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Holding behavior of Chinook salmon (*Oncorhynchus tshawytscha)* and steelhead (*O. mykiss)* smolts, as influenced by habitat features of levee banks, in the highly modified lower Sacramento River, California

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Abstract Using acoustic telemetry methods on large numbers of tagged fish, we studied how the holding behavior of Chinook salmon and steelhead smolts could be related to habitat features and spatial and temporal variables on a highly altered section of the Sacramento River. We viewed downstream migration as a process in which fish transition between moving and holding states, and used a binomial and negative binomial Generalized Linear Model to analyze two aspects of holding: 1) probability of holding, and 2) holding time. For Chinook salmon, the probability of holding increased as wood size and fine substrates increased; holding time increased as overhead shade increased. For steelhead, holding behavior was only weakly related to habitat variables, in contrast to the strong relationships with spatial and temporal variables. For both species, the probability of holding increased when distance from the release location decreased and instream flows decreased. We found support for three main findings: 1) spatial and temporal factors have considerably greater influence on Chinook salmon and steelhead smolt holding behavior than nearshore habitat features; 2) holding behaviors of Chinook salmon smolts are influenced more strongly by habitat features than steelhead smolts; and 3) incorporation of habitat features such as large woody material and overhead shade should be considered when conducting nearshore bank rehabilitation projects to increase cover from predators and provide velocity refuge, improving holding habitat during downstream migration.

Keywords Acoustic telemetry · Chinook salmon · Downstream migration · Holding · Steelhead

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Introduction

When salmonid (*Oncorhynchus spp.*) smolts migrate from freshwater to marine habitats, their survival rates may be affected by their travel rate, route taken, predation pressure, and habitats encountered; these factors affect their susceptibility to predation as they move towards the sea. The survival rates of downstream migrating salmonid smolts in the Sacramento River have recently been quantified by telemetry-based studies (Burau et al. 2007; Michel 2010; Perry et al. 2010). Telemetry-based studies in the Sacramento River have also quantified residence times (Burau et al. 2007), travel

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rates (Michel 2010; Bruce MacFarlane, National Marine Fisheries Service (NMFS), pers. comm., 29 June 2011), and travel routes (Burau et al. 2007; Perry et al. 2010).

Travel rates are dependent on many physical factors, as may be expected. In general, most downstream migrating salmonid smolts travel rapidly (Giorgi et al. 1997; Friesen et al. 2007; Michel 2010) and use the main channel; however, some tagged salmonid smolts have been detected near river banks, such as in the Willamette River (24 % of tagged fish, Friesen et al. 2007) and the Sacramento River (Burau et al. 2007). Travel rates near the banks are typically much slower than within the main channel (Williams 2006). Although the majority of salmonid smolts appear to migrate downstream in the thalweg, fish are likely influenced by habitat features along banks, and their movement patterns may reflect their interactions with these features and their associated vegetation and fish communities.

Our study builds on the telemetry-based findings of travel rates and routes from previous studies in the Sacramento River (Burau et al. 2007; Michel 2010; Perry et al. 2010; Bruce MacFarlane, NMFS, pers. comm., 29 June 2011; Arnold Ammann, NMFS, pers. comm., 10 July 2011; Chapman et al. 2012). We used similar data collection methods, shared the same tagged fish, and collected the same types of data, as other telemetry studies on the Sacramento River that were conducted by the California Fish Tracking Consortium (CFTC).

Our study differs from others in that we evaluated relationships between spatial and temporal variables (i.e., flow, smolt release location, time of year), habitat features (e.g., large wood, bank slope, substrate), and smolt migration pattern. We define smolt migration pattern as the transition between moving and holding states; as a smolt migrates downstream, it can swim for a long period (move) and then stop (hold) (Steel et al. 2001). Our objective is to evaluate the importance of spatial and temporal variables and habitat features for whether a smolt holds, and if it holds, the duration of its holding time.

Methods

Study area and sites

Study site locations on the Sacramento River ranged from river kilometer (rkm) 38.6, which is just upstream of the Delta, to rkm 160.9, which is approximately 80 km upstream of the City of Sacramento (Fig. 1). The study area is mostly confined by large, rip-rapped levees with discontinuous narrow bands of riparian vegetation. Flows in the Sacramento River and its tributaries are regulated by water supply and flood control dams that alter flow regimes by stabilizing river flow, and that have changed the river's erosion and sediment transport characteristics (Mount 1995). Discharge in the study area is measured at rkm 126 (USGS Station #11425500). During the study, discharge ranged from 205 to 1392 m^3/s in 2009 and from 264 to 1645 m^3/s in 2010.

