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Physical Characteristics Influencing Nearshore Habitat Use by Juvenile Chinook Salmon in the Sacramento River, California

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Abstract

Urban and agricultural development has resulted in drastically modified riverine corridors that are often considered to be detrimental to the recovery of anadromous salmonid populations. Although mitigation features (e.g., large wood and shallow-water areas) are frequently incorporated in flood control infrastructure to offset the impacts of stream-bank stabilization, little is known regarding their effectiveness and the habitat characteristics associated with enhanced nearshore rearing conditions in large rivers. We evaluated two measures of habitat use by emigrating juvenile Chinook Salmon *Oncorhynchus tshawytscha* relative to different shoreline types (rock revetment [riprap], mitigated, and natural) and analyzed associations between environmental characteristics and habitat occupancy using a large number of presence/absence samples in the lower Sacramento River, California. We found both measures of habitat use to be significantly higher at natural shorelines and those including mitigation features than at shorelines consisting predominantly of rock revetment. A predictive logistic regression model suggested that the density of woody material and inundated terrestrial vegetation, depth, and substrate type significantly affected habitat occupancy. Despite a moderate predictive capability (62% of correctly classified records in a leave-one-out simulation), the model was useful in identifying habitat characteristics associated with significantly increased habitat use in this large, low-gradient river, most notably the presence of instream cover (wood or vegetation), gently sloping streambanks, fine substrate, and variable nearshore current velocity. Conversely, habitat occupancy by juvenile Chinook Salmon diminished with large, rocky substrate and increased depth, characteristics favored by introduced predatory Smallmouth Bass *Micropterus dolomieu*. This study illustrates the value of incorporating mitigation features and identifies characteristics that enhance habitat use by emigrating juvenile Chinook Salmon.

Urban and agricultural development along large, salmon-bearing streams of the Pacific Northwest has resulted in the need for and construction of extensive flood control

features, such as levees and weirs, to protect valuable agricultural lands, public infrastructure, and private property. As a consequence, nearshore riverine habitat, which is

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particularly important for the juvenile stages of anadromous Chinook Salmon *Oncorhynchus tshawytscha* (e.g., Murphy et al. 1989; Beechie et al. 2005; McLain and Castillo 2009), has been extensively modified. However, the effects of bank protection features—particularly rock revetment armoring (riprap)—on habitat use by this species remain poorly understood (Schmetterling et al. 2001).

The rarity of investigations pertaining to habitat use by juvenile salmonids in large rivers is likely due to the challenging sampling environment, as high flows and low visibility limit the applicability of visual (snorkel) surveys for assessing habitat use. Shoreline armoring using rock revetment can be one of the driving factors determining localized fish assemblages (e.g., Schiemer and Spindler 1989; Jurajda et al. 2001) and may locally increase the diversity of physical habitat, as large rocks provide more complex substrate over sand and silt, which comprise the dominant substrate in large, low-gradient rivers (Gordon et al. 1992). Shoreline armoring is also associated with reduced riparian vegetation coverage and related instream habitat features, such as exposed roots, undercut banks, and naturally deposited woody material, which are considered important constituents of high-quality habitat for juvenile salmonids (Schmetterling et al. 2001). Furthermore, introduced species, such as Smallmouth Bass *Micropterus dolomieu*, are often found in high densities along riprap habitats (Tiffan et al. 2016) and may exert predation pressure on juvenile salmonids (Fritts and Pearsons 2004; Naughton et al. 2004), further hampering efforts at population recovery.

Research on nearshore habitat use by subyearling Chinook Salmon in low-velocity impoundments on the Columbia River suggests that the probability of habitat occupancy by subyearlings is higher along natural, unaltered shoreline habitat compared to those armored with rock revetment (Garland et al. 2002). In addition, temperature, current velocity, substrate, and lateral bank slope are thought to affect habitat use by juvenile Chinook Salmon (Tiffan et al. 2006, 2016). For lotic reaches of large, main-stem rivers, however, information on habitat use by juvenile Chinook Salmon and how it pertains to modified streambanks is limited, particularly outside of the Columbia River basin. Nearshore habitat is considered important for the rearing of juvenile Chinook Salmon (i.e., periods of residency) as well as during downstream dispersal and migration (Connor et al. 2003). Although rearing juvenile Chinook Salmon may have the ability to find and remain in habitats with preferable characteristics for some time, emigrating juveniles are confined to main-stem reaches of large rivers in highly developed areas where the shoreline often consists of a patchwork of distinct habitats, arguably with different levels of quality. Therefore, it is important to understand how this species uses such modified habitat, particularly if the opportunity exists to incorporate

features that may enhance habitat value by future river-bank modification.

One of the large rivers affected by extensive shoreline modification is the Sacramento River. It is California's largest salmon-producing river and is unique across the geographic range of Chinook Salmon by virtue of its four temporally and genetically distinct salmon runs (Moyle 2002). A large part of the reach that remains accessible to anadromous species (below Keswick Dam at river kilometer [rkm] 490) has been modified for flood conveyance through the construction of levees and bypasses, often through extensive armoring with rock revetment to protect densely populated areas and one of the most economically valuable agricultural production areas in the world. Juvenile salmonids that are produced in the main-stem Sacramento River (spawning only occurs upstream of rkm 350) and those originating from numerous salmon-bearing tributaries rear in or migrate through the lower main stem primarily during late winter and spring. Due to the diversity in reproductive timing and life history strategies among the distinct salmon runs, some juvenile Chinook Salmon may be present in the lower main stem at any time of the year (Williams 2006).

