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Movements of steelhead (*Oncorhynchus mykiss*) smolts migrating through the San Francisco Bay Estuary

**Eric D Chapman · Alex R Hearn · Gabriel P Singer ·
William N Brostoff · Peter E LaCivita ·
A. Peter Klimley**

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Abstract We used acoustic telemetry to monitor the out-migration of 1,000 steelhead smolts (*Oncorhynchus mykiss*) through the San Francisco Bay Estuary during spring of 2009 and 2010. The smolts transited the estuary rapidly (2–4 days) and utilized flows in the main channel during their migration. Fewer smolts were detected in marinas, tributaries and other shallow areas surrounding the estuary. Many of the smolts made repeated upriver and downriver movements that were related to the tidal flow, moving upstream during flood tides and downstream during ebb tides. These results show that steelhead smolts migrating from the Sacramento River transit rapidly through the lower reaches and do not use the estuary for feeding, rearing, or smoltification purposes.

Keywords Steelhead · Migration · Tide · Acoustic telemetry · Sacramento River · San Francisco Bay Estuary

E. D. Chapman (✉) · A. R. Hearn · G. P. Singer ·
A. P. Klimley
Department of Wildlife, Fish and Conservation Biology,
University of California,
1331 Academic Surge, One Shields Ave, Davis, CA 95616,
USA
e mail: edchapman@ucdavis.edu

W. N. Brostoff · P. E. LaCivita
U.S. Army Corps of Engineers,
San Francisco District, 1455 Market Street, San Francisco,
CA 94103, USA

Introduction

Steelhead are an anadromous and iteroparous form of rainbow trout (*Oncorhynchus mykiss*) indigenous to the Pacific coasts of Asia and western North America. In California, Central Valley steelhead are listed as threatened under the Endangered Species Act and the Central Valley Evolutionary Significant Unit occupies the Sacramento and San Joaquin rivers and their tributaries (Busby et al. 1996). Only a winter run of Central Valley steelhead is currently recognized, although there may have also been a summer run (Needham 1940). Historically, the run size may have approached one to two million adults but by the 1960s had declined to about 40,000 (McEwan 2001). Current estimates place the number of female spawners at 3,628 (Good et al. 2005). The Coleman National Fish Hatchery in Anderson, CA has a long term production goal of 600,000 (+/− 90,000) yearling steelhead smolts per year (K Neimala, pers. comm., 28 March 2014).

The San Francisco Bay Estuary is the largest estuary on the west coast, and covers more than 1,500 mile^2 of central California. The salinity ranges from fresh to brackish water in the lower Delta and Suisun Bay to the marine waters of San Francisco Bay. The depths in the estuary extend to 53 m in the central part of the Bay and eventually to 115 m just outside the Golden Gate Bridge (Chin et al. 2004). Information is lacking on the estuarine movements of steelhead throughout the Pacific Northwest and, in particular, the San Francisco Bay Estuary. The amount of time a steelhead smolt is present in an estuary may vary greatly from days Johnston et al.

(2010); McMichael et al. 2011; Moore et al. 2010; Harnish et al. 2012; Romer et al. 2013) to months (Hayes et al. 2008). The purpose of this study was to examine habitat use and movement rates of hatchery-reared steelhead smolts during their migration through the San Francisco Bay Estuary using ultrasonic telemetry.

Methods

Study area

This study was conducted in the San Francisco Bay Estuary from Benicia Bridge to the Golden Gate Bridge in San Francisco, CA. We divided our study area into three reaches: Carquinez Strait - from Benicia Bridge to Carquinez Bridge (10.4 km); San Pablo Bay - from Carquinez Bridge to the Richmond-San Rafael Bridge (26.6 km); and Central Bay - from the Richmond-San Rafael Bridge to the Golden Gate Bridge (17.7 km), delimited by the Bay Bridge to the south (Fig. 1).

We deployed 152 ultrasonic receivers (Vemco Ltd., VR2W, 69 kHz) throughout the San Francisco Bay Estuary. Eighty-eight receivers were deployed in the form of cross–sectional arrays at each reach boundary (Benicia, Carquinez, Richmond, Bay, and Golden Gate Bridges) with receivers spaced 150 m apart across the entire span. Receiver spacing was based on range tests published in two yearly reports (Chapman et al. 2009; Hearn et al. 2010). In 2009, the receivers did not extend completely to the eastern or western edge of the Richmond Bridge. In 2010, we added receivers to each end of the Richmond Bridge in order to complete the coverage across the entire span. We also deployed 48 stand-alone receiver stations on acoustic releases (Sub Sea Sonics, AR-50) in 2009 and attached 10 receivers to permanent moorings. In 2010, we added an array of

