

Migration route selection of juvenile Chinook salmon at the Delta Cross Channel, and the role of water velocity and individual movement patterns

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Abstract We examined movement tracks of ultrasonic-tagged juvenile Chinook salmon (*Oncorhynchus tshawytscha*) smolts at the juncture of two migratory pathways. This migratory juncture occurs where the Delta Cross Channel splits from the Sacramento River in California's Sacramento–San Joaquin Delta. Smolt tracks were analyzed to compare the importance of river flow and individual parameters in migratory route selection. The two routes differ significantly in smolt survival probabilities (Perry et al. *N Am J Fish Manag* 30:142–156, 2010), thus a clearer understanding of the variables contributing to route selection will be valuable for management of this declining species. A comparison of the two migratory groups showed that fish remaining within the Sacramento River: 1) Encountered the migratory juncture when river water velocities were much higher than those in the Delta Cross Channel ($p < 0.0001$), 2) showed more direct swimming paths ($p = 0.03$) and 3) migrated at higher speeds ($p = 0.04$). Logistic regression models showed that the ratio of

mean water velocity between the two routes was a much stronger predictor of ultimate route selection than any other variable tested. However, parameters for both the lateral position of smolts within the river and smolt size added predictive power to the final model. Our results suggest that river flow remains the most important variable for predicting smolt migration route, but note that knowledge of individual smolt attributes and movement patterns can increase our predictive ability.

Keywords Ultrasonic telemetry · Positioning system · Sacramento–San Joaquin Delta · Water velocity

Introduction

The Central Valley of California has historically supported several runs of salmonids, all of which are now listed as either endangered, threatened, or of special concern under the Federal Endangered Species Act (Nehlsen et al. 1991; NOAA 2004, 2005). The decline of these salmonid populations is likely due to multiple environmental changes, including the alteration of natural flow-regimes (Nichols et al. 1986; Moyle 1994; Zeug et al. 2011). More than half of the estimated historic outflow from the Sacramento–San Joaquin Delta (hereafter referred to as the Delta) is now diverted for urban and agricultural uses before reaching the ocean (Nichols et al. 1986). This has dramatically altered the magnitude and timing of flows

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(Brown and Bauer 2010), and can periodically reverse the direction of flow through some channels (Fig. 1; Brandes and McLain 2001).

Juvenile salmon are well adapted to use hydrodynamic patterns for navigation and outmigration (Montgomery et al. 2000). These hydrodynamic cues are likely to be especially important in a system such as the Delta characterized by an intricate network of channels and multiple possible migration routes, each associated with different survival probabilities (Brandes and McLain 2001; Newman and Brandes 2010; Perry et al. 2010). Therefore, the alteration of natural flow patterns may have important consequences for smolts in the Central Valley. This is supported by the work of Perry et al. (2010), which examined the distribution of juvenile Chinook salmon across multiple

migration pathways. Perry et al. (2010) showed a relationship between the probability of migration and the fraction of discharge in a migratory route. However, the authors noted that the form of this relationship may be influenced by variation in flow distribution at finer time scales, and by the spatial distribution of smolts within a river. The probability of an individual smolt entering a given migratory route may be a function of both instantaneous hydrology and the movement patterns of individual fish.

We recorded the positions of acoustically tagged smolts at the juncture of the Sacramento River and Delta Cross Channel (DCC) to examine the importance of individual smolt characteristics and movement patterns in migration route selection of Chinook smolt. We hypothesized that higher water velocities in the DCC would increase the likelihood of smolts migrating within this route, and that smaller smolts would be more susceptible to these higher water velocities. We also expected that movement patterns of individual smolts would further modify the probability of migration through the DCC. The movement metrics we considered included local migration speeds, the directionality of the detection track, and the smolts' lateral river position upon first arriving at the juncture. The primary objective of this study was to gain a clearer understanding of the factors associated with migratory route selection by juvenile salmonids.