Although rock revetment has long been the predominant type of bank protection on the Sacramento River and elsewhere, more recent alterations to the flood control infrastructure often include habitat features that are intended to mimic natural stream characteristics and mitigate habitat loss. Engineered habitat features often consist of deliberately placed and anchored large woody debris and contoured shallow-water areas, which are generally expected to ameliorate the loss of natural riverine habitat and enhance conditions for juvenile anadromous salmonids. Recent (post-2006) levee repair on the Sacramento River included the implementation of designs that provided an alternative to rock revetment and resulted in the opportunity to study habitat use by juvenile salmonids at rock revetment, mitigated, and natural shorelines. This allowed us to (1) evaluate whether engineered shorelines incorporating presumably beneficial habitat features increased habitat use by the target species as compared to banks consisting exclusively of rock revetment and (2) investigate which particular habitat characteristics significantly affected the probability of occupancy. The objectives of this study were to (1) investigate potential differences in habitat use between shoreline characterized by rock revetment, mitigated levee designs, and natural riverbanks; (2) evaluate which microhabitat characteristics affect habitat use by juvenile Chinook Salmon; and (3) formulate predictive models that can provide information regarding the suitability of future streambank modification for juvenile Chinook Salmon. As a consequence, this study can serve to identify features that should be considered for inclusion—or, conversely, features that should be

avoided—in future bank stabilization and restoration activity, given localized hydraulic and water level elevation constraints. Such consideration could serve to enhance the habitat value for juvenile Chinook Salmon when the opportunity for mitigation along flood control infrastructure exists.

METHODS

Study Area

The Sacramento River is a large river (mean annual flow = 800 m³/s; watershed area = 70,000 km²) that drains much of interior northern California and flows in a southerly direction into San Francisco Bay and ultimately the Pacific Ocean. The main-stem Sacramento River and its larger tributaries have been extensively modified through construction of large storage reservoirs and levees, resulting in a laterally constrained riparian corridor along predominantly steep banks in the study area. The Sacramento River and its tributaries support California's largest fall-run Chinook Salmon population in addition to three other, temporally distinct Chinook Salmon runs (spring-, winter-, and late-fall runs). With the exception of large discharge events (flows greater than approximately 2,000 m³/s) that provide favorable off-channel rearing habitat by inundating floodplains (in about 60% of years; Sommer et al. 2001; Limm and Marchetti 2009), juvenile Chinook Salmon are confined to the main-stem Sacramento River for rearing and during out-migration. Sampling locations included in this study were located between rkm 65 and rkm 150 (Figure 1). In this area, depth in the thalweg typically exceeds several meters, and the river is between approximately 90 m (upstream) and 170 m (downstream) wide, with a gradient of less than 0.05%.

Field Sampling

Sampling locations.—Due to greatly fluctuating water levels in the study reach, an a priori stratification into distinct habitats was not possible. As a consequence, we relied on multiple sampling events during spring 2013 (January 25–March 13; $n = 6$) and spring 2014 (February 11–April 10; $n = 5$), which were timed to coincide with the peak abundance of juvenile fall-run Chinook Salmon and were intended to encompass a wide range of conditions and to include representative combinations of habitat parameters (Snider and Titus 2000; Williams 2006). During each event, we sampled the same 16 distinct locations (rkm 65–150; Figure 1) that were selected to be representative of one of three general shoreline categories most commonly encountered in this reach: (1) rock revetment sites ($n = 3$), which are shorelines armored with riprap but lacking additional features to enhance habitat; (2) mitigated sites ($n = 9$), which, despite including slight

variations in design, are characterized by contoured, gradually sloping banks, substrate consisting of soil or fine sediment, deliberately planted native riparian vegetation, and anchored or embedded large woody debris; and (3) natural sites ($n = 4$), which have not been engineered, are devoid of rock revetment, and are dominated by native, naturally established vegetation.

An illustrative and representative example of each shoreline category is shown in Figure 2. Sampling reaches were defined by clear breaks in habitat characteristics and varied between 107 and 216 m in length (mean length = 179 m). The length of individual sample units remained constant throughout the study period.

Occupancy sampling.—We sampled the nearshore fish community by boat electrofishing with a point sampling approach (Persat and Copp 1990; Garland et al. 2002; Tiffan et al. 2002, 2006). Sampling occurred only during daylight hours, when fish are expected to be active and feeding in the water column (Edmundson et al. 1968; Venditti and Garland 1996; Tiffan et al. 2010). The electrofishing boat, equipped with two 80-cm-diameter umbrella anode arrays, was driven toward the bank with the electrodes activated (for 10–15 s; 2 A; 60-pulses/s DC) and then proceeded upstream, making multiple incursions until the site boundary was reached. Point spacing ranged between 10 and 20 m depending on the overall length of the sampling unit but always exceeded 10 m so as not to disturb fish at the adjacent sampling point, thus maintaining independence of occupancy status between point samples while obtaining a sufficiently large sample size (Beechie et al. 2005). At each sampling point, the presence or absence of juvenile Chinook Salmon and other species was determined from reviewing video and audio recordings of a camera mounted on the bow rail of the electrofishing boat, which included netted fish as well as definitively identified observed fish that evaded capture. This approach was used to streamline the field component of this study and permitted a standardized field of view for classifying the density of instream cover (see *Habitat characteristics* section).