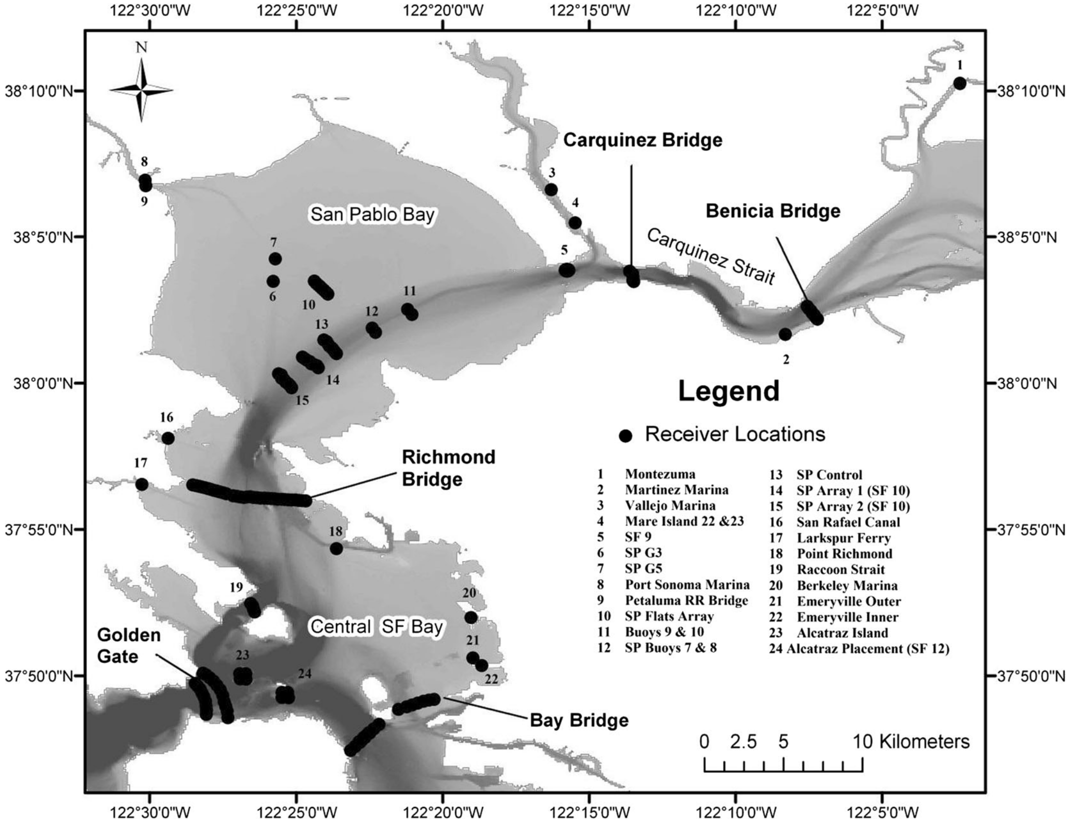

Fig. 1 Receiver arrays deployed throughout the San Francisco Bay Estuary. Lines of receivers were deployed at the boundaries (on bridges) of each of the three reaches: Carquinez Strait, San Pablo Bay, and Central Bay so as to detect across the entire cross section of the waterway. Receivers were also deployed at marinas around the shallower edges of the bay. One hundred and fifty two autonomous receivers were deployed as single or multiple receiver stations

eight receivers (Flats Array) in San Pablo Bay and four receivers at a site (SF9) near Carquinez Bridge. Finally, ten receivers were placed at marinas surrounding the estuary (Fig. 1).

Tagging and release

For each of our two study seasons (spring 2009 and 2010), we obtained 500 steelhead smolts/yearlings (fish in the second year of life) from the Coleman National Fish Hatchery of the US Fish & Wildlife Service in Anderson, CA. The smolts were transported to the University of California Davis, Center for Aquatic Biology and Aquaculture to be reared until tagging. Each fish was tagged with an internal ultrasonic tag that did not exceed 5 % of its body weight (average 1 %). In each study year we used V7−4 L tags (Vemco, Ltd.) weighing 1.84 g in air, 0.8 g in water, 136 dB, 138 day lifespan, 30–90 s nominal delay, and measured 7.0 mm in diameter × 20.0 mm in length. No mortalities or tag shedding were observed during the two days between tagging and release in either year. The tagging procedure was identical to Ammann et al. (2013), and was reviewed and approved by the University of California Davis Institutional Animal Care and Use Committee.

Steelhead smolts were released at Elkhorn Landing in two batches of 250 fish per year, on February 27 and March 6, 2009 and on January 30 and February 5, 2010. Steelhead smolts were trailered from UC Davis in a tank with O_2 diffusers. Temperature and dissolved oxygen were monitored once during the half hour transport to the release site. There was no need to temper the fish as in both years the river temperature was within one degree of the water in the tank. The fish were released into the river after dark to decrease the risk of predation from visually oriented piscivorous fish within the first few hours of acclimatization. The trailer was backed down the boat ramp into the river and a submerged door opened to allow the fish to exit the trailer.

The mean fork length of steelhead smolts was 258.6 mm (±0.9 S.E.) in 2009 and 223.1 mm (±0.8 S.E.) in 2010. There was no significant difference in fork length between batches in 2010 ($p=0.48$) or in 2009 ($p=0.08$) but steelhead were significantly longer in 2009 than in 2010 ($p<0.001$, Table 1). The mean weight of steelhead smolts was 192 g (±1.6 S.E.) in 2009 and 119 g (±1.2 S.E.) in 2010. There was no significant difference in weights between batches in 2010 ($p=0.1$) or in 2009 ($p=0.4$) but, consistent with the fork lengths, steelhead were significantly heavier in 2009 than in 2010 ($p<0.001$).

Table 1 Means and Standard Errors for acoustic tagged steelhead smolts

Year	Weight±SE (g)	Fork length±SE (mm)	Sample Size
2009	192±1.6	258.6±0.9	500
2010	119±1.2	223.1±0.8	499

Data analysis

We used the non-parametric Mann–Whitney Rank Sum Test to determine if there were differences in fork length between release groups in the same year and between years. The reach-specific survival of the fish tagged and released in this study was described in detail by Singer et al. (2013). Therefore, we present only a cursory analysis of migration success and tag-detection efficiency. We recorded the number of individuals detected at the beginning of each reach – Benicia Bridge represented the start of the study area, Carquinez Bridge represented entry to San Pablo Bay, Richmond Bridge represented entry to Central San Francisco Bay, and the Golden Gate represented exit of the study area into the marine environment. The proportion of smolts detected at the beginning of a particular cross-sectional array was calculated as the sum of all individuals detected at that array plus those individuals not detected at that array but detected downstream of that array. The detection efficiency was calculated by dividing the number of individuals detected at that array by the number of individuals detected at that array and below. Successful migration was expressed as the numbers of individuals surviving through each cross-sectional array as a proportion of the number originally released at Elkhorn Landing, and also as a proportion of those entering the study area at Benicia Bridge. The reach specific migration success was expressed as the number of fish at the start of the reach divided by the number detected at the end of the reach, or in the next reach if not detected at the end of the reach being examined.