To account for the influences of large tributaries, changes in channel morphology, and tidal influence, we divided the study area into three reaches: Ko-Ket (rkm 38.6 to 56.3), Garcia Bend (rkm 64.4 to 112.7) and Knights Landing (rkm 136.8 to 160.9). The Knights Landing reach extends south from rkm 160.9 to just north of the Feather River confluence; in this reach the Sacramento River is comparatively narrow (60 to 120 m) with no tidal influence; here, steep banks are largely bordered by agricultural fields. The Garcia Bend reach starts approximately midway between the Feather and American river confluences, and ends just south of the City of Sacramento; the river here is broader (80–200 m) and more sinuous, becoming increasingly tidal (1-m tidal variation at rkm 74) with occasional depositional beaches and bars in an urban/suburban setting. The Ko-Ket reach extends from south of the City of Sacramento towards the Delta, with increasing tidal influence, although the salinity remains <1 ppt; in this reach, the river narrows (75 to 180 m), and the banks often feature derelict pilings and other structures in a mixed suburban and agricultural setting.

Within these three reaches, we selected 14 sites at levee repairs (n=9) and natural areas (n=5). Over the years, failing levees have been repaired using rip-rap while maintaining existing vegetation where possible; levee repairs were characterized by one or a combination of features that included supplemental woody material, reduced slope compared to historical designs, and off-channel ditch habitat. The natural areas were dominated by naturally established riparian vegetation.

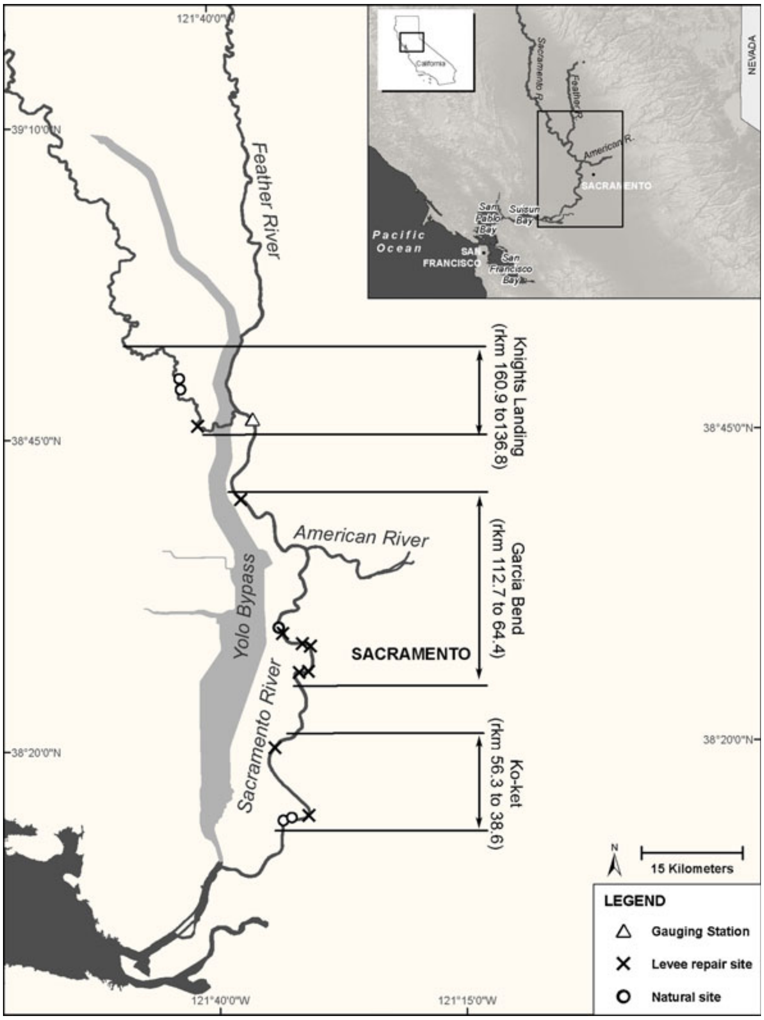

Fig. 1 Locations of reaches and the 14 telemetry receivers placed at levee repair sites and natural sites, from rkm 38.6 to rkm 160.9 on the Sacramento River, California

Habitat measurements and variables

At each levee repair and natural site, we collected measurements that characterized seven habitat variables:

- % shade
- % cobble/boulder
- bank slope
- submerged vegetation
- instream woody material (IWM) diversity
- average large woody material (LWM) density, and
- dominant IWM size.