Materials and methods

Study area and telemetry array

The Sacramento–San Joaquin Delta in California's Central Valley is a critical hub for the water supply system of California. Nearly 50 % of the state's surface runoff passes through the Delta (Nichols et al. 1986), which provides approximately 25 million Californians with water for municipal use and irrigates agricultural lands supporting a multi-billion dollar agricultural industry (Brown and Bauer 2010). The Delta itself is a brackish and freshwater system with an intricate network of pre-existing waterways and engineered connections, such as the Delta Cross Channel (Nichols et al. 1986; Brown and Bauer 2010). The present study was conducted at the juncture of the Delta Cross Channel (DCC) and the Sacramento River (Fig. 1), from

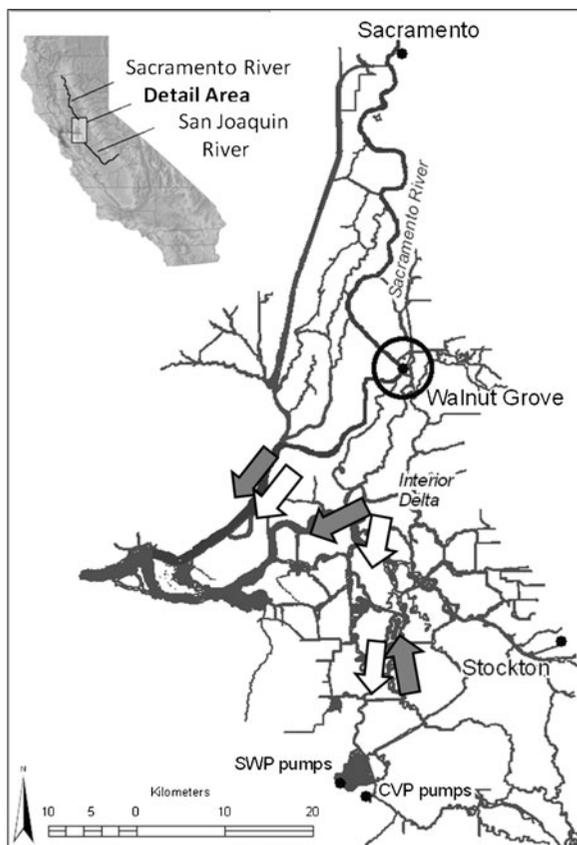


Fig. 1 Map of the study site (circled) within the Sacramento–San Joaquin Delta in California, USA. Arrows show altered flow patterns due to water exports. Dark arrows indicate historic flow direction; light arrows indicate current cross-delta flows that occur when large volumes of water are pumped into the Central Valley Project (CVP) and State Water Project (SWP) aqueducts

1 Dec 2008 to 22 Dec 2008 during a Critical Water Year in the Sacramento Valley, as defined by the California State Water Resources Control Board, Decision 1641.

The DCC is located along the Sacramento River at river km 60 in the northern Delta. It was designed to selectively divert water, using a pair of control gates, from the Sacramento River into the interior Delta where gravity can more quickly carry the water to pumping plants in the south. The mean annual maximum flow in the DCC between 2005 and 2010 was roughly one tenth that of the Sacramento River at this junction. The timing of tidal influence differs between the DCC and Sacramento River, with peak flows occurring in the DCC approximately 3.5 h after those in the Sacramento River (Fig. 2; US Geological Survey gauges 1133660 and 11447890).

Advances in ultrasonic technologies have led to the development of transmitters small enough to be implanted in outmigrating juvenile salmonids (Lacroix et al. 2004; Perry et al. 2010; other articles in this issue). In addition to allowing researchers to record large-scale migratory movements, these new technologies can be used to record localized fine-scale positions. To record the movement patterns of juvenile Chinook salmon, we deployed an automated, two-dimensional tracking system (VPS; VEMCO Ltd, Halifax). The ultrasonic array consisted of four monitors (VR2W, VEMCO) that detected the ultrasonic pulses from tagged fish within the array. Detections were then post-processed to calculate two-dimensional positions by means of triangulation equations (VEMCO 2008).