Transit time was calculated as the time elapsed from the first detection at Benicia Bridge to the last detection at the Golden Gate Bridge. We calculated the transit rate across each reach for those fish that successfully migrated through the reach. The time was also determined between the first detection at the beginning of the reach to the last detection at the end of the reach, divided by the length of the reach and expressed as "body lengths per second". We used individual length at the time of tagging for this calculation. We explored the factors affecting transit rates by constructing a lognormal generalized linear mixed effects model (GLMM) using the "lme" package (Pinheiro et al. 2011) in R software version 2.13.1 (R Development Core Team 2011). Bolker et al. (2009) describe GLMMs as a combination of linear mixed models (which incorporate random effects) and generalized linear models (which handle non-normal data by using link functions and exponential family distributions). Given that many of the data are repeated measurements on the same fish, we used the variable "Fish ID" as a random effect to avoid pseudoreplication. Our initial fixed variables were fork length, fish weight, tag-to-weight ratio, surgery duration and river reach. We created a beyond-optimal model, using all possible explanatory variables and their interactions, to find the optimal structure of the random component. To accomplish this, restricted maximum likelihood (REML) estimators were utilized (Zuur et al. 2008). We then used a stepwise approach to remove non-significant terms of the fixed variables from the model until we found a best fit, using Akaike Information Criterion (Akaike 1974) to compare models. In the results section we present the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and negative log likelihood values of the full suite of models. We subsequently checked the model for homogeneity of residuals.

Many fish were observed making upstream and downstream movements. We defined a "movement" to have occurred whenever a fish was detected at a new receiver site. We defined an "upstream" movement as a detection that was observed at a greater river kilometer (rkm) than the previous one and "downstream" as a detection observed at a lesser river kilometer than the previous one (Golden Gate was considered rkm zero). To avoid compounding several tidal cycles within one movement, we used a subset of data, which included only those movements occurring within a 6 h period but greater than 14 min. This was based on minimum expected movement times between receivers. We hypothesized that these movements were related to tidal flows, and that smaller fish were more likely to be swept upstream by the currents. We obtained data on current speed and direction from two locations within the estuary (Davis Point, 38.0620°N, 122.2767°W; and Alcatraz South, 37.8167°N, 122.4166°W) using models made available by the University of South Carolina (http://tbone.biol.sc.edu/tide). We assigned a current speed to each detection, based on the closest time and the location of the fish. All fish detected at Richmond Bridge and downstream were assigned the current speed measured from Alcatraz, whereas those above Richmond Bridge were assigned current speeds measured from Davis Point (just south of Carquinez Bridge). We then ran a recursive partitioning algorithm using Hothorn's "party" package (Hothorn et al. 2006) to construct a conditional inference tree. We used temperature, fork length, current, and river kilometer as predictors of upstream and downstream movements. We then constructed a generalized additive mixed model (GAMM) using current and river kilometer based on the results of recursive partitioning using the "mgcv" package (Wood 2004) in R.

To determine whether there was a relationship between the depth of the water column and the number of fish passing through each receiver station, we measured the water depth at each receiver station at the Bay Bridge and Richmond Bridge. We plotted the number of fish detected across each cross-section array. A linear regression was fitted to the number of fish detected for each depth and tested for significance.

Results

Migration success

The migratory success of steelhead smolts varied between the three regions of the San Francisco Bay Estuary. A greater percentage of tagged fish reached the beginning of the study area at Benicia Bridge (47.6 %) in 2009 than in 2010 (22.2 %). However, a similar proportion of fish released at Elkhorn Landing migrated successfully to the Golden Gate in both years, 14.6 % in 2009 compared to 13.8 % in 2010. Mortality in San Pablo Bay (Carquinez-Richmond reach) was particularly low in 2010, with only eight individuals not reaching the Richmond Bridge, compared to 54 in 2009 (Table 2). This suggests that the mortality was inverted between years (greatest below Benicia in 2009 but greatest above in 2010) although the addition of receivers on the eastern and western end of the Richmond Bridge greatly improved the detection efficiency at that location.

Table 2 Numbers of steelhead smolts detected at bridge arrays and estimated detection efficiencies. Figures for Golden Gate (*shown in italics*) are estimates based on fish detected on a line of monitors deployed in the ocean

Year	Site	Success to Site	Actual Detections	From Benicia %	From Release Site %	Reach Specific %	Detection Prob. %
2009	Benicia	238	163		47.6	47.6	68.5
	Carquinez	214	101	89.9	42.8	89.9	47.2
	Richmond	160	86	67.2	32.0	74.8	53.8
	Golden Gate	73	62	30.7	14.6	45.6	*96.9*
2010	Benicia	111	97		22.2	22.2	87.4
	Carquinez	100	63	90.1	20.0	90.1	63.0
	Richmond	92	84	82.9	18.4	92.0	91.3
	Golden Gate	69	65	62.2	13.8	75.0	*94.2*