Percent shade and % cobble/boulder were determined using a transect line established at each site as described in the Standardized Assessment Method (Stillwater Sciences and Dean Ryan Consultants 2004). At sites above rkm 50, the transect line was placed at the average low (summer/fall) water surface elevation. The transect line at sites in the Ko-ket reach (rkm 43.3, 40.2, and 38.6) were placed along the mean low tidal elevation. Percent shade was determined at 30 evenly-spaced points along the transect line at each site; at each point the presence or absence of shade was determined along a line perpendicular to and extending from the transect line toward the water. The mean percentage of shaded shoreline was calculated for each site. Shade was measured in August and September, and was defined as riparian canopy or any other vertical obstruction that provided shade above the seasonal water surface elevation at midday. To characterize bank substrate, we estimated the total percentage of substrate >15.2 cm diameter, and named the variable "%

cobble/boulder", which was estimated for the area extending from the transect towards the water at each site.

Bank slope was measured in the summer, and calculated as the average change in channel width with respect to depth (dW/dH) at each site. Higher values for the bank slope variable represent more gradual slopes, and lower values represent steeper slopes.

We found that the variables for submerged vegetation and woody material as suggested in the Standardized Assessment Method (Stillwater Sciences and Dean Ryan Consultants 2004) poorly represented field conditions at our sites. We created three alternative woody material variables that could be calculated from our field measurements: instream woody material diversity, average large woody material (LWM) density, and dominant IWM size. We created these alternative wood variables because we realized that a site could have a high LWM density and a large dominant IWM size, and yet still offer lesser quality habitat because the diversity of woody material could be low.

Field data for submerged vegetation and wood were collected at 10 to 15 evenly-spaced, 3-m diameter sampling points established in the water at each site (the number of points was based on site length) during April. Submerged vegetation was defined as plant material that provides instream cover, including submerged riparian vegetation, shrubs (i.e., blackberries), and aquatic plants. Submerged vegetation was characterized as being present (defined as >10 % of the area covered by submerged vegetation) or absent (<10 % covered). The three wood field measurements were wood density, wood size, and wood in/out of water (Table 1). Wood density was classified as the percentage of total area of wood visible below the surface of the water at each sampling point. Wood size was classified as the most frequently observed size class of wood at each sampling point. Wood in/out of water was classified as submerged, above the surface, or floating at each sampling point.

We used the field measures of wood to subsequently determine values for the submerged vegetation variable and the variables IWM diversity, average LWM density, and dominant IWM size. Values for the submerged vegetation variable were determined by dividing the number of points where >10 % of the area was covered by submerged vegetation, by the total number of sampling points at that site. Values for the variable IWM diversity were calculated as the number of unique combinations of wood density, size, and in/out of water among all sampling points at a site, divided by the total number of sampling points at that site. For example, if all 15 sampling points at a site had the same values for wood density, size, and in/out of water, the site would have an IWM diversity of 0.067 (i.e., calculated as one divided by 15). To calculate average LWM density, for any sampling point containing one or more pieces of wood >10.2 cm diameter, the midpoint of that sampling point's wood density class designation (i.e., 12.5 % for wood density class <25 %; 37.5 % for wood density class 25–50 %) was calculated; for points lacking any wood pieces >10.2 cm diameter, zero was used instead. These density values were then averaged across all sampling points within the site. Dominant IWM size was the midpoint of the most common size class at each site. If the most common size class at a site was 10.2–20.3 cm diameter, the value for dominant IWM size was 15.25 cm.

Table 1 Instream woody material (IWM) measures collected at each sampling point at 14 sites on the Sacramento River. These measurements were used to calculate the variables IWM diversity, average LWM density, and dominant IWM size

IWM Measurements	Classification
IWM density	None
	Low (<25 %)
	Medium (25 to 50 %)
	High (>50 %)
IWM size	<10.2 cm diameter
	10.2–20.3 cm diameter
	>20.3 cm diameter
IWM in/out water	>50 % submerged
	>50 % above the surface
	Floating

Telemetry receiver deployment

The study was conducted over two years; receivers were deployed from 21 November 2008 to 27 April 2009 for the first year and from 17 December 2009 to 13 May 2010 for the second year. Telemetry receivers (Vemco, Ltd.; Model VR2W) were placed at the 14 levee repair and natural sites to monitor migratory movements and site association patterns of acoustically tagged Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) (Fig. 1). At each site, receivers were deployed within 4 to 34 m of the bank while ensuring that water was sufficiently deep so that gear would be submerged under typical flow conditions. The CFTC implanted Vemco, Ltd. tags (models V7 and V9 series) into Chinook salmon and steelhead smolts. Each tag's effective range is 100–200 m (with a consistency of >80 % detection) (Arnold Ammann, pers. comm., 10 July 2011, NMFS). In 2009, field conditions were more severe than anticipated, and data were not available for the two most downstream stations in the Knights Landing reach, because receivers could not be retrieved.