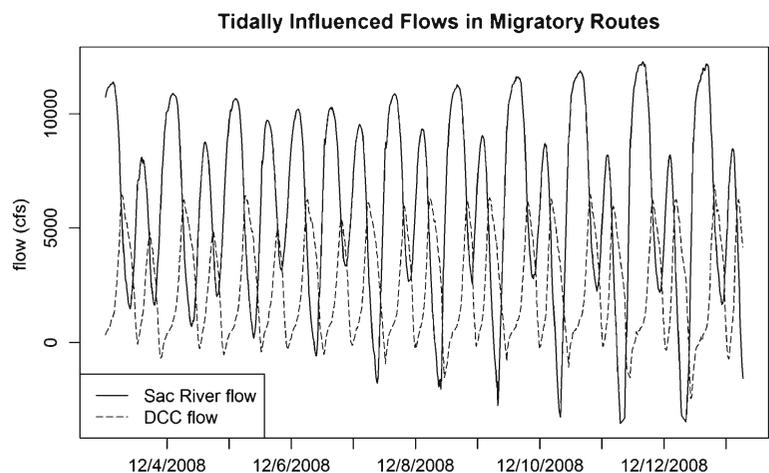
The array monitors were located at the entrance to the channel, encompassing an area of approximately 1.3 km², extending slightly upstream and downstream

of the DCC. Monitors were placed in an approximate rectangle with no monitors greater than 120 m apart (Fig. 3). Prior range tests suggested this to be an appropriate spacing to ensure high probabilities of detection. The deployment strategy was meant to utilize optimal array geometry while keeping gear out of the boat traffic lanes, as surface floats were used to retrieve and mark the final positions of all four monitors. A single reference tag was located on the right bank of the river, across from the Delta Cross Channel and between the upstream and downstream monitors. The tag was a V9-2L-R64K which had an output power 3 dB stronger than that of the V7 tags implanted in Chinook salmon smolts. Monitors consistently heard this reference tag throughout the course of the study, verifying the functionality of the array.

Tagged fish

The juvenile late-fall run Chinook salmon considered in this study ($n=28$) were among a larger cohort of smolts tagged and released for an assessment of out-migration survival rates ($n=292$; Perry 2010). The juvenile salmon were raised at Colman National Fish Hatchery (Red Bluff, CA) and tagged by biologists of the University of California, Davis and the National Marine Fisheries Service. Coded beacons (V7-2L-R64K, Vemco Ltd.) were programmed to emit a unique series of pulses at a mean interval of 40 s. These tags were surgically implanted into the peritoneal cavity of the fish, following the procedure outlined by Adams et al. (1998). A tag size was chosen that would constitute between 2 % and 5 % of the body weight of the juvenile salmon to avoid potential

Fig. 2 Illustration of tidal influence in the Sacramento River and the Delta Cross Channel (DCC) at monitoring stations 1.3 km and 0.5 km, respectively, from the study site



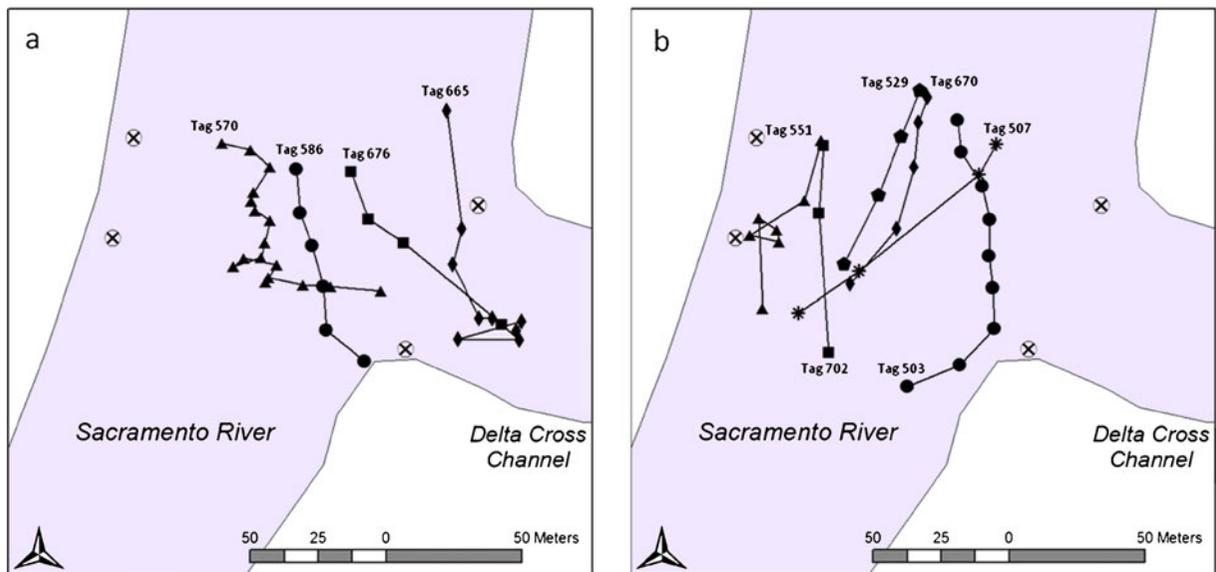


Fig. 3 Map of the ultrasonic positioning system—monitors represented with circled Xs. Selected tracks of individual juvenile salmon shown for illustration: **a** smolts that migrated through the DCC, **b** smolts that migrated through the Sacramento River.