We did not distinguish occupancy between single and multiple individuals for logistic regression analysis, but we did record the number of observed Chinook Salmon for determining the mean number of individuals per sampling point (see Data Analysis). After completion of sampling at a particular site, all captured fish were measured to the nearest millimeter (FL), but no point-specific length measurements of captured fish were obtained. Although the Sacramento River supports four temporally distinct runs of Chinook Salmon and there is substantial overlap in out-migration timing between the different races, we did not attempt to classify sampled juveniles to their respective race, as classification according to size and capture date is associated with great ambiguity (Harvey et al. 2014).

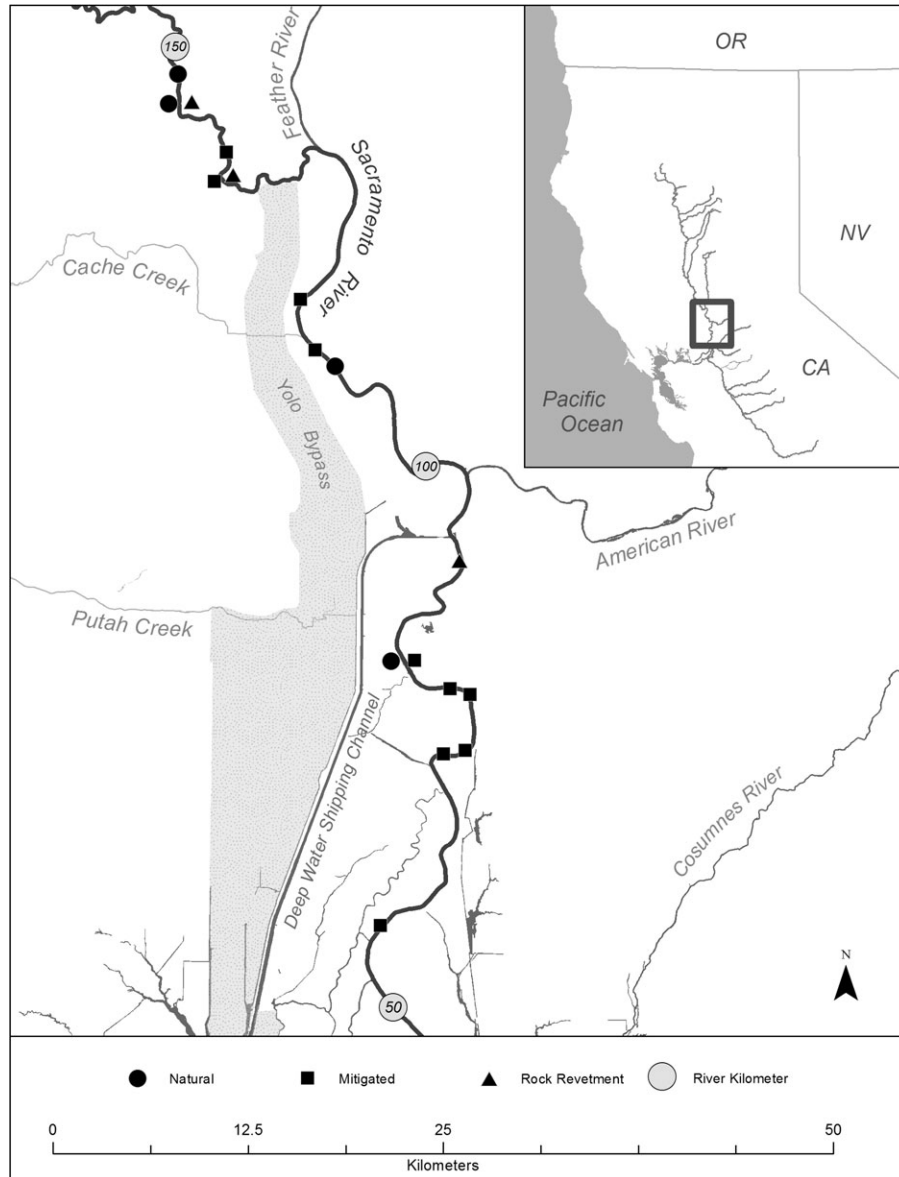


FIGURE 1. Sampling locations (rock revetment, mitigated, and natural shorelines) on the lower main-stem Sacramento River, California. Inset depicts the study area's location within the state.

Habitat characteristics.—At each sampling point, a weighted piece of highly visible flagging was placed on the bank near the water's edge to mark the sampling point for a second crew of technicians who then measured the various habitat characteristics of interest. We measured current velocity (nearest 0.01 m/s) by using a portable digital velocity meter (HACH FH950; based on a 10-s measuring interval, measured at 80% of water depth [or at 80 cm below the surface if depth exceeded 1 m]). We measured velocity and depth 1.5, 3.0, and 4.5 m from the water's edge and then used these measurements to calculate current gradient and bank slope (intercept forced through the origin) using linear regression. We categorized the

dominant substrate at each sampling point as fines (sand/silt), cobble/gravel (rounded; diameter ~100 mm), or rock (angular; diameter generally >200 mm) based on probing the bottom with a stadia rod. Substrates of intermediate sizes were rarely observed in the study reach; even when intermediate substrates were present, one of the three categories listed above remained the dominant substrate type. At each site, mid-channel temperature (°C) was recorded immediately prior to sampling to determine the relative differences in water temperature between the main channel and each sampling point. In addition, cover in the form of vegetation (inundated terrestrial vegetation) and woody material was qualitatively categorized according to density