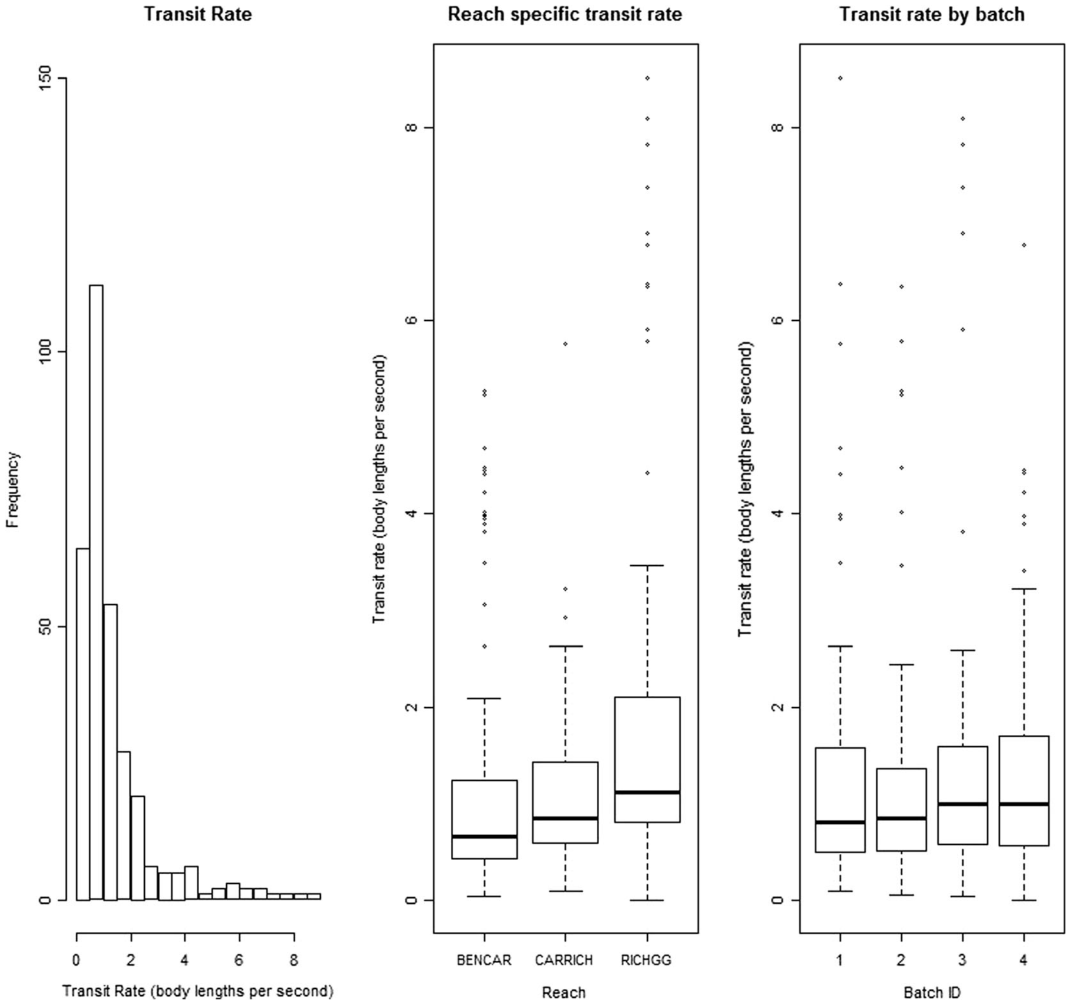

Fig. 2 Transit rates (in body lengths per second) through each reach of the San Francisco Bay Estuary (Benicia to Carquinez, Carquinez to Richmond Bridge, and Richmond Bridge to the Golden Gate). From left to right: frequency of transit rates through all reaches, boxplot of transit rates through each reach, boxplot of transit rates for each release batch (1 and 2 released in 2009, 3 and 4 released in 2010). Boxplots display median and upper/lower quartiles, with outliers displayed as points

Table 3 Model statistics for all smolt transit rate and sloshing movement models, with following parameters Transit time: u = transit rate (in body lengths per second), RR = river reach, FL = forklength, BT = release batch); Sloshing: down (downstream movement =1, upstream movement =0), CU = current speed ms 1, FL = forklength, RKM = river kilometer. For both models, k = number of parameters, neg.log.lik = negative log likelihood, BIC = Bayesian Information Criterion, AIC = Akaike's Information Criterion. Models have been sorted from best to worst, in order of increasing AIC values

Transit Rate	k	neg. log. lik.	BIC	AIC
u~ RR	1	154	336	317
u~ RR + FL	2	158	350	328
u~ RR + FL + BT	3	162	375	341
u~ 1	0	556	1129	1118
u~ RR + FL + BT + RR:FL	4	164	414	358
u~ RR + FL + BT + RR:FL + RR:BT	5	173	443	381
u~ RR + FL + BT + RR:FL + RR:BT + FL:BT	6	186	485	411
u~ RR + FL + BT + RR:FL + RR:BT + FL:BT + RR:FL:BT	7	205	556	461

Transit rates

Transit rates of smolts were similar between years. The total transit time through the study area, from the first detection at Benicia Bridge to the last detection at the Golden Gate was an average of 3.3 days in 2009 and 3.0 days in 2010. When one outlier (18 days) was removed, the 2009 average was also 3.0 days.

