

Selection of Spawning Sites by Coho Salmon in a Northern California Stream

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Abstract.—We assessed the relative importance of various factors contributing to spawning site use by a population of threatened coho salmon *Oncorhynchus kisutch* in Freshwater Creek, California, and created a predictive model of spawning habitat selection based on logistic regression analysis. We excluded sampling sites that previous studies had established as unsuitable on the basis of depth and substrate criteria and asked why fish chose particular locations and not others in seemingly suitable habitat. We evaluated surface water velocity, depth, substrate size composition, gravel inflow rates, vertical hydraulic gradient, geomorphic channel units, hyporheic water physicochemistry, cover, and proximity to other redds not in sampling sites during the 2004–2005 spawning season. In univariate comparisons with unused sites, coho salmon selected sites with a smaller median particle diameter, a larger percentage of gravel–pebble substrate, and higher gravel inflow rates. Based on multivariate logistic regression, the probability of a site’s being used for spawning was best modeled as a positive function of the gravel–pebble fraction of the substrate, location at a pool or run tail, and the presence of existing redds in close proximity to the site. This model explained 38% of the variation in the data and was a better predictor of spawning habitat use than a more traditional model based on depth, velocity, and substrate. Our results highlight the potential importance of social behavior in contributing to habitat selection by spawning salmonids.

Habitat use by salmonids in streams is typically described on the basis of water depth, water velocity, and substrate composition. These three variables are widely used in traditional models, such as the physical habitat simulation system (PHABSIM) (Milhous et al. 1989), and their importance has been demonstrated in several studies of spawning site selection by salmonids (e.g., Reiser and Wesche 1977; Witzel and MacCrimmon 1983; McHugh and Budy 2004), as well as in the predictive model of Knapp and Preisler (1999). However, some studies have suggested that depth, velocity, and substrate alone may underestimate or overestimate the area suitable for spawning, and PHABSIM has been shown to have limited accuracy in predicting the use of spawning habitat. For example, Shirvell (1989) found that 70% of the spawning area used by a population of Chinook salmon *Oncorhynchus tshawytscha* was predicted to be unusable, and 87% of the area predicted to be usable never had spawning activity. This result suggests that spawning

site selection may be more complex than traditional models indicate.

For example, additional variables that describe the movement of water through the substrate may be required to capture more fully the influence of water velocity in site selection by spawning salmonids. Several studies have identified rates of intragravel flow and water exchange between surface and subsurface flows as potentially important in affecting site choice. Baxter and Hauer (2000) showed that bull trout *Salvelinus confluentus* redds were associated with areas of high intragravel flow, and Chapman (1988) found that permeability in egg pockets was higher than in areas adjacent to spawning activity. Increased intragravel flow probably improves conditions for embryonic development (Reiser and Wesche 1977), although the ability of salmonids to detect differences in intragravel permeability has not been established. Spawning locations of several species of salmonids have been associated with upwelling hyporheic flow (e.g., Witzel and MacCrimmon 1983; Geist and Dauble 1998; Baxter and Hauer 2000). Alternatively, Vronskii and Leman (1991) found that Chinook salmon selected areas of downwelling. Whether salmonids prefer areas of upwelling or downwelling or simply require a significant exchange of water

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between subsurface and surface flows is unknown (Baxter and Hauer 2000), and preferences may vary with species and location.

Water quality variables, including dissolved oxygen, conductivity, and temperature, may also be important in the selection of redd sites by salmonids and lead to better predictive models than velocity, depth, and substrate alone. For example, Baxter and McPhail (1999) found that areas selected for spawning by bull trout in a British Columbia stream had higher water temperatures than unused locations. Differences in dissolved oxygen, conductivity, and temperature between redd sites and unused sites might be expected if salmon prefer sites with high intragravel permeability or surface water-groundwater exchange. In general, upwelling flows tend to have lower dissolved oxygen levels, but higher temperature, conductivity, and nutrient levels than downwelling flows (Bjornn and Reiser 1991). These physicochemical characteristics may provide a set of cues potentially used by spawning salmonids to detect suitable spawning sites.

The literature also points to channel geomorphology and proximity to cover as potentially important in the selection of salmonid spawning sites. Salmonids often spawn in areas of transition between pools and riffles, where the variability in streambed slope creates a vertical hydraulic gradient that results in upwelling and downwelling (Bjornn and Reiser 1991). Hoopes (1972) found that spawning sockeye salmon *Oncorhynchus nerka* preferred the downstream end or tail of pools where the transition from pool to riffle induces downwelling. Salmonid redds are often located near undercut banks, overhanging vegetation, and instream structures such as large boulders or accumulations of large woody debris (Hoopes 1972; Witzel and MacCrimmon 1983; Merz 2001). Merz (2001) offered an explanation that instream structures simultaneously create areas of increased velocity suitable for spawning and back eddies that provide a resting place adjacent to redds. Inclusion of cover and channel unit variables may, thus, also add predictive power to traditional models of habitat selection.