tag effects such as reduced swimming performance, increased vulnerability to predation, and reduced growth. Previous studies showed no tag effects for tag-to-bodyweight ratios of less than 5 % (Moore et al. 1990; Adams et al. 1998; Brown et al. 1999; Anglea et al. 2004; Lacroix et al. 2004). The fish used in our analysis were a subset of these tagged smolts, with a mean weight of 43.8 g (SD = 9.1) and mean fork length of 154.9 mm (SD = 9.6).

After implantation, fish were released at two locations along the Sacramento River, with 100 fish released downstream of our detection array and the remaining 192 released upstream. All fish included in the current analysis were released from the upstream location, approximately 30 km from the study area, near the city of Sacramento, California. All upstream releases occurred between 30 Nov 2008 and 4 Dec 2008. Smolts were selected for analysis if they encountered the study site when the DCC control gates were open, and were positioned at least three times within the array. We required a minimum of three positions for each study fish in order to calculate a metric for the directionality of the track.

Tag detections were recorded by both the two-dimensional positioning array at the DCC and by a system-wide array in place throughout the Sacramento

River and Delta. Using this larger detection network, we removed from the analysis any tags that appeared to be within predators rather than the original smolts. Tags were considered likely to be in predators if they showed non-migratory tracks, which we defined as multiple detections in one area over a long duration, or repeated movements between a set of locations with no ultimate progress out of the system. While continuous tracking of juvenile salmonids (steelhead trout) has shown that they will reverse their direction of movement based upon flow (Sandstrom et al. unpublished data), these fish also display a net movement towards the ocean which was not seen for any of the fish we classified as predators.

Statistical analysis

For each track analyzed we calculated the ratio between the mean water velocity in the Sacramento River channel and the mean water velocity in the DCC at the time when the smolt first arrived at the juncture. Mean channel velocity measurements, averaged over 15 min intervals were obtained from US Geological Survey gauges 11336600 and 11447890. The former gauge is located in the DCC, while the later is approximately 1 km upstream of the juncture in the mainstem of the Sacramento River. We chose to use

velocity rather than discharge because the former is more comparable between migratory routes of different channel areas, based on the continuity equation ($Q = vA$), it is more readily detected by a migrating fish (Nestler et al. 2008) and has been shown to be correlated with other aspects of outmigration (Michel et al. 2011). Because velocity varies spatially within a river channel, we note that a further assessment using a detailed hydrodynamic model might provide additional insight into the mechanisms of migratory route selection. The ratio between velocities in the two migratory routes was the most appropriate variable for modeling route selection because it eliminates collinearity between multiple related variables, yet still captures the contrast between velocities caused by tidal stage. Velocity measurements were transformed by adding a small constant (0.1 msec^{-1}) to each measurement to eliminate three instances of negative velocities in the DCC.

The following movement patterns were considered possible correlates of the ultimate migratory pathway: 1) Local migration speed, or the speed of movement relative to the ground, 2) river position upon encountering the juncture, and 3) directionality of movement. Local migration speeds will impact the period of time during which a smolt is present at the migratory juncture, and therefore may be an important predictor of the ultimate migratory pathway. This variable was calculated as the quotient of the total distance traveled (the sum of the distance between sequential points) divided by the time elapsed between the first and last recorded positions. The lateral river position of a smolt upon first encountering the juncture may impact the degree to which a smolt detects or can access the alternate migratory pathway. The position of a smolt within the river was quantified as the distance between the first recorded position for each fish and the bank on river left (east), where the DCC is located. Finally, we hypothesized that fish with highly directional tracks would be less likely to deviate into the side channel, whereas those fish which expressed less directionality and more exploratory behavior would be more likely to enter the DCC. To measure the directionality of a track we computed the changes in the bearing of the track at each recorded position, describing this shift as a turn angle. The mean of the absolute values of these turn angles allowed us to estimate the degree of directionality of the track. Additionally, we considered the impact of smolt size on migratory route selection through measurements of fork length and weight.