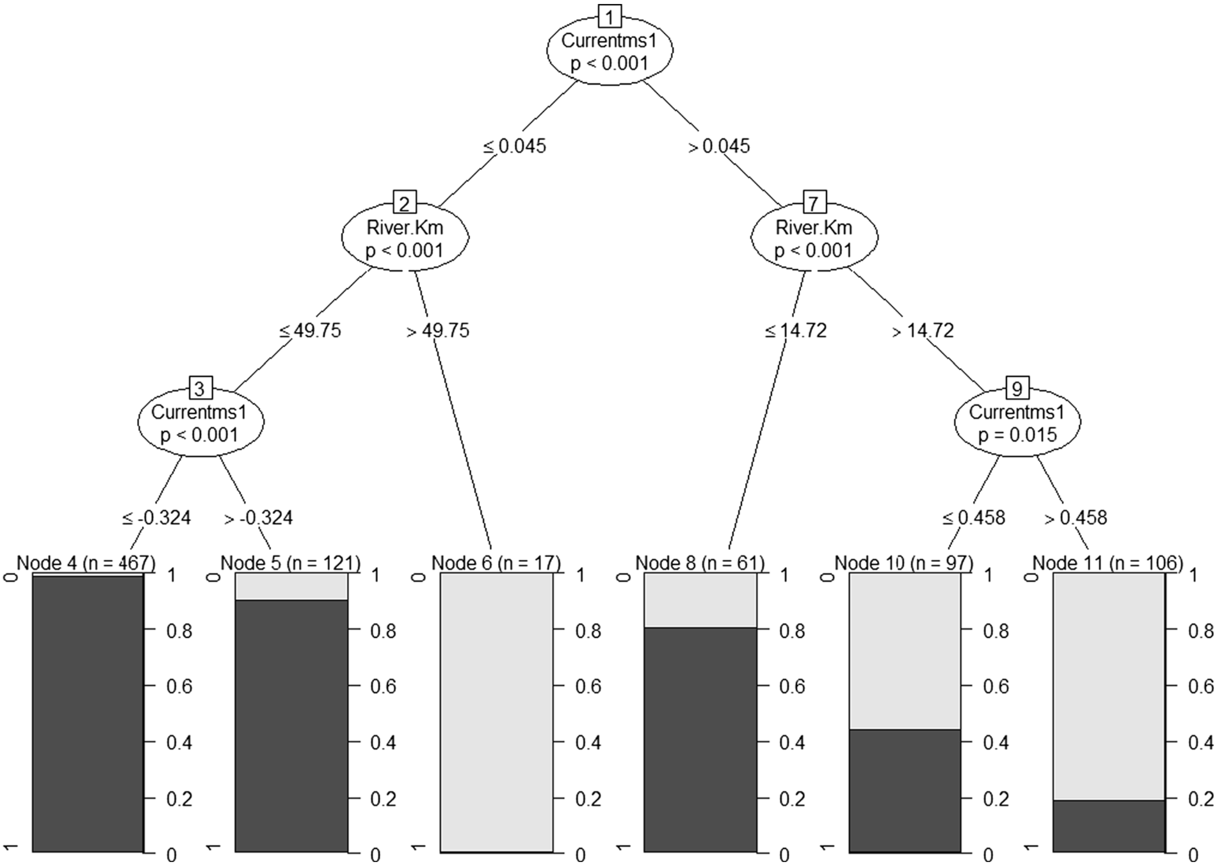

Fig. 3 Conditional inference tree for movement data. For each inner node, the Bonferroni adjusted P values are given, the fraction of upstream movements is displayed for each terminal node

Transit rates increased as fish moved downstream, with the fastest rates observed in the Richmond to the Golden Gate reach. There were no statistically significant differences in transit rates observed between batches (Fig. 2). The best model (GLMM) included "river reach" as the fixed variable and suggests that movement rates varied between reaches (Table 3). This model performed better than all other models including the null model.

Tidal effects

Many of the steelhead exhibited upstream movement during both years. Of the fish reaching the start of the study area, 77 steelhead (32.4 %) in 2009 and 57 (51.4 %) in 2010 were observed to make at least one upstream movement. The maximum distance a fish was observed to make an upstream movement was 16.8 km. The conditional inference tree (Fig. 3) showed that the most important factors were current velocity and to a lesser extent river kilometer. Temperature and fork length were not identified as important. The GAMM that was run using these two predictors showed a smooth effect of water velocity, indicating that movements were highly correlated with upstream and downstream flows created by the ebbing and flooding tides (Fig. 4).

Channel depth

Steelhead smolts were detected on most receivers along the Richmond Bridge. In 2010 there were no steelhead detected by the four receivers that were added to the far eastern side of the Richmond Bridge just prior to the fish release in 2010. The majority of fish were detected on the western side of the bridge (Fig. 5). There was a significant correlation between the number of fish detected and the depth of the water column in 2010 ($F_{1,\ 34}$=5.1, $p<0.05$) but not in 2009 ($F_{1,\ 17}$=0.233, ns).

Steelhead smolts were detected on most receivers along the Bay Bridge. The majority of detections were along the western side of the bridge between Treasure Island and San Francisco with fewer on the eastern edge of the Bay between Treasure Island and Oakland (Fig. 6). There was a significant correlation between the number of fish detected and the depth of the water column in 2010 ($F_{1,\ 16}$=19.1, $p<0.001$) but not in 2009 ($F_{1,\ 16}$=0.539, ns).

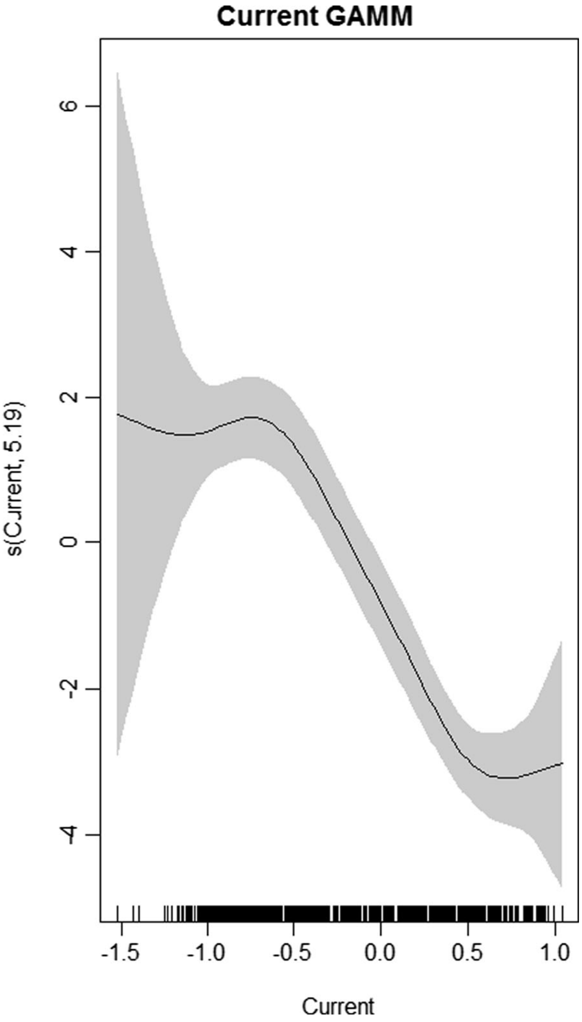

Fig. 4 Estimated conditional dependence of the occurrence of movements on currents. Estimate (solid line) and confidence interval (shaded area), derived from generalized additive mixed model (GAMM), with rug plot along bottom indicating observation density. The y axis label indicates that upstream movement has been modeled as a smooth function of current with an estimated degree of freedom (for the smooth term)