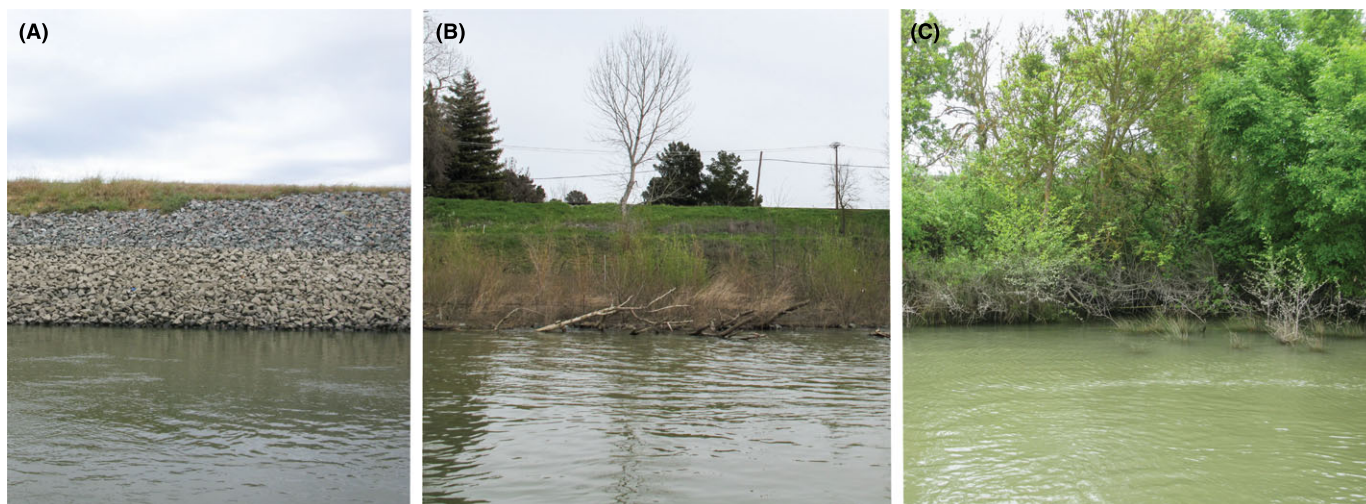


FIGURE 2. Representative illustration of the different shoreline categories sampled in this study: (A) rock revetment, (B) mitigated, and (C) natural.

for a standardized area at each sampling point by reviewing video footage recorded by a camera mounted on the bow rail of the electrofishing boat during sampling (categories: absent [0%], sparse [1–10%], medium [11–50%], and dense [>50%]). Standardized area was determined from the field of view of the video recording at the time when the umbrella electrodes reached the water's edge.

Data Analysis

Shoreline category.—Differences in habitat occupancy by juvenile Chinook Salmon for the different shoreline categories (revetment, mitigated, and natural) were compared using two distinct metrics: the mean proportion of occupied sampling points (over all sampling events) and the mean number of individuals per sampling point. Due to spatial and temporal nesting (multiple sites per category, each visited 11 times), we used generalized mixed models to evaluate the effects of shoreline category and sampling event (Poisson distribution for the mean number of juveniles; binomial distribution for the proportion of occupied points).

Point occupancy and model development.—We used point occupancy and habitat data, which were collected over the course of two spring sampling seasons (2013 and 2014) and encompassed a broad range of inundation levels and habitat characteristics, to develop a logistic regression model to identify factors that influenced the probability of habitat occupancy by juvenile Chinook Salmon. We withheld 450 randomly selected observations from the data set for later model validation (see *Model validation*) and used the remaining 2,000 observations for model development. Variables included in model selection, their type (design/numeric), and their definitions (if applicable), are summarized in Table 1. The linearity between each predictor

variable and its logit was evaluated using the methods described by Demaris (1992). If the relationship was highly nonlinear, it was modeled as a design variable.

To identify habitat characteristics that influenced the probability of habitat occupancy by juvenile Chinook Salmon (P_i), we performed univariate logistic regression for each habitat variable. This probability can be expressed as the logit function,

$$P_i = \frac{e^{g(x)}}{1 + e^{g(x)}}$$

where $g(x)$ represents a linear combination of parameter estimates of the predictor variables. We then used a likelihood ratio test to establish whether a particular single-variable model differed from the null (constant) model at $P = 0.25$. Variables that were identified as significant using this criterion were included in subsequent multivariate model fitting (Hosmer and Lemeshow 2000).

To fit the most appropriate multivariate logistic regression model, we used a forward model selection approach, beginning with a null model (specified as a constant probability of point occupancy) and then adding variables identified in the previous step one at a time based on a combination between a low Akaike's information criterion (AIC) score and maximum rescaled R^2 . The fit of the resulting logistic regression model was assessed using Hosmer–Lemeshow goodness-of-fit statistics (high, nonsignificant P -values are indicative of good model fit; Hosmer and Lemeshow 2000).

Model validation.—We tested the predictive capabilities of the juvenile Chinook Salmon model by using an unbiased jackknife routine. To apply this method, each observation was sequentially removed from the data set, and

TABLE 1. Summary of environmental variables measured in association with point presence/absence records of juvenile Chinook Salmon in the Sacramento River, California.