All statistical analyses were conducted with the software program 'R', version 2.2.1 (R Development Core Team 2010). We considered any p -value less than or equal to 0.05 to be significant. Initially we grouped smolts by migratory pathway to compare the mean or median measurements of each variable between migratory routes. We then built logistic regression models to further examine the relationship between independent variables and migratory pathway. For modeling purposes, passage through the DCC was considered an event, while migration within the Sacramento River was considered a non-event. We chose logistic regression because migration route was a dichotomous dependent variable, and the relationship between the log odds of the migration route and the majority of independent variables suggested that a linear approximation was appropriate. Because logistic regression also assumes little multicollinearity within the model, we were unable to include the metric for track directionality in the model selection process as it was significantly correlated with the ratio of water velocities (*Spearman's rho* = -0.394 , $p=0.039$) and local migration speed (*Spearman's rho* = -0.602 , $p=0.0008$). Furthermore, the correlation of length and weight was accounted for by defining a size index as the product of length and weight measurements. Due to problems of separation, we used Firth's logistic regression, which uses a penalized log likelihood approach to estimate parameter values and confidence intervals (Heinze and Schemper 2002). Models were evaluated by AICc values, corrected for small sample size. All possible models were evaluated to find the model(s) with the lowest overall AICc.

Results

Tracks analyzed

A total of 62 fish were positioned by the array during this study, with an additional 23 positioned after the final closure of the control gates on the DCC. Based on estimates of routing and survival from the release point to the DCC (Perry 2010), we expect that 99 of the original 192 fish passed the DCC. Therefore, the array recorded positions for approximately 86 % of passing smolts. These smolts which were positioned during the study period ($n=62$) passed the DCC over a 16 day period from 3 to 18 Dec 2008, with the middle 50 % passing

from 5 to 7 Dec 2008. From 13 to 22 Dec 2008 the DCC control gates were open during the day and closed in the evening and night. Fourteen of the fish detected passed during these closures, while 48 were positioned when the control gates were open. Of those detected when the gates were open, 10 smolts were removed from the analysis because they only had one or two recorded positions while 10 additional smolts were excluded because the patterns of the tracks suggested the tags were within predatory fish. After the removal of these tags, the final study group contained 28 individuals. Based upon downstream detections of all fish by monitors in the system-

wide array, we determined that 12 of the study fish migrated through the DCC while 16 remained within the Sacramento River. Aside from the final destination, there were no clear qualitative differences between tracks (Fig. 3).

Examination of variables

A comparison of the two migratory groups showed the median ratio of water velocities was significantly different between groups (Mann Whitney test: $p < 0.0001$; Fig. 4). Fish that migrated through

