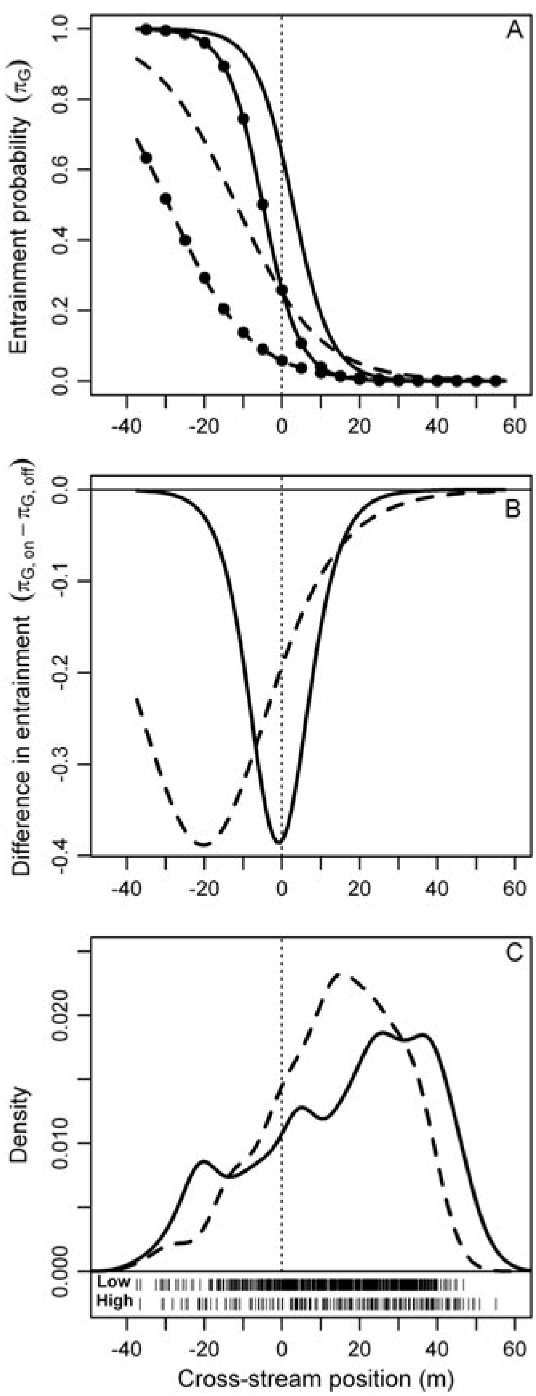

Figure 4. Effect of cross-stream position on estimated probability of entrainment into Georgiana Slough for high-flow and low-flow periods (solid and dashed lines, respectively) for BAFF on (lines with circles) and BAFF off (lines without symbols; A); the difference in estimated entrainment between BAFF on and BAFF off (B); and the cross-sectional distribution of fish (C). In (A), curves were plotted based mean values of discharge and streakline given in Table III. In (C), the distribution was based on a kernel density estimator, and the rug plot (i.e. the tick marks) shows observed cross-stream positions of fish for high-flow and low-flow periods. Only daytime data are shown because the results for nighttime data were similar.

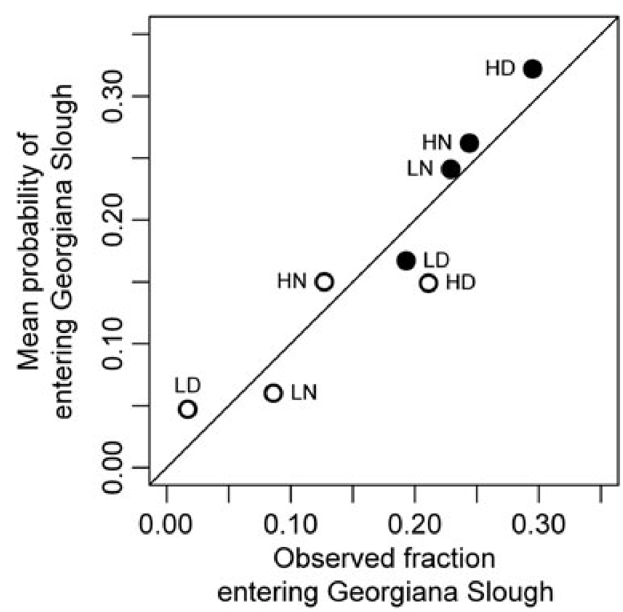

Figure 5. Mean estimated probabilities from the best-fit logistic regression model compared with the observed fraction of fish entering the Georgiana Slough. Symbols represent data stratified by BAFF on (open circles) and BAFF off (filled circles) for day and night during high and low flow periods (see Table III). The reference line shows where mean probabilities equal observed fractions. Data labels indicate high-flow (H) or low-flow (L) and day (D) or night (N) groups

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entrainment probabilities on the Georgiana Slough side of the river channel and reduced the spatial zone of influence of the BAFF.