Variable	Description	Variable type	Categories
Shoreline type	Different shoreline categories	Design	Rock revetment (reference), mitigated, or natural
Shade	Shaded water surface at sampling point	Design	Absent (reference) or present
Substrate	Classification of dominant substrate based on probing with stadia rod	Design	S (silt, sand, or other fine substrate; reference), R (rock), or G (gravel)
Instream woody material	Abundance of emergent woody material	Design	Absent (reference), sparse (1–10%), medium (10–50%), or dense (>50%)
Inundated terrestrial vegetation	Abundance of emergent vegetation	Design	Absent (reference), sparse (1–10%), medium (10–50%), or dense (>50%)
Temperature difference	Difference (°C) between mid-river and sample point	Design	Same (within 0.1°C; reference), cool (–2.0°C to –0.1°C), elevated (+0.1°C to +0.5°C), or warm (+0.5°C to +2.0°C)
Mean depth	Mean depth (m)	Continuous	NA
Slope	Bank slope, estimated by linear regression	Continuous	NA
Mean velocity	Mean current velocity (cm/s)	Continuous	NA
Velocity gradient	Gradient of current velocity, estimated by linear regression	Continuous	NA

the model parameters were re-estimated using the remainder of the data set. The resulting model parameters were then applied to classify the excluded occupancy record, and the process was repeated for each observation on the data set. The resulting classifications were tabulated and compared to observed, actual values to determine the percentage of correctly classified records. As classification favors assignment to larger groups, we used Cohen's kappa (κ) statistic as a chance-corrected measure of predictive accuracy (i.e., a measure of correct classification/predictive improvement over random classification; Titus et al. 1984).

We also used the final regression model to classify the 450 observations that were withheld from the data set for model development. Again, predicted and actual occupancy points were tabulated to evaluate the performance of the model in predicting the occupancy of juvenile Chinook Salmon in nearshore riverine habitat.

All statistical analyses were performed using the program R (R Core Team 2017).

RESULTS

Sampling

Over the course of 11 sampling events in 2 years, we collected a total of 2,450 point-specific records of juvenile Chinook Salmon occupancy and associated habitat

characteristics (revetment shoreline: $n = 526$; mitigated shoreline: $n = 1,278$; natural shoreline: $n = 646$). We detected the presence of juvenile Chinook Salmon at 608 (25%) sampling points, although the proportion of occupied points varied among sampling events and ranged from 10% to 39%. Juvenile Chinook Salmon ranged in FL from 29 to 167 mm (median = 44 mm; mean = 49 mm). We acknowledge that based on their size, some stream-type yearling Chinook Salmon (Healey 1991) juveniles were included in our sample; however, because no size-specific information was collected for each sampling point, we grouped all juvenile individuals for purposes of subsequent analysis. Mid-channel water temperature ranged from 7.2°C to 19.7°C (mean = 12.8°C), while point-specific temperatures ranged from 7.2°C to 20.1°C (mean = 12.9°C). Conductivity ranged from 113 to 274 $\mu\text{S}/\text{cm}$ (mean = 179 $\mu\text{S}/\text{cm}$). Ranges of values or frequencies of occurrence (for categorical variables) for each shoreline category are summarized in Tables 2 and 3.

Shoreline Category

Along rock revetment shoreline, the mean number of juvenile Chinook Salmon per sampling point was 0.23 (95% confidence interval [CI] = 0.14–0.32) compared to 0.66 (95% CI = 0.56–0.75) at mitigated shoreline and 0.83 (95% CI = 0.62–1.03) at natural shoreline (Figure 3). Differences in mean abundance between the three categories were significant ($P \leq 0.01$).

TABLE 2. Summary of categorical variables and their frequencies of occurrence according to different shoreline types (revetment, mitigated, and natural) in the Sacramento River. The percentage of occupied points refers to sampling points in the respective category where juvenile Chinook Salmon were observed.

Categorical variable	Revetment		Mitigated		Natural	
	<i>N</i>	% occupied	<i>N</i>	% occupied	<i>N</i>	% occupied
Shade						
Absent	522	13.79	1,195	26.61	629	29.57
Present	4	25.00	83	31.33	17	29.41
Substrate						
Rock	395	14.43	922	24.19	2	50.00
Sand/silt	88	13.64	353	33.99	643	29.55
Gravel	43	9.30	3	33.33	1	0.00
Instream woody material						
Absent	513	13.65	771	22.96	219	28.77
Sparse	12	25.00	402	34.83	239	27.62
Medium	0	NA	82	28.05	81	45.68
Dense	1	0.00	23	17.39	107	23.36
Inundated terrestrial vegetation						
Absent	413	10.90	996	24.90	479	26.93
Sparse	41	29.27	154	37.01	71	43.66
Medium	5	60.00	97	28.87	62	35.48
Dense	67	19.40	31	35.48	34	26.47
Water temperature difference						
Cool	51	11.76	63	15.87	33	21.21
Same	212	12.74	494	31.58	324	25.62
Elevated	263	15.21	657	23.59	259	36.68
Warm	0	NA	64	35.94	30	20.00

TABLE 3. Summary of numeric variables and their ranges (minimum, maximum) according to different shoreline types (revetment, mitigated, and natural) in the Sacramento River.