General pathways

Steelhead smolts generally passed through the channel toward the Golden Gate. In 2009, 10 % of the steelhead reaching the start of the study area at Benicia Bridge did not subsequently reach Carquinez Bridge, compared to 7 % in 2010. The majority of fish in the study areas moved through the system without moving into tributaries or marinas along the shores. Those fish which did move up the Petaluma River or Mare Island Strait in most cases subsequently returned to the main estuary

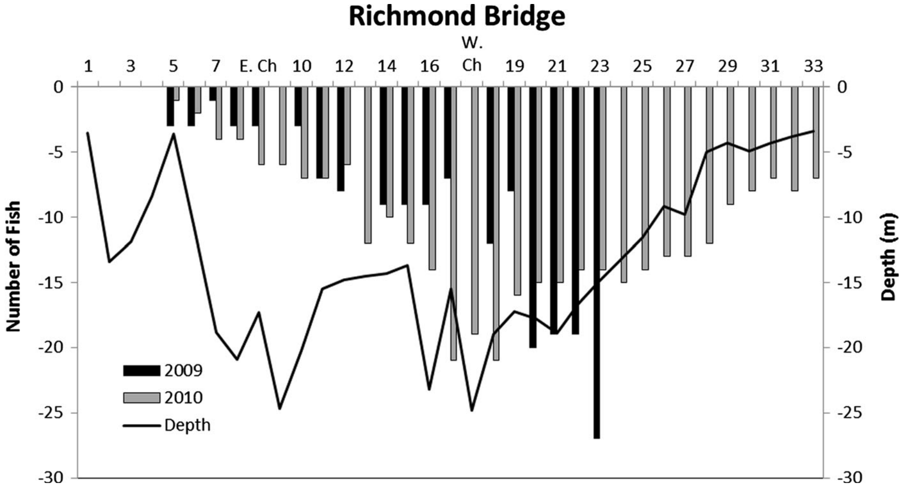

Fig. 5 Number of steelhead smolts detected at each receiver (east to west from left to right) along the Richmond San Rafael Bridge in 2009 and 2010. The solid line depicts the depths listed on the right axis. Note: Two receivers malfunctioned in 2009 (9 and 13), the receiver in the west channel that was deployed on an acoustic release popped up early in 2009, and receivers 24 33 and 1 4 were added in 2010

and did not appear to be affected in terms of successfully reaching the Golden Gate. In 2009, no steelhead moved up Mare Island Strait (Fig. 7, reference Fig. 1 for stations). In 2010, seven steelhead moved up Mare Island Strait, all but one of which returned to the main estuary and five were later detected at the Golden Gate (Fig. 8, reference Fig. 1 for stations). In 2009, five steelhead smolts moved up the Petaluma River, of which four returned to San Pablo Bay and all arrived at the Golden Gate. In 2010 only one steelhead was detected here, but it was not detected anywhere else subsequently. As a proportion of the number of fish known to have reached San Pablo Bay in 2010, only 6.5 % of steelhead utilized the Flats Array (added in 2010) whereas over 50 % utilized the channel-based Control Array.

Five steelhead in 2009 and one in 2010 were detected at a marina site bordering San Pablo Bay (Larkspur Ferry Terminal). Of the former, two were subsequently detected at the Golden Gate. The latter fish returned to the Richmond Bridge but was not detected further. Two steelhead were detected at Point Richmond (Central Bay) in 2009 and a further one fish was detected in 2010. All three fish were subsequently detected at the Golden Gate.

The number of steelhead moving through Raccoon Strait increased from 15 in 2009 to 21 in 2010. A similar number of fish were detected at Alcatraz in both years, and detections at these sites were often preceded and followed by detections at the Golden Gate. In 2009, two steelhead were later detected at the offshore array at Point Reyes, approximately 60 km to the north of San Francisco Bay, whereas in 2010 this number increased to 17.

Discussion

In 2009, 47.6 % of the fish reached the start of the study area at Benicia Bridge. In 2010, only 22.2 % of the fish reached the study area. Even though far fewer fish reached the study area in 2010, a similar proportion of the fish in both years were detected at the Golden Gate Bridge (14.6 % and 13.8 % respectively). The influence of tides in the San Francisco Bay Estuary extends above the beginning of our study area. Singer et al. (2013) postulated that the dissimilarity between years may have resulted from flows which, surprisingly, were higher in 2010. Since the majority of mortality in 2010 occurred above Benicia Bridge, the increased survival in the lower estuary may have extended to the ocean. The large difference in detections at Point Reyes between years (two in 2009, 17 in 2010) could be attributed to ocean conditions or simply by chance. Further differences in behavior may occur with wild fish, for example, in the Mokelumne River (also in the Central Valley of California), Del Real et al. (2012) reported successful migration of 10 % for hatchery steelhead compared to only 1 % of wild fish.