Covariates other than river flow and BAFF operation also varied among strata and influenced entrainment probabilities. For example, during high-flow periods, both the mean streakline and mean of the cross-stream fish distribution was shifted toward the Sacramento River, relative to the low-flow period (Table III). However, the cross-stream distribution for the group with the highest entrainment (high flow, day, BAFF off) was shifted more toward the Georgiana Slough side of the channel (Table III). For this group, 33% of the fish were located to the Georgiana Slough side of the streakline compared with 17% to 23% for the other high-flow groups. Consequently, the interaction between the location of the streakline and the cross-stream distribution of the fish, combined with the effect of BAFF off and high flow, acted to increase individual entrainment probabilities resulting in a high fraction of fish being entrained into Georgiana Slough. In contrast, the lowest observed and predicted entrainment occurred during the day for the low-flow period with the BAFF on (Table III). For this group, only 18% of fish were located to the Georgiana Slough side of the streakline, compared with 18% to 26% of the other low-flow groups. These factors, combined with the effect of low flow and operation of the BAFF, led to a low fraction being entrained into Georgiana Slough. Our analysis illustrates how multiple factors interacted to influence the fraction of fish entrained into Georgiana Slough.

DISCUSSION

Using a non-physical behavioural barrier as a management tool requires understanding its effectiveness under a range of environmental and operational conditions. Our analysis showed that operation of the BAFF reduced entrainment into a low-survival migration route, but more importantly, we were able to quantify how factors such as discharge and the cross-stream distribution of fish influenced the performance of this non-physical barrier. Such insights are critical to inform future design and performance of non-physical barriers. Our analysis was made possible by obtaining two-dimensional tracks of fish moving through the study area, which allowed us to include the location of the fish in the channel cross-section as a covariate in the model. Ultimately, the location of fish approaching the BAFF proved to be the most important factor affecting migration routing.

It should come as no surprise that fish location in the cross-section was the most important determinant of an individual's probability of entrainment into Georgiana Slough. We showed that fish closest to either shore enter the channel along that shore with near certainty. Furthermore, our analysis revealed *where* in the cross-section fish became vulnerable to entrainment into Georgiana Slough and *where* the BAFF reduced, or failed to reduce, an individual's probability of entrainment. For instance, we identified that the BAFF failed to substantially reduce entrainment probabilities of fish closest to the Georgiana Slough shoreline during the high-flow period (i.e. fish located between $X = -37.5$ m and $X = -15$ m). Cross-stream position was also critical for understanding how the cross-sectional distribution of fish drives overall entrainment by dictating the fraction of the population likely to come into contact with the BAFF or likely to enter Georgiana Slough. Such insights are critical for understanding how a non-physical barrier such as the BAFF affects individual entrainment probabilities and subsequently, overall entrainment.

We have shown that the BAFF was effective at reducing entrainment into Georgiana Slough during both high and low flow conditions. However, the BAFF was less effective at higher flows for fish located close to the Georgiana Slough side of the river channel. The mechanism behind this finding is likely the inability of a fish to alter its course away from the BAFF before being swept across the barrier into Georgiana Slough. Given typical burst swimming speeds of smolts (~1.5 $m \cdot s^{-1}$ or 10 body lengths$\cdot s^{-1}$) relative to water velocities approaching the BAFF, swimming speeds required to avoid the BAFF may have been physically unattainable at high flows. Therefore, even if fish were deterred by the BAFF, they may not have been able to avoid entrainment into Georgiana Slough.