Numeric variable	Revetment		Mitigated		Natural	
	Mean	Min, max	Mean	Min, max	Mean	Min, max
Mean depth (m)	1.26	0.67, 2.03	1.08	0.19, 2.43	1.23	0.22, 4.06
Bank slope	0.42	0.23, 0.66	0.36	0.06, 0.76	0.40	0.08, 1.25
Mean velocity (cm/s)	19.93	0.10, 40.64	11.83	0.00, 58.32	15.83	0.20, 59.13
Velocity gradient	6.61	0.22, 13.57	4.01	0.09, 19.17	5.33	0.15, 19.42

The percentage of points occupied by juvenile Chinook Salmon was 14.3% (95% CI = 10.9–17.6%) at rock revetment shorelines, 27.2% (95% CI = 24.5–29.8%) at mitigated shorelines, and 30.3% (95% CI = 26.3–34.3%) at natural shorelines (Figure 3). Differences in the proportion of occupied points were significant ($P < 0.01$).

Point Occupancy and Model Development

Of the all variables included in the univariate analyses (Table 1), only the categorical predictor “shade” was not

included in the final multivariate model fitting process. Additionally, we did not include rkm as a potential predictor variable, as the intent of this investigation was to evaluate the effect of shoreline category and microhabitat variables on juvenile Chinook Salmon habitat use. Exploratory analysis revealed that rkm was a significant predictor of habitat occupancy, which was expected due to two large tributaries with substantial natural and hatchery production entering the Sacramento River within our study reach (the Feather and American rivers; Figure 1).

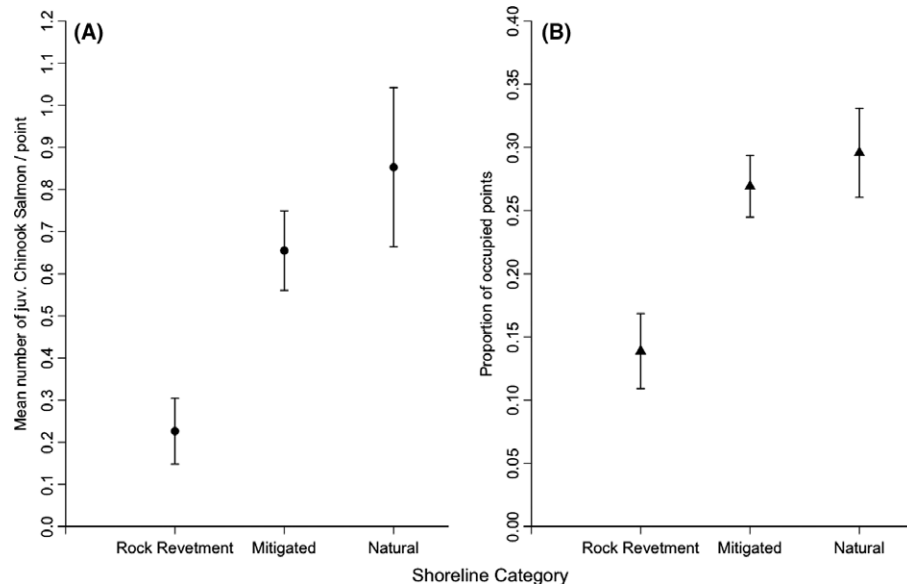


FIGURE 3. Mean (A) number of juvenile Chinook Salmon per sampling point and (B) proportion of occupied points along different shoreline categories based on a cumulative 2,450 samples collected during 11 repeated visits to Sacramento River sites characterized by rock revetment ($n = 3$), mitigated ($n = 9$), and natural ($n = 4$) shorelines in spring 2013 and 2014. Vertical bars indicate 95% confidence intervals.

As a consequence, juveniles are more abundant (increased occupancy) in the downstream section of the study reach, yet this increase is not attributable to differences in habitat use.

Of the remaining variables, the categorical predictors of density of instream woody material, density of inundated terrestrial vegetation, substrate, and temperature difference (between a sampling point and mid-channel) and the continuous predictor variables of bank slope, mean velocity, and velocity gradient were retained in the final predictive model for juvenile Chinook Salmon (Table 4).

Sparse levels of instream woody material increased the probability of occupancy by nearly 70% over locations where wood was absent; a medium density of wood material increased occupancy probability by 124%. A high density of woody material did not significantly influence the probability of habitat occupancy. All levels of inundated terrestrial vegetation were associated with a higher probability of occupancy than the absence of vegetation, and sparse terrestrial vegetation was identified as increasing the chance of habitat occupancy the most (by 127%). Hard substrate was associated with a significant reduction in occupancy probability (–27% for rock; –83% for gravel) compared to fine substrate (sand or silt). The temperature difference between mid-channel and the shoreline sampling point significantly affected occupancy probability only when temperatures at the sampling point were cooler (chance of occupancy was reduced by 48.5%).

The continuous variables included in the model all significantly affected occupancy probability. The regression

TABLE 4. Summary of coefficients of the final logistic regression model for nearshore riverine habitat occupancy by juvenile Chinook Salmon. Reference categories for the categorical predictors are described in Table 1 (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variable	Regression coefficient	SE	Odds ratio
Intercept	–0.445	0.178	
Instream woody material (reference: absent)			
Sparse	0.521***	0.121	1.683
Medium	0.804***	0.203	2.235
High	0.038	0.253	0.039
Inundated terrestrial vegetation (reference: absent)			
Sparse	0.818***	0.158	2.267
Medium	0.572**	0.201	1.771
High	0.590*	0.248	1.804
Substrate (reference: silt, sand, or other fine substrate)			
Rock	–0.308**	0.113	0.735
Gravel	–1.775**	0.632	0.169
Temperature difference (reference: same)			
Cool	–0.664*	0.280	0.515
Elevated	–0.069	0.113	0.934
Warm	0.060	0.262	1.062
Bank slope	–1.986***	0.443	0.137
Mean velocity	–0.082*	0.037	0.921
Velocity gradient	0.234*	0.118	1.264

coefficients for bank slope (change in depth [m] per meter of distance from the bank) and mean current velocity (cm/s) were strongly negative, indicating a substantial decrease in occupancy probability at steep banks/shorelines and areas with faster currents. Velocity gradient (change in current speed [cm/s] per meter of distance from shore), in contrast, was positively associated with habitat occupancy, indicating a preference for habitats with diverse hydraulic conditions (slow current in proximity to fast current velocities).