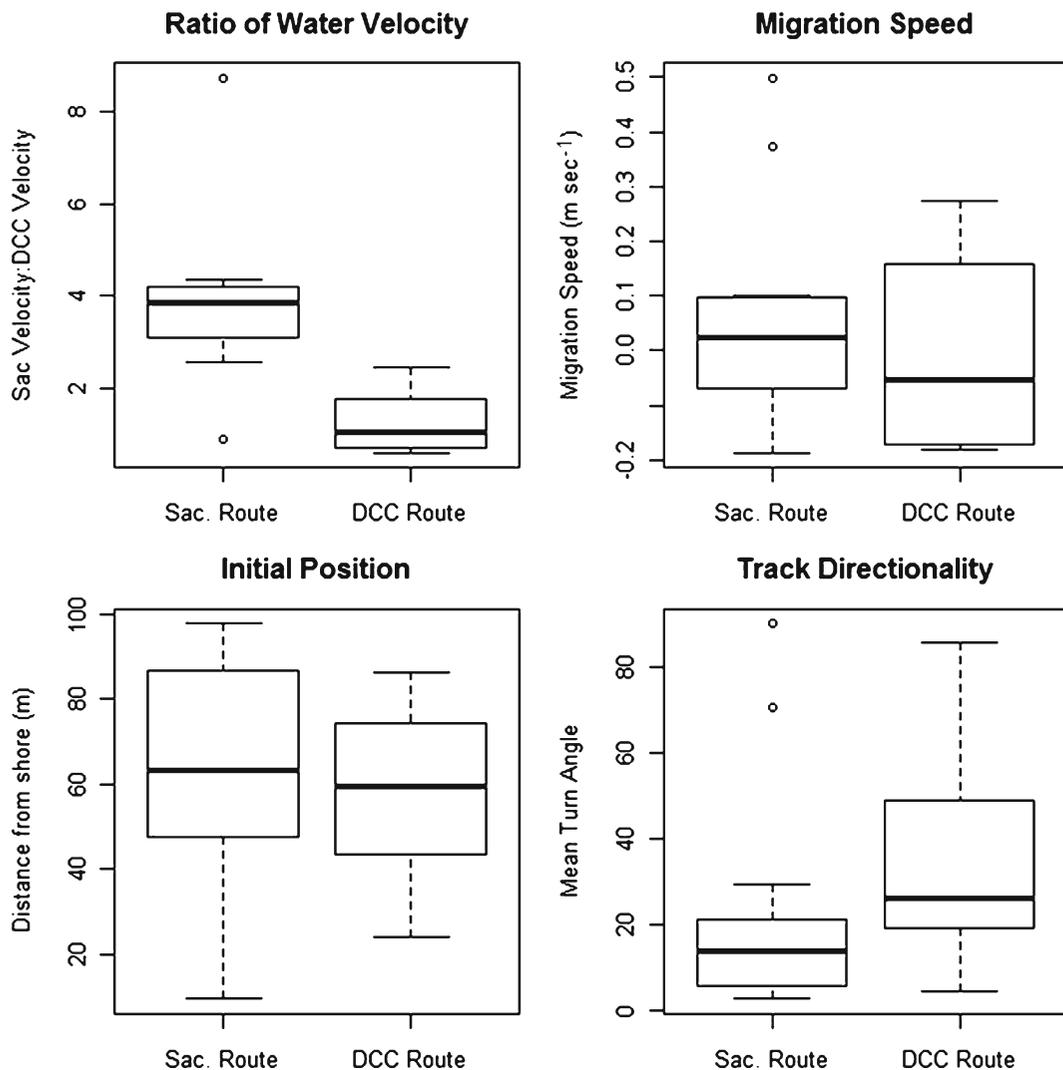


Fig. 4 Summary of the relationship between each variable analyzed and the final migratory route taken by smolts ($n_{sac} = 16$; $n_{dcc} = 12$). All variables except for initial position showed significant differences between groups (see text). Boxplots

include the median (line) and the Inter Quartile Range (IQR; lower and upper margins of box). Whiskers extend to the farthest points within 1.5*IQR of the margins of the box

the DCC encountered the juncture when the median of water velocities in the Sacramento River just upstream of the juncture was only slightly faster than that in the DCC (ratio = 1.26). Comparatively, fish that remained in the Sacramento River encountered the juncture when velocities in the river were much higher than in DCC (ratio = 3.81). While there was no statistically significant difference in the size of fish in the two migratory groups, the fish which passed through the DCC tended to be smaller with a mean weight of 40.7 g and a mean fork length of 151.2 mm when compared with fish that remained in the mainstem of the Sacramento River which showed a mean weight of 46.1 g and a mean fork length of 157.8 mm (Student's *t*-tests: weight $p=0.106$, length $p=0.055$; Fig. 5).

Two of the three movement variables examined showed statistically significant differences between the two migratory groups. Juvenile salmon that migrated through the DCC exhibited a mean migration speed of 0.29 msec⁻¹, significantly slower than the mean migration speed of 0.41 msec⁻¹ for smolts that remained within the Sacramento River (Student's *t*-test: $p=0.040$; Fig. 4). Smolts that migrated through the DCC had a median turn angle of 26.1°, significantly greater than the median turn angle of 14.0° for smolts that remained within the Sacramento River (Mann–Whitney test: $p=0.029$; Fig. 4). The two groups did not significantly differ in their mean lateral

positions when first entering the migratory juncture (Student's *t*-test: $p=0.489$; Fig. 4).