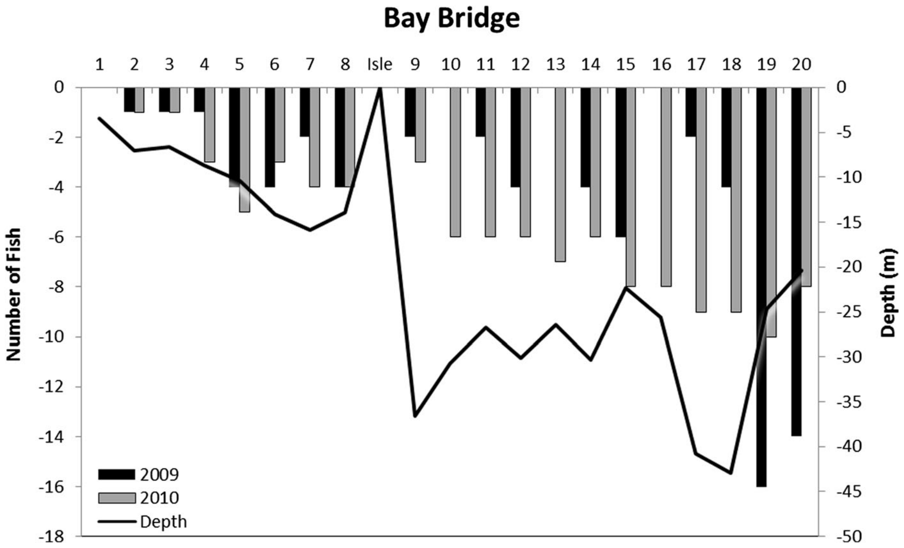

Fig. 6 Number of steelhead smolts detected at each receiver (east to west from left to right) along the Bay Bridge in 2009 and 2010. The solid line depicts the depths listed on the right axis. Note: receivers 10, 13, and 16 were deployed on acoustic releases that popped up early in 2009

The majority of steelhead migrating through the San Francisco Bay Estuary transited in less than four days. These hatchery-reared smolts utilized the estuary as a migratory corridor. Based on our GAMM model, tidal currents were the main force pushing fish back upstream. We also observed upstream movements at the Golden Gate Bridge, which indicated that fish had already completed smoltification requirements before entering the ocean (e.g. osmoregulation). Similar results were seen by Clements et al. (2011) where steelhead

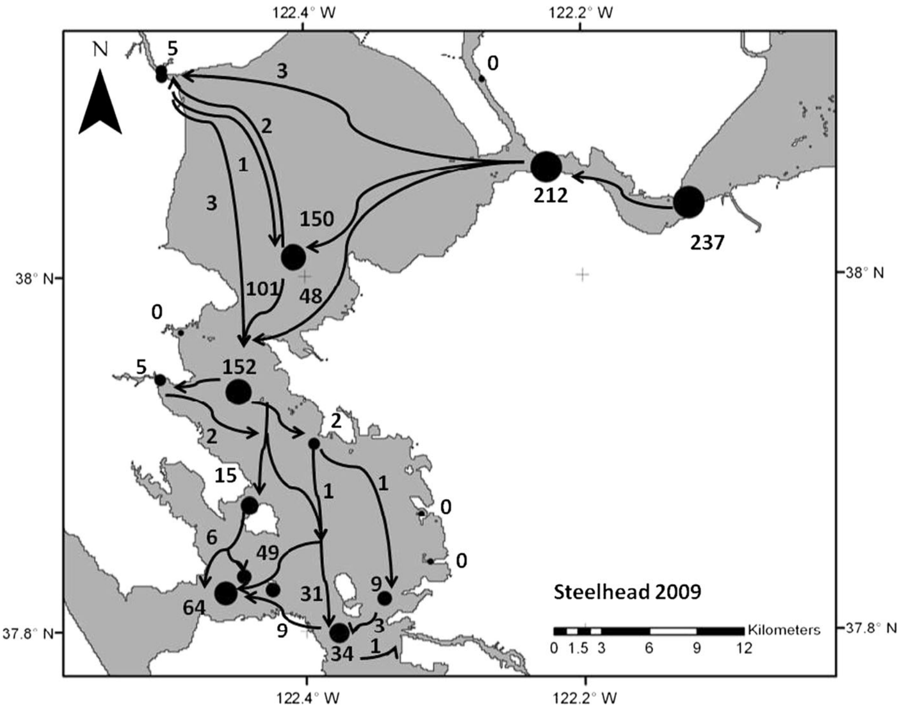

Fig. 7 Movement patterns by outmigrating steelhead in San Francisco Bay Estuary in 2009. Black dots refer to receiver sites or arrays, and are sized relative to the number of fish detected at each site (numbers also shown). Note that the lines portray movements between sites, not actual pathways

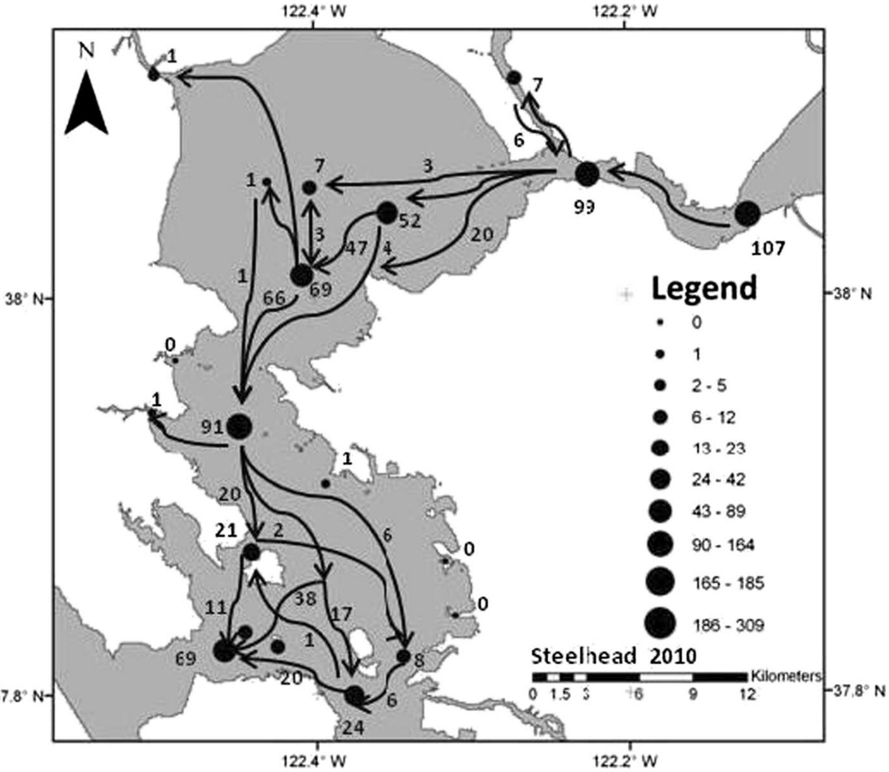

Fig. 8 Movement patterns by outmigrating steelhead in San Francisco Bay Estuary in 2010. Black dots refer to receiver sites or arrays, and are sized relative to the number of fish detected at each site (numbers also shown). Note that the lines portray move ments between sites, not actual pathways