The final model had an AIC value of 2,159 (null model: AIC = 2,260). The Hosmer–Lemeshow statistics indicated that the model fit the data well ($P = 0.82$). Coefficients for the juvenile Chinook Salmon model are summarized in Table 4.

Chinook Salmon Model Validation

The jackknife evaluation procedure resulted in overall 61.8% correct classification. Cohen's κ indicated that the occupancy predictions by the model constituted a slight improvement over random classification ($\kappa = 0.19$; $P < 0.001$). Error rates of omission (occupied habitat despite predicted absence) and commission (unoccupied habitat despite predicted presence) were 38.3% and 38.2%, respectively.

Of the 450 occupancy records that were withheld from the data set prior to model fitting for validation, 47.6% were classified correctly. Cohen's κ indicated that the occupancy predictions by the final model constituted an improvement over random classification ($\kappa = 0.22$; $P = 0.029$). Error rates of omission and commission were 31.7% and 38.7%, respectively.

DISCUSSION

The results presented herein show that habitat use by juvenile Chinook Salmon was significantly higher at natural and mitigated shorelines in the lower reaches of the Sacramento River than at shorelines consisting of rock revetment (Figure 3). This result mirrors the findings of Garland et al. (2002) in low-velocity impoundments on the Columbia River, where the probability of habitat occupancy by this life stage was higher along unaltered shoreline habitat as compared to those armored with rock revetment. Similarly, in the Sacramento–San Joaquin Delta, downstream of our study reach, Chinook Salmon fry were found in lower densities over revetment substrate than over sand or mud substrate (McLain and Castillo 2009). In the present study, both measures of habitat use—the mean proportion of occupied points and mean number of juvenile Chinook Salmon per sampling point—were highest along natural shoreline. This finding indicates that engineered flood control features can at least partially offset the loss in habitat quality associated with rock

revetment shoreline armoring. Incorporating particular habitat features in bank protection structures can therefore significantly enhance rearing and migratory habitat for juvenile Chinook Salmon. However, to deliberately include features that promote habitat use by emigrating and rearing Chinook Salmon, it is important to define the habitat features that are associated with increased occupancy.

Logistic regression is frequently applied in investigations on the importance of various habitat variables in predicting fish occupancy (Beauchamp et al. 1992; Knapp and Preisler 1999; Tiffan et al. 2002, 2006) and was useful in determining influential habitat features in the Sacramento River. The performance of the model established herein was marginal in predicting point occupancy using the jackknife validation and when applied to the data set that was withheld for model validation. Resulting error rates are partially attributable to the greatly differing overall abundances (occupancy frequencies) between sampling events (11 sampling events over 2 years; occupancy range = 0.10–0.39). Although juvenile Chinook Salmon can be found in the study reach at any time of the year owing to the diverse life histories exhibited by the four races of Chinook Salmon in the Sacramento River, abundance within the reach peaks in late winter and early spring (January–April) and is strongly affected by rainfall-driven increases in discharge (USFWS 1997). Juvenile Chinook Salmon are expected to migrate through the study reach rather quickly and do not rear for extended periods of time. Studies using (yearling) late-fall-run Chinook Salmon indicate migration rates between approximately 30 km/d (Michel et al. 2012) and over 60 km/d (McNair 2015). Residence time of subyearling Chinook Salmon may be higher, but highly variable levels of abundance (capture) between sampling events are indicative of short residence time. It should be noted that the model and subsequent classification accuracy could have been improved substantially by inclusion of a unique categorical identifier for each sampling event, but we chose to forgo the inclusion of this variable as such a predictor, thereby allowing us to focus on physical habitat parameters that were more universally applicable.

Our results suggest that instream cover, either in the form of woody material or inundated terrestrial vegetation, was significantly associated with increased habitat use by juvenile Chinook Salmon as compared to locations where such cover was absent (Table 4). Over the course of the past century, extensive shoreline modification has led to a large reduction in recruitment of woody material to the Sacramento River and has disconnected the now narrowly constrained riverine corridor from large, shallow floodplains. The lack of instream structure along representative study locations was reflected in the frequency of sampling points that lacked woody material or inundated

terrestrial vegetation; woody material was present at the majority of sampling points only along natural shorelines (Tables 2, 3). The association between increased probability of occupancy and the presence of woody material likely contributed to the higher habitat use by juvenile Chinook Salmon along mitigated shorelines, which were often characterized by deliberately placed woody material to enhance habitat value. Despite this positive association, woody material only increased habitat use by juvenile Chinook Salmon when such material was present in sparse and medium densities (Table 4). Restoration activities often deliberately place woody material to enhance habitat for salmonids, yet our results indicate that although wood in low and medium densities can be beneficial, high-density woody material did not significantly enhance habitat value for juvenile Chinook Salmon.