We also tagged and released 99 steelhead smolts obtained from Coleman National Fish Hatchery (CNFH), located on Battle Creek, a tributary of the Sacramento River at rkm 438, on 5 January 2009. We surgically implanted the Vemco, Ltd. V9-2 L individually coded acoustic transmitter tags (operating at 69 kHz; estimated tag life 37 days; 9×21 mm, weight in water 2.9 g, with a randomized transmission interval of 15 to 45 s) in the peritoneal cavity of steelhead smolts. The mean total length for the tagged steelhead was 209 mm (11.57 SD), and the mean weight was 101 g (17.94 SD). With the V9-2 L weighing 2.9 g in water, this gives a tag to body weight ratio of 0.029. Handling, anesthesia, and surgical procedures followed those described by Hall et al. (2009). The tagged fish were held for 24 h post-surgery at the CNFH, and then transported in twin temperature-controlled, re-circulating tanks to the release sites, within 3 to 7 h. Each of the three reaches received approximately one-third of the tagged fish (at rkm 43, n=34 fish released; at rkm 83, n=28 released; and at rkm 159, n=37 released, on 6 and 7 January 2009).

The vast majority of our detections were from Chinook and steelhead smolts tagged and released by other researchers participating in the CFTC. By accessing the CFTC database, we were able to obtain information (i.e., species, release date, release location, and responsible researchers) on those fish detected by our receivers. We limited our analyses to fish that were released between November 2008 and March 2009, and between December 2009 and March 2010. More details and an illustration of telemetry receiver deployment and tagging can be found in other reports (H. T. Harvey & Associates and PRBO Conservation Science 2010).

Analysis

Telemetry data consisted of the times of site-specific detections of individually tagged hatchery fish. Holding time was the time spent at a site (in h), determined using the first and last detections of a tagged fish at a given site. All telemetry data were used except for data indicating evidence of a shed tag, mortality, or predation. We assumed that voluminous consecutive records associated with a single station indicated a shed tag or mortality, and that rapid upstream movement likely indicated predation of a tagged smolt by a larger fish such as a striped bass (*Morone saxatilis*) that is more likely to move rapidly upstream. Tag detections were removed if there were several consecutive days at the same station with >1000 detections per day, and/or if upstream travel was greater than 16 km in a single day.[1]

Generalized linear models (GLMs) were used to identify key spatial, temporal, and habitat variables for Chinook salmon and steelhead smolts. The spatial variable was distance from release; temporal variables included the year of study (2009 or 2010), date of release, number of days between first detection at a site and release (days since release), and daily average discharge on the first date of detection at a site. Daily average discharge was log-transformed to mute statistical effects of very large events when there is likely some threshold above which the biological response is the same. Another temporal variable, the day/night variable, was included to indicate whether the first detection at a site occurred during day, defined as from sunrise to sunset, or night, defined as from sunset to sunrise, because this could influence the decision to hold at a site. Based on prior knowledge, we determined that reasonable potential interaction terms were Year x Release date and Year x Days since release, because the relationship with release timing could vary between years. Habitat variables included % shade, % cobble/boulder, bank slope, submerged vegetation, and IWM diversity, average LWM density, and dominant IWM size.

We also considered tag type and fish length, in an attempt to account for potential effects on holding due to detection range or body size. For Chinook salmon, only one tag type was used (V7), therefore, only fish length was added. For steelhead, both tag type and fish length were added to the analyses. Although not technically spatial or temporal variables, tag type and/or

[1] We chose to use 16 km upstream travel in single day based on telemetry results that indicated a range of 0.2 to 42.3 km for Chinook salmon and from 0.2 to 37.7 km for steelhead; only nine Chinook salmon and seven steelhead smolts were found to travel greater than 16 km upstream in a single day.

fish length were included so that they could be controlled for, thus reducing the amount of unexplained variance in the dependent variable. This improved our ability to identify and quantify habitat variables.