Logistic regression models

Of the five univariate logistic regression models considered, the model incorporating the ratio of water velocities had the lowest AICc value ($AICc = 14.50$). This model was also the only significant univariate model, based on log likelihood ratio tests ($p<0.0001$; Table 1). When movement parameters were incorporated into this model, it was improved by the addition of parameters for the initial position of smolts at the juncture ($p<0.0001$, $\Delta AICc = -9.02$; Table 1) and for the size index of smolts ($p<0.0001$, $\Delta AICc = -13.67$; Table 1). Further examination of all possible models showed that the model with the lowest AICc included all three of these parameters: The ratio of water velocities, initial position, and the index for smolt size ($p<0.0001$, $\Delta AICc = -22.26$; Table 2). However, the parameter estimate for the size index of smolts was small and not significant (Table 2).

Discussion

The data presented here show that the relationship between mean channel velocities in the two migratory routes is highly predictive of the ultimate route

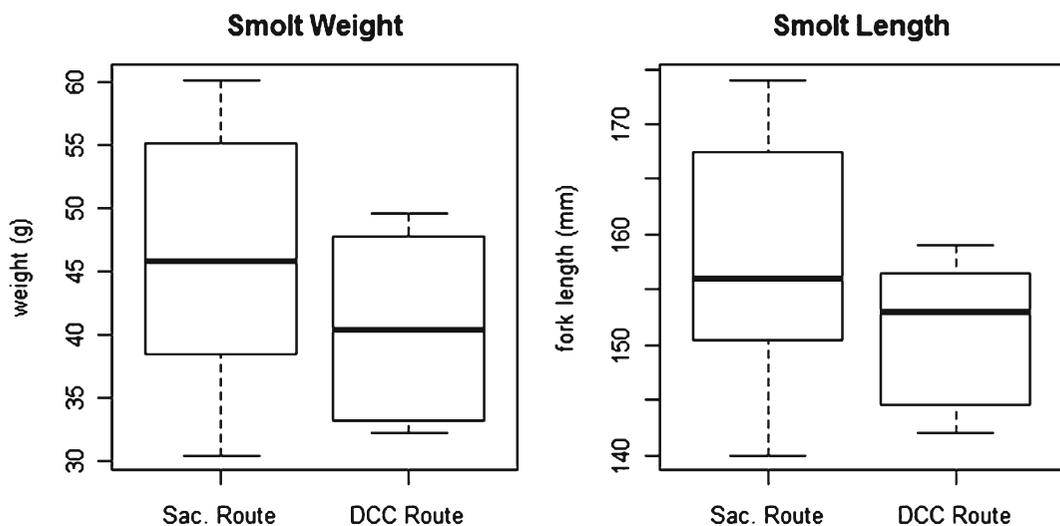


Fig. 5 Fork length (mm) and weight (g) of fish in each migratory group ($n_{Sac} = 16$, $n_{DCC} = 12$). There are no statistically significant differences between groups. Boxplots include the

median (*line*) and the Inter Quartile Range (IQR; *lower and upper margins* of box). Whiskers extend to the farthest points within 1.5*IQR of the margins of the box

Table 1 Logistic regression models considered in model selection process. Vel Ratio = the ratio of water velocities of the Sacramento River and the Delta Cross Channel; Size = index of smolt size; Dir = directionality of the track, not included in multivariate models due to problems of multicollinearity;

Pos = initial smolt position upon encountering the juncture; Mig Speed = local migration speed. Models were compared using AICc values. Also shown are number of parameters (k), natural log of the likelihood of the full model, and natural log of the likelihood ratio (LL Ratio) and associated *p*-value

Parameters	k	Model log likelihood	LL ratio	<i>p</i> -value	AICc	Δ AICc
Vel Ratio	1	-6.172	20.908	<0.0001	14.50	-
Size	1	-8.360	2.657	0.103	18.87	+4.38
Dir	1	-13.058	1.918	0.166	28.27	+13.77
Pos	1	-13.899	0.448	0.503	29.95	+15.45
Mig Speed	1	-17.153	3.699	0.054	36.46	+21.96
Vel Ratio + Size	2	1.825	20.117	<0.0001	0.83	-13.67
Vel Ratio + Pos	2	-0.497	24.190	<0.0001	5.47	-9.02
Vel Ratio + Mig Speed	2	-7.865	19.582	<0.0001	20.21	+5.71
Vel Ratio + Size + Pos	3	7.382	23.165	<0.0001	-7.76	-22.26
Vel Ratio + Size + Mig Speed	3	0.179	19.011	0.0003	6.64	-7.86
Vel Ratio + Pos + Mig Speed	3	-2.398	22.489	<0.0001	11.80	-2.70
Vel Ratio + Size + Pos + Mig Speed	4	5.493	21.612	0.0002	-1.25	-15.74