Similar to woody material, inundated terrestrial vegetation was associated with substantial increases in occupancy probability (Table 4). This finding attests to the value of submerged vegetation for rearing or emigrating Chinook Salmon, presumably by providing cover and foraging opportunity. By definition, terrestrial vegetation is only inundated during periods of above-average discharge. To maximize the frequency of inundation and access to such habitat for juvenile Chinook Salmon, mitigation and restoration efforts should attempt to incorporate gently sloping streambanks that are readily submerged. Shallow, seasonally inundated habitat is often associated with high-quality nursery habitat and increased juvenile abundance; particularly large, seasonally inundated areas, such as the Yolo Bypass on the Sacramento River, have been shown to provide enhanced growth conditions for rearing Chinook Salmon (Sommer et al. 2001).

We interpret the estimated significant increase in occupancy probability at higher densities of inundated vegetation to constitute an indirect validation of the sampling methodology; dense vegetation may reduce the capture success for small fishes during sampling, which could lead to an underestimation of parameters. An increase in occupancy probability, however, suggests that bias-related capture success is not a factor in determining the importance of various habitat characteristics. Conversely, it may be argued that a lack of cover increases the reactive distance of fish. Reactive distance is also strongly influenced by fish size (smaller fish have a shorter reactive distance; Grant and Noakes 1987), and we assume that any bias introduced by differences in reactive distance between cover densities was negligible.

This study also indicates that rocky substrate (defined as large, angular rock, typical of revetment), which often comprises the majority of streambank stabilization, was associated with a decreased probability of occupancy by juvenile Chinook Salmon (a 37% reduction in probability as compared to fine substrate, such as sand or silt).

Previous work on the Snake River indicated that Smallmouth Bass were more likely to be found over rocky substrate (Tiffan et al. 2016). Smallmouth Bass have been shown to prey on juvenile salmonids (e.g., Tabor et al. 2007) and are common in the Sacramento River, where they support a popular sport fishery, particularly in the lower reaches. No Smallmouth Bass abundance estimates are available for the study area; however, our sampling suggests that at least during daylight hours in nearshore habitat, Smallmouth Bass are more abundant than other piscivores, including the native Sacramento Pikeminnow *Ptychocheilus grandis* and non-native Striped Bass *Morone saxatilis* and Largemouth Bass *Micropterus salmoides*. It is possible that predator presence discourages habitat use by juvenile Chinook Salmon, yet reduced prey availability/production, low habitat variability, and higher velocity are likely additional factors that discourage occupancy along rock revetment shorelines. Lateral bank slope was also an important predictor of juvenile Chinook Salmon presence, whereby steep banks are less likely to be occupied, similar to the findings of Tiffan et al. (2006). Lastly, while higher mean velocity was associated with a decrease in occupancy by Chinook Salmon, an increasing velocity gradient also increased habitat use. This suggests that juvenile Chinook Salmon preferentially occupy habitat that provides refuge from fast current—thereby minimizing energy expenditure—but is in close proximity to faster current, which perhaps enables more efficient feeding.

At mitigated shoreline reaches, it is likely that a combination of factors resulted in increased habitat use over revetment shorelines. The presence of instream cover, gradually sloping banks and the predominance of small sediment (silt/sand) likely contributed to the enhanced habitat value of mitigated shorelines. As a consequence, we encourage the continued implementation of mitigation features where localized hydraulic conditions and construction cost permit. Interestingly, we found no significant positive association between elevated temperatures at sampling points and occupancy by juvenile Chinook Salmon, which has been previously identified to increase the probability of occupancy in the Columbia River (Tiffan et al. 2006). This is surprising, as slightly elevated temperature compared to the main river channel is frequently invoked as one of the main benefits of springtime floodplain inundation and is thought to facilitate increased growth through more favorable metabolic conditions (e.g., Sommer et al. 2001; Takata et al. 2017). The final logistic regression model did indicate that areas where temperatures are lower than mid-channel surface temperature may be avoided by juvenile Chinook Salmon (a 38% reduction in occupancy probability; Table 4). The difference between the results of the present study and other studies may be attributable to the generally warmer temperatures found in the Sacramento

River compared to more northerly streams where similar work has been carried out, diminishing the metabolic benefit of slightly elevated temperatures.

This study identifies a number of variables that affect the probability of habitat occupancy by emigrating juvenile Chinook Salmon in the lower reaches of a large, low-gradient river. On the Sacramento River, juvenile Chinook Salmon from several large and small spawning tributaries and juveniles reared in state and federal fish hatcheries must migrate through the lower river to reach the ocean, including several runs/races that are afforded special protection by state and federal endangered species legislation. This special protection is often the driving factor leading to the incorporation of mitigation features in contemporary riverbank modification activity. As such, the variables we identified can guide restoration and mitigation planning. Although implementation of alternative levee designs and mitigation features can be constrained by localized hydraulic conditions and construction cost, our results suggest that alternatives to steep rock revetment (1) create riverine habitat that is of higher value to native juvenile salmonids, and by extension, (2) reduce habitat favored by non-native predators. Although the habitat value of mitigated shoreline habitats may be lower than that of large, seasonally inundated floodplains, nearshore habitats in the main channel or large streams are available to emigrating Chinook Salmon during all years, whereas floodplains are only accessible for rearing in some years for relatively short periods of time and therefore are accessible to a comparatively small fraction of the overall juvenile salmonid population. We suggest that levee designs incorporating mitigation features should be implemented whenever localized constraints permit; furthermore, mitigation features should be incorporated at elevations that are expected to be inundated during the majority of flows typically observed during peak rearing and emigration of juvenile Chinook Salmon.

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