We fit a binomial and truncated negative binomial GLM to the telemetry data to address two subtle but distinct aspects of fish behavior and their ecological responses to the study sites. The binomial model was used to describe 'holding' versus 'moving' where the two conditions are defined as follows: 'moving' fish were those whose elapsed times from first detection to last were below a determined threshold, based on an analysis of the distribution of hours between first and last detections at a site. The threshold that we determined was 1 h (see "Results" section for determination of this time threshold). The use of this 1-h threshold provides a means for differentiating between fish that were clearly spending appreciable amounts of time within the detection range of a given receiver, and therefore likely influenced by the local environment, versus those fish that may instead have had a more transitory relationship to a given site. The truncated negative binomial model (truncated at zero) was used to model those fish whose elapsed times were greater than the threshold, and were understood to be 'holding.' This approach allowed us to explore the ways in which fish appear to have potentially interacted with a site, where the habitat features were presumably influential in terms of behavior.

For the binomial model, the dependent variable was the probability of holding, and for the truncated negative binomial model, it was holding time. The probability of holding is the probability that a fish holds for at least the threshold time of 1 h. Holding time is the number of hours that a fish holds, if it holds for more than 1 h. Before the analysis was conducted, we modified the potential pool of variables for multicollinearity by inspecting variance inflation factors, using a cut-off of 5 (Zuur et al. 2009). For Chinook salmon, we excluded the habitat variable LWM density; for steelhead, we excluded the temporal variable date released and the habitat variable IWM diversity.

We approached the modeling in two steps:

Step 1: Identify significant spatial and temporal variables associated with the probability of holding or holding time.

Step 2: Identify significant relationships between habitat variables and the probability of holding or holding time. Significant spatial and temporal variables identified in Step 1 were retained in the model in order to control for their effects.

During each step, variables were dropped one at a time, and likelihood ratio tests were used to compare successive models. Likelihood ratio tests with $p>0.10$ led to the variable being removed; otherwise it was retained. Variables leading to a likelihood ratio test result of $p<0.05$ were considered significant and $p>0.10$ not significant; results were considered to be inconclusive when $0.05<p<0.10$. In Step 1, spatial and temporal variables were removed. In Step 2, the spatial and temporal variables identified and retained in Step 1 were included with potential habitat variables, with habitat variables being dropped based on likelihood ratio tests. We used R software (RDCT 2009) to conduct all analyses.

Results

The proportions of tagged Chinook salmon and steelhead smolts that were detected at one or more of the sites within the study area varied, depending upon release location (Table 2). In 2009 and 2010, 2,187 acoustically tagged Chinook salmon and 1,718 acoustically tagged steelhead smolts were released (mostly by other CTFC researchers as described above). The proportions of tagged Chinook salmon and steelhead smolts detected were 0.64 and 0.43, respectively, with large variation depending on release location. Chinook salmon and steelhead detected by the receivers exhibited two distinct behavioral patterns related to their downstream movements: 1) migration through the site (i.e., moving), and 2) remaining at the site for ≥1 h (i.e., holding). We identified 1 h as the threshold between moving and holding, because the vast majority of fish that stayed less than 24 h at a site had stayed less than 1 h there; 85 % of Chinook salmon smolts and 90 % of steelhead smolts that were staying less than a day stayed for less than 1 h.

Chinook salmon

Spatial and temporal variables

Based on likelihood ratio tests, most of the spatial and temporal variables identified were significant for both probability of holding and holding time, although the "date released" variable was only significant for the

Table 2 Summary information for tagged Chinook salmon and steelhead smolts released into the Sacramento River, from December 2008 to March 2010. "Proportion detected" is the proportion of fish released that were detected at one or more sites within the study area. "Above study area" ranges from rkm 270 to 412

Study year	Release location variable	Month/Year released	No. fish released	Fork Length (mm)		Proportion detected
				Mean	Range	
Chinook salmon						
2009	Above study area	Dec 2008, Jan 2009	300	152.1	139–175	0.53
	Between Feather, American rivers	Feb, Mar 2009	500	173.5	143–218	0.36
	Study area below American River	Dec 2008, Jan 2009	384	152.0	136–180	0.94
2010	Above study area	Dec 2009, Jan 2010	306	152.5	135–176	0.37
	Study area above Feather River	Jan 2010	100	163.7	150–185	0.81
	Between Feather, American rivers	Jan, Feb 2010	597	174.9	93–206	0.85
Steelhead						
2009	Above study area	Dec 2008, Jan 2009	300	228.2	192–278	0.30
	Study area above Feather River	Jan 2009	37	210.4	190–240	0.41
	Between Feather, American rivers	Feb, Mar 2009	500	258.6	147–314	0.50
	Study area below American River	Jan 2009	62	208.6	181–234	0.84
2010	Above study area	Dec 2009, Jan 2010	300	196.1	155–238	0.14
	Between Feather, American rivers	Jan, Feb, Mar 2010	519	222.5	108–277	0.55