smolts migrated rapidly through the small Nehalem Estuary (Oregon, USA) and generally on an outgoing tide. They concluded that smolts were stationary on a slack or incoming tide and that holding behavior was due to the influence of the tides rather than any apparent "decision" by the fish to remain in a particular area, and were strongly influenced by the tidal currents. It appears that hatchery-reared Central Valley steelhead attempt to hold as well. The difference appears to be that steelhead migrating through this larger estuary were unable to maintain position throughout the entire incoming tide. They were forced back up river maybe by stronger currents or lack of structure, particularly in the channel that these smolts often occupied. Yet despite this, they still moved through the system at a faster rate than might be expected from simple passive transport. Hearn et al. (2013) found that estimated passive transport based on current predictions for Davis Point (approximately midway across the study area) suggest that a fish would take 5 days from the first detection at Benicia Bridge to the last detection at the Golden Gate. They postulated that fish might move horizontally or vertically into slower upstream currents on incoming tides.

Johnston et al. (2010) reported that more than 50 % of hatchery steelhead smolts reversed direction and were detected at a receiver located upstream of the receiver they were previously detected at upon reaching various locations with the Alsea Bay Estuary (Oregon, USA). We also observed greater than 50 % of steelhead in 2010 and 32 % in 2009 making at least one upstream movement – many fish were observed to make repeated upstream movements. However, it was rare to detect fish making more than three upstream movements. Given a semi-diurnal tidal cycle and an average transit time of 3.0 days, we might expect fish to be subjected to approximately six incoming tides as they move out through the estuary. Many more upstream movements likely went undetected out of the range of the receiver array. Some receiver arrays were deployed in close proximity to others, some were deployed much farther away than adjacent receivers. For example, in the center of San Pablo Bay, three lines of eight receivers each were spaced one and a half kilometers apart. In this area of the estuary (between river km 23 to 26), movements were detected in far greater numbers than receivers placed up to 15 km apart and at single receiver stations. River kilometer came out as the second most important predictor of upstream movements in the classification tree. However, receiver deployment strategy may have had a big impact on the "interpretation" of upstream and downstream movement. Successful migration to the Gulf of Maine increased for Atlantic salmon smolts that reversed direction on multiple tide cycles (Kocik et al. 2009). Hostetter et al. (2012) found that steelhead in poor external condition were subjected to predation significantly more often than fish in good condition. This implies that fish with good condition have more energy. It is possible that steelhead and Atlantic salmon smolts, which expend less energy by not swimming against strong flood tides have more energy reserved for predator avoidance.

Steelhead transited the San Francisco Bay Estuary faster through each consecutive reach as they neared the ocean. The average rate was 1.4 body lengths per second although some fish migrated up to 8.0 body lengths per second. Travel speeds for steelhead smolts migrating through the Strait of Georgia (British Columbia, Canada) averaged 1.0 body lengths per second (Melnychuk et al. 2007). They also observed an increase in transit rate as fish neared the ocean until exit from Howe Sound on the Cheakamus River.

We detected greater numbers of steelhead in the deeper channelized areas than in the shallower water along the edges at both the Richmond and the Bay Bridge. At the Richmond Bridge, where we assume detection probability is the same at all locations, smolt presence during downstream migration was correlated with the deep channels in the center. While smolts were also detected in the channelized deep area of the western side of the Bay Bridge it is likely tidal effects rather than an affinity for that particular area. The incoming water during flood tide would be unlikely to carry a fish up around Yerba Buena/Treasure Island to the eastern shallower side of the Bay Bridge. On an outgoing tide, flows move south and west from Richmond and north and west from the South Bay. It is also unlikely that a steelhead smolt would swim against an outgoing tide and be detected on the eastern side of the Bay Bridge.

In conclusion, the San Francisco Bay Estuary is mainly a migratory corridor for migrating hatchery steelhead smolts. This is in contrast to what was expected of these hatchery fish in the Central Valley. The assumption was that steelhead would feed or rear in the estuary during the migration. Moyle (2002) mentions that upon leaving their home streams, steelhead feed on estuarine invertebrates. They are likely opportunistic feeders picking off prey as it presents itself during outmigration but steelhead from the Coleman National Fish Hatchery certainly do not key in on one food source for any substantial amount of time as they do in the hatchery or a wild fish in its natal streams. As they reach the estuary they encounter flooding tides that push them back upstream. They attempt to transit the estuary quickly (and they do) but the distance they must travel (>50 km) makes it difficult for them to migrate seaward unimpeded. We believe that these fish would migrate directly out with the current if the distance were short enough for them to cover in one outgoing tide. Late-fall run Chinook salmon smolts behaved in similar fashion, migrating rapidly through the Bay and mostly through the main channels, while being subjected to upstream movements on flood tides (Hearn et al. 2013). Both species transit the Bay faster than would be expected if they were simply floating passively in the water column. This suggests that steelhead smolts swim downriver against the oncoming tide, until they are no longer willing or able to expend the energy swimming against the current, in an effort to reach the ocean in as little time as possible. Though cost prohibitive, it is likely that a study in the San Francisco Bay Estuary utilizing a grid type receiver deployment strategy, with velocity meters at each station, would conclude that steelhead smolts move upstream throughout the entire estuary and upstream movement is more prevalent in areas with highest current speed.

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