selection of juvenile Chinook salmon at the junction of the Sacramento River and Delta Cross Channel. This conclusion is supported by the highly significant difference in the ratio of water velocities between the two migratory groups (Fig. 4), as well as the highly significant univariate logistic regression model (Table 1). This is in agreement with previous studies which have demonstrated that migrating smolts follow the primary flow path in a river (Moser et al. 1991; Moore et al. 1995, 1998). While previous work in this system has shown a relationship between the probability of smolts entering the DCC and the fraction of total Sacramento River discharge that flows through the channel (Perry et al. 2010), the current study provides insight into individual smolt responses to flow patterns at an finer time scale.

This study also examined the relative importance of individual characteristics and movement patterns

associated with smolts' migratory route selection. We conclude that while these biologic factors are far less predictive than mean channel velocity, the consideration of a smolt's size and its initial position within the river strengthened our ability to predict migration route. Because of the significant correlation between the directionality of smolt tracks and the ratio of water velocities, we were unable to include track directionality in our models. However, it is worth recognizing that under conditions of higher water velocities in the Sacramento River, smolts displayed a more directional migration path. One possible mechanism to explain this observation is that under conditions of high water velocity, greater energy is required for smolts to navigate across or against the flow of the river, and therefore they move downstream in a more directional manner.

Interestingly, while smolt migration speed showed significant differences between groups, multivariate

Table 2 Estimates of parameter coefficients in final model. Vel Ratio = the ratio of water velocities of the Sacramento River and the Delta Cross Channel; Pos = initial smolt position upon

encountering the juncture; Size = index of smolt size. CI = 95 % confidence interval

Parameter	Estimate (SE)	Lower CI	Upper CI	χ ²	<i>p</i> -value
Intercept	15.955 (9.416)	2.645	106.808	8.282	0.004
Vel Ratio	-3.804 (2.041)	-22.772	-1.034	20.432	<0.0001
Pos	-0.124 (0.081)	-8.453	-0.001	3.983	0.046
Size	-0.0001(0.000)	-0.001	0.001	0.177	0.674

models were not improved when this variable was incorporated. This could be because migration speed does not contribute new explanatory power to the model due to the weak correlation between migration speed and Sacramento River velocity (*Spearman's rho* = 0.287, $p=0.139$). Alternatively, by excluding fish with fewer than three detections from the analysis we may have eliminated those smolts which moved most quickly through the array, thus reducing our ability to detect an effect due to migration speed.

The initial position of smolts encountering the migratory juncture is not a significant variable when compared between migratory groups or considered in the univariate logistic regression model. However, when we account for river velocities in a multivariate model, the data suggests that smolts which entered the juncture farther from the DCC were more likely to remain in the Sacramento River than those that entered nearer to the DCC. It is possible then that smolt position is only important under conditions of high proportional velocities in the DCC, when smolts are most at risk of entrainment.

Finally, while there was no statistically significant difference between the sizes of smolts in each of the two migratory groups, when this variable was considered in a multivariate model including river velocities it added additional predictive power to the model. However, the parameter estimate was very small, the confidence interval included zero, and the parameter was not statistically significant, all suggesting that in fact smolt size is a weak predictor.

Results of this study support previous salmonid migration work in finding that river flows are a primary factor in migration route selection (Moser et al. 1991; Moore et al. 1995, 1998). Furthermore, unlike previous studies, the present work demonstrates that this relationship is consistent at a sub-hourly scale. We also show that the lateral position of a smolt within the river can improve predictive models. Note that the scope of this work is limited to hatchery-raised late-fall run Chinook smolts, therefore these results should be extended with caution as differences in outmigration behavior are known to exist between species, races, and rearing history (Moser et al. 1991). Because water velocities are influenced by both modified connectivity and the management of California's water projects, these findings further encourage managers to consider the multiple impacts of flow alterations on declining populations of California's salmon.

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