probability of holding (Table 3). Holding behavior was most strongly affected by flow, day/night, and distance from release location. Chinook salmon were less likely to hold at higher flows, but held longer during higher flows. Chinook salmon were much less likely to hold at night than during the day, and Chinook salmon that did hold at night held for longer periods. Finally, fish that were released farthest from the study sites were least likely to hold, and tended to hold for the shortest duration if they did hold.

Table 3 Significant spatial and temporal variables based on GLMs fit to telemetry data of Chinook salmon smolts, Sacramento River, 2009 and 2010, based on likelihood ratio tests. The dependent variables were holding time (h) or probability of holding

Variable	Category[a]	Coefficient	SE	χ^2	$\Pr(>\chi^2)$
Holding time					
Year	2010	−0.490	0.271	6.121	0.0134
log10(flow)	n/a	2.873	0.671	24.595	<0.0001
Day/night	Night	0.548	0.169	8.329	0.0039
Distance from release	n/a	−0.005	0.001	34.530	<0.0001
Days since release	n/a	0.036	0.013	8.178	0.0042
Year x Days since release	2010 x Days since release	0.067	0.024	9.497	0.0021
Probability of holding					
Year	2010	−0.296	0.115	6.627	0.0100
log10(flow)	n/a	−3.272	0.278	166.527	<0.0001
Date released	n/a	−0.005	0.002	7.856	0.0051
Day/night	Night	−0.722	0.073	96.255	<0.0001
Distance from release	n/a	−0.001	0.000	20.097	<0.0001
Days since release		0.010	0.004	5.314	0.0212
Year x Days since release	2010 x Days since release	0.056	0.009	39.338	<0.0001

[a] Reference categories for categorical variables are "2009" for Year, and "Day" for Day/night. Category = "n/a" for numeric variables

Habitat variables

One habitat variable, IWM diversity, was significant for both the probability of holding and holding time; however, other variables were only significant for one or the other. Chinook salmon had a higher probability of holding in habitats where substrate is finer, IWM diversity is lower, and dominant IWM size is larger (Table 4). Holding time was associated with greater shade, lower IWM diversity, and the absence of submerged vegetation.

Steelhead

Spatial and temporal variables

Three temporal variables, year, days since release, and the Year x Days since release interaction were significant for both steelhead probability of holding and holding time. In 2009, the longer a steelhead took to reach the study site, the less likely it was to hold at the study sites; if it did hold, it held for shorter periods. However, in 2010, the converse effects were observed (Table 5). The strongest relationships were found for days since release, tag type, and flow. The probability of holding was greater for the V9 tag type and during lower flows.

Habitat variables

One habitat variable, LWM density, was significant for both probability of holding and holding time. Steelhead had a higher probability of holding in habitats where the bank slope was steeper and LWM density was lower (Table 6). Holding time was associated with the presence of submerged vegetation and higher LWM density.

Discussion

Our study indicates that smolt holding has significant and strong associations with certain habitat features, however the habitat potentially has greater value for rearing. Young-of-the-year salmonids are known to rear in nearshore habitats in the Sacramento River (Williams 2006; McLain and Castillo 2010), however most smolts are moving rapidly towards the sea (Giorgi et al. 1997; Friesen et al. 2007; Michel 2010), and are less likely to be using nearshore habitats (Friesen et al. 2007). At the same time as this telemetry study, we conducted an electrofishing study that captured hundreds of young-of-the-year Chinook salmon in nearshore habitats but comparatively few Chinook salmon or steelhead smolts (H. T. Harvey & Associates and PRBO Conservation Science 2011). Current tagging technology does not allow us however to tag and study smaller young-of-the-year fish that are likely to be using specific habitat features for rearing. Emerging technologies such as the Juvenile Salmon Acoustic Telemetry System (McMichael et al. 2010) may eventually allow acoustic telemetry and tagging of smaller Chinook salmon and steelhead, but even these tags are currently too large for fish smaller than 90 mm in length. Nonetheless, studies such as ours provide value by describing smolt downstream movement patterns that can aid in understanding the potential benefits of bank rehabilitation projects for holding.