Discharge entering this river junction is often lower than that observed during our study, and hydraulic conditions differ considerably at lower flows. At discharge less than approximately 280 $m^3 \cdot s^{-1}$ entering the junction, tidal forcing causes the river to reverse direction on flood tides. Under these conditions, up to 50% of fish passing this river junction can be entrained into Georgiana Slough (Perry, 2010), substantially higher than observed during our study. Entrainment is higher under these conditions because fish may pass by the Georgiana Slough safely when the river is flowing downstream, only to be advected back upstream on the flood tide and ultimately entrained into Georgiana Slough. It is difficult to infer the performance of the BAFF under these conditions from our study, but our findings provide some insight into the expected change in individual entrainment probabilities. Because velocities approaching the BAFF decline with discharge, we might expect the BAFF to further reduce individual entrainment probabilities of fish at a particular cross-stream location when discharge is lower than observed in our study. However, on the transition from ebb to flood tide, water is funnelled into Georgiana Slough simultaneously from both the upstream and downstream directions. Under these conditions, all fish passing the junction will have a high probability of entering

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Georgiana Slough. What remains to be seen under these conditions is how the cross-stream distribution of fish changes with flow, how multiple encounters with the BAFF affect an individual's total probability of entrainment and how these processes integrate across tidal cycles to drive the fraction of the population entrained into Georgiana Slough.

The critical streakline clearly influenced entrainment probability, indicating that this is a useful measure for aiding in the design and location of non-physical barriers in settings similar to our study. The critical streakline essentially represents the fraction of flow entering Georgiana Slough [see Equation (2)], but on a scale that is relevant to the location of the fish in the river channel. As the location of the streakline became more positive and moved toward the Sacramento side of the junction, entrainment into Georgiana Slough increased. This process illustrates why fish location relative to the streakline is an important determinant of an individual's fate. Fish located near the streakline will have a greater ability to alter their fates in response to a non-physical barrier, whereas fish located at greater distances from the streakline will have less ability to alter their trajectories across the streakline into the opposing parcel of water, thus rendering a non-physical barrier less effective. These findings suggest that placing a non-physical barrier close to the critical streakline will result in the highest likelihood of altering a fish's migration pathway.

Although time of day (day versus night) was included in the model, it did not explain much variation in the data. Furthermore, the interaction between BAFF operation and time of day was not supported by model selection criteria, suggesting that the BAFF performed equally well during day and night periods. In contrast, Welton *et al.* (2002) found that the BAFF was much more effective at deterring juvenile Atlantic salmon (*S. salar*) at night as opposed to during the day. They attributed the difference in performance to the ability of fish to navigate through the bubble curtain using visual cues during the day, which were unavailable at night. During our study period, turbidity averaged 19.48 Nephelometric Turbidity Units (NTUs). Such high turbidity likely limited the use of visual cues to navigate the bubble curtain during the daytime, possibly leading to similar performance between day and night.

Our findings show how an integrated, multi-sensory, non-physical barrier was able to reduce entrainment into a low-survival migration route. Coutant (2001b) makes a strong argument that behavioural guidance devices are likely to be most effective when different technologies are used in concert and tailored to a specific application. Along these lines, we hypothesize that entrainment into Georgiana Slough could be further reduced by altering the cross-stream distribution of fish just upstream of the river junction before fish arrive at the BAFF. Given that entrainment probability dropped rapidly to zero at $X > 10\,\mathrm{m}$ (Figure 4A), our findings suggest that a small shift in the spatial distribution of fish could have a large effect on the fraction of fish entering Georgiana Slough. Relatively simple guidance structures, such as a shallow-draft floating boom, could be used to shift the cross-stream distribution of fish toward the Sacramento River side of the channel. For example, a floating log boom at Lower Granite Dam on Snake River was successful at guiding migrating juvenile salmon toward a surface passage structure (Wilson *et al*., 1991; Cash *et al*., 2002).

CONCLUSIONS

Our findings support Coutant's assessment, showing that use of multiple behavioural stimuli could alter the movement paths and fates of migrating juvenile salmon (Coutant, 2001b). However, variation in environmental conditions and complex physical settings pose both challenges and opportunities for devising a behavioural guidance system capable of directing fish away from potentially dangerous locations. Our study shows how careful monitoring in a field setting can aid in quantifying factors affecting performance of non-physical barriers and provide critical information for their design and implementation. Only with such insights can managers make informed decisions about whether non-physical barriers can be used as an effective tool in the management of water and fisheries resources.

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