Table 4 Significant habitat variables based on GLMs fit to telemetry data for Chinook salmon smolts in Step 2, Sacramento River, 2009 and 2010. The dependent variables were holding time (h) or probability of holding

Variable	Coefficient	SE	χ^2	Pr(>χ^2)
Holding time				
% Shade	0.689	0.229	9.604	0.0019
IWM diversity	−2.238	0.489	17.404	<0.0001
Submerged vegetation	−1.022	0.309	7.791	0.0052
Probability of holding				
% cobble/boulder	−0.747	0.131	32.588	<0.0001
IWM diversity	−0.678	0.272	6.214	0.0127
Dominant IWM size	0.207	0.025	73.392	<0.0001
Submerged vegetation	−0.279	0.154	3.283	0.0700

Table 5 Significant spatial and temporal variables based on GLMs fit to telemetry data for steelhead smolts, Sacramento River, CA, 2009 and 2010, based on likelihood ratio tests. The dependent variables were holding time (h) or probability of holding

Variable	Category[a]	Coefficient	SE	χ^2	Pr(>χ^2)
Holding time					
Year	2010	0.795	0.196	17.772	<0.0001
Days since release	n/a	−0.025	0.005	21.658	<0.0001
Year x Days since release	2010 x Days since release	0.041	0.010	16.832	<0.0001
Probability of Holding					
Year	2010	−0.348	0.124	7.799	0.0052
log10(flow)	n/a	−1.758	0.347	27.135	<0.0001
Day/night	Night	−0.236	0.094	6.378	0.0116
Distance from release	n/a	−0.003	0.001	20.757	<0.0001
Days since release	n/a	−0.019	0.003	42.084	<0.0001
Tag type	V9	1.130	0.178	39.125	<0.0001
Year x Days since release	2010 x Days since release	0.027	0.005	24.121	<0.0001

[a] Reference categories for categorical variables are “2009” for Year, “Day” for Day/night. Category = “n/a” for numeric variables

Based on this study’s data, we can not discern steelhead that are residualizing (staying non-anadromous due to the halting of smoltification) from those that are holding. Therefore, longer holding time values could potentially be associated with steelhead that are residualizing. However, only 10 % of steelhead holding times exceeded 1 day.

The movement patterns of migrating Chinook salmon and steelhead smolts appear to be influenced by large scale spatial and temporal factors, as well as by local habitat features. Both species had similarly strong relationships with spatial and temporal variables release location and flow. Chinook salmon exhibited relatively strong relationships with habitat, particularly large wood and shade, whereas steelhead exhibited much weaker relationships with habitat.

Commonalities

One of the strongest influences on downstream migration of smolts is distance from release location. For both species, fish released farther above the study sites were more likely to migrate quickly (that is, less likely to hold) than those released closer to the study sites. Similarly, Michel (2010) found that fish released farther upstream had faster movement rates. In addition, holding time was greater for those released closer to the study sites, because they likely needed to acclimate prior to migration. Michel (2010) found evidence of acclimatization following release of tagged hatchery Chinook salmon, based on increased holding with increased downstream distance from the source hatchery. Acclimatization may have included the time for

Table 6 Significant habitat variables based on GLMs fit to telemetry data for steelhead smolts in Step 2, Sacramento River, CA, 2009 and 2010. The dependent variables were holding time (h) or probability of holding

Variable	Estimate	SE	χ^2	Pr(>χ^2)
Holding time				
LWM density	1.789	0.843	4.386	0.0362
Submerged vegetation	1.078	0.426	6.470	0.0110
Probability of holding				
Bank slope	−0.039	0.020	3.924	0.0476
LWM density	−1.190	0.446	7.164	0.0074

tagged fish to recover from surgery; however, all members of the CFTC followed similar tagging protocols as described in this study, which aimed to minimize effects due to tagging.

The strong relationships with flow for both species suggest that flow is one of the strongest environmental cues for downstream migration. One of the primary directional cues for migrating juveniles is flow (Williams 2006). Strong relationships between flow and the movement of smolts have been documented in the Sacramento River (Michel 2010), the Columbia River, Washington (Giorgi et al. 1997), and the Willamette River, Oregon (Friesen et al. 2007). In our study, both species exhibited strong relationships with flow that are consistent with the idea that most smolts are less likely to hold in faster water currents (Williams 2006).

Chinook salmon

Even though most smolt movement patterns are dominated by downstream movement, in the Sacramento River, there are clearly times when Chinook salmon smolts hold during their downstream migration (this study; Williams 2006; Burau et al. 2007). Our study indicates that Chinook salmon smolts tend to move more at night and hold more during the day, when visual predators such as birds and introduced predatory fish are expected to have greater success in preying on juvenile fish. Other researchers have also found that movement is more frequent at night for juvenile Chinook salmon (Southard et al. 2006; Burau et al. 2007; Michel 2010; Smith et al. 2010; Chapman et al. 2012). There are also other conditions in the lower Sacramento River that may potentially be providing cover from predators, such as turbidity; this was hypothesized by Michel (2010), based on results from his telemetry study showing weaker relationships with day/night in a downstream direction. He suggested that fish in the lower Sacramento River did not need to move strictly at night due to decreasing predation pressure with increased turbidity levels. However, our study in the lower Sacramento River suggests a strong tendency for Chinook salmon to migrate at night.

Since there is some need for holding during downstream migration, and Chinook salmon smolts tend to hold during the day, managers involved with habitat rehabilitation or improvement should consider managing habitat features that provide cover from predators. In large rivers generally, shade and wood cover have been indicated as important for juvenile Chinook salmon and steelhead. A positive association between juvenile Chinook salmon and steelhead and wood cover was identified in the Skagit River (Beamer and Henderson 1998). In the Feather River, a tributary to the Sacramento River, Cavallo et al. (2003) found a positive relationship between juvenile Chinook salmon and shade, though their study was based on smaller fish in a smaller river. Larger wood and shade may be important habitat features that provide cover from both avian and fish predators.

In addition to cover, a fish that is holding is likely to do so in areas where the water velocities are lower to minimize metabolic costs. Two habitat features indicative of decreased velocity or velocity refuge, large wood and finer substrates, were found to be strongly associated with holding duration in our study. The presence of velocity refuges related to structure or bathymetric features is a likely factor in where a fish holds (Burau et al. 2007). Chinook salmon smolts held in velocity refuges as long as an entire day in the Sacramento River at Clarksburg Bend (also located in our study area) (Burau et al. 2007). Based on modeling and empirical data, some evidence suggests that downstream travel rates are largely governed by a fish's swim speed and mean water velocities (Blake and Horn 2003), with greater water velocities resulting in faster travel rates. Therefore, if a fish can find refuge from higher water velocities, it may hold longer at a site. The qualities of habitat features that provide velocity refuge (such as large woody material) appear to influence whether and for how long a fish holds.

Steelhead

Relatively little is known about how steelhead migration patterns differ from other anadromous salmonid species, however, steelhead appear to respond strongly to large-scale environmental cues (Phil Sandstrom, UC Davis, 24 January 2011, pers. comm., unpubl. data) and only rarely utilize nearshore habitats (H. T. Harvey & Associates and PRBO Conservation Science 2011). Based on an active tracking study conducted in our study area, tagged steelhead would move out of the middle of the channel towards the bank, and along the bottom, holding during incoming tides and moving with the outgoing tide (Phil Sandstrom, UC Davis, 24

January 2011, pers. comm., unpubl. data). Our electrofishing study (H. T. Harvey & Associates and PRBO Conservation Science 2011) rarely captured steelhead smolts in the shallow nearshore habitats where habitat features were characterized. Based on these two studies, steelhead smolts may move closer to banks when they are holding, but appear to be utilizing bottom features at the transition from the main channel to shallower water nearshore habitat, which would result in weaker nearshore habitat relationships for steelhead.

Among the large-scale variables that appear to strongly affect steelhead holding was the number of days since release, perhaps due to acclimatization near the release location. Hatchery steelhead smolts released above the study area had a greater number of days in the river before reaching the study area, and were moving rapidly to the ocean. However, there was evidence of the opposite movement pattern with days since release in 2010. Interannual variability in flows may have affected the relationship in 2010; on average, there were higher flows during January and February of 2010 compared to 2009 (Shahcheraghi and Chu 2011).

Conclusion

In summary, the influences of certain spatial and temporal factors on Chinook salmon and steelhead smolt movement are considerably greater than nearshore habitat features, and should not be ignored. However, habitat features (e.g., large woody material sufficient to create velocity breaks, and overhead shade) that offer velocity refuge and cover from predators for Chinook salmon smolts should be considered when conducting nearshore bank restoration or rehabilitation projects. Nearshore habitat features are probably equally valuable, if not moreso, for smaller juvenile salmonids that are rearing in these shallow water habitats.

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