Finally, evidence suggests that at some level the social behavior of salmonids may also be an important variable in selecting spawning sites. As reviewed by Fleming and Reynolds (2004), the literature has become richer on social elements of salmonid mating systems, including relationships between sexual selection and behaviors such as breeding time and selection of redd sites. Clumping of redd sites and nest superimposition are common in salmonids (e.g., Witzel and MacCrimmon 1983; Blanchfield and Ridgway 1997), even when habitat availability is apparently not limiting (Essington et al. 1998). Shared preference

criteria among females leads to competition for nest sites and may give rise to frequency-dependent distribution of redds, as some individuals occupy less preferred sites at high spawning densities. Choice of redd sites by females probably represents a balance between intrinsic habitat quality and the costs associated with competition or mortality risks (Hendry et al. 2001).

The relative suitability of stream sites for salmonid spawning is thus probably related to several physical, chemical, and biological factors, and high quality spawning habitat may be scarcer than traditionally believed. The distribution of redds in a stream is patchy, even within short stream reaches that appear to be suitable to spawning fish (Dauble and Watson 1990). Owing to the complexity of redd site selection and the possible involvement of many interacting variables, models tailored to specific river systems may more accurately predict spawning habitat use (Shirvell 1989; Geist and Dauble 1998; McHugh and Budy 2004).

The objectives of this study were to evaluate the relative importance of various physical and biological factors contributing to spawning site use by a population of threatened coho salmon *Oncorhynchus kisutch* in a coastal northern California stream and to create a model of spawning habitat selection based on logistic regression analysis. This study focused on reaches in the Freshwater Creek watershed that appeared to be suitable for coho salmon redds based on published depth and substrate criteria in regional streams (e.g., Hassler 1987; Regnart 1991). Because we sought to determine why fish chose particular locations and not others in seemingly good habitats, we did not sample all available habitats but rather excluded sections of the study reaches that previous research had established as unsuitable. Within suitable areas we measured and evaluated the relative importance of surface water velocity, depth, substrate size composition, gravel inflow rates, vertical hydraulic gradient, geomorphic channel units, hyporheic water physicochemistry, cover, and proximity to other redds in sites selected and not selected by spawning coho salmon. In developing candidate models to predict spawning habitat use, we started with the hypothesis that depth, velocity, and substrate would represent the best model of site selection. Additional models were explored based on hypotheses that inclusion of variables pertaining to the movement of water through the substrate (gravel inflow rate and vertical hydraulic gradient), water quality (dissolved oxygen, conductivity, and temperature), geomorphic channel unit, and proximity to cover and to other redds would each improve the fit of the traditional model.

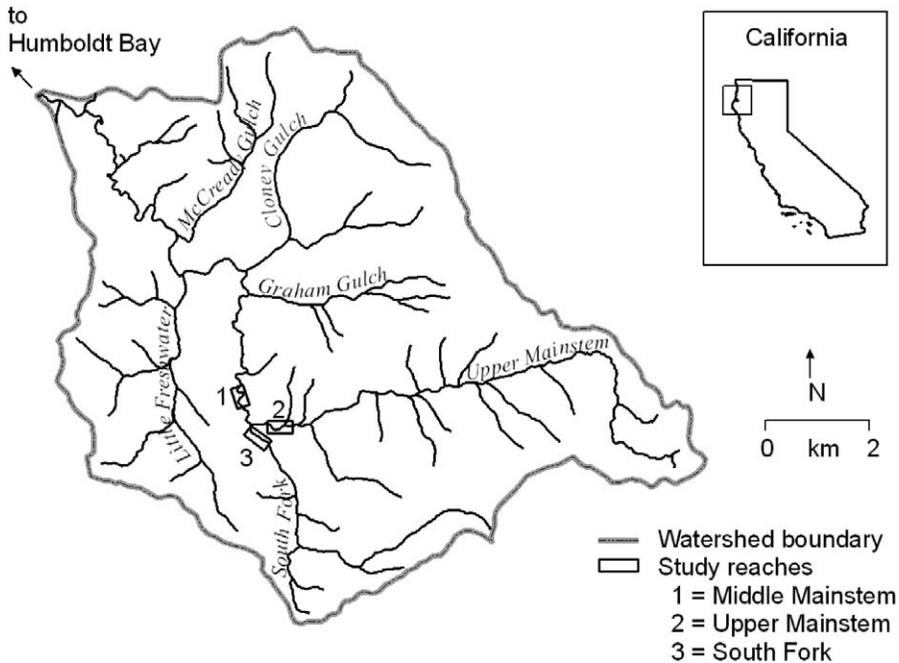


FIGURE 1.—Watershed map showing the primary coho salmon spawning tributaries and the locations of the three 500-m study reaches in Freshwater Creek (40°44'N, 124°02'W) in northern California.

Study Site

Freshwater Creek drains into Humboldt Bay just north of the city of Eureka in coastal northern California. The watershed is approximately 67.3 km² in area, of which approximately three-quarters is managed for timber production. The main stem and five major tributaries provide an estimated 30 km of habitat for anadromous salmonids (Figure 1).

The temperate climate of the region is characterized by wet winters and dry summers. Most of the annual rainfall (mean, >150 cm) occurs between November and March. Water temperatures in the three study reaches ranged from 6.1 to 9.9°C with a mean of 7.8°C between 15 December 2004 and 5 February 2005, and streamflow in the main-stem Freshwater Creek averaged 1.189 m³/s (42.0 ft³/s) during this study. The highest peak flows were 9.401 m³/s (332 ft³/s) and 8.637 m³/s (305 ft³/s) on 31 December 2004 and 7 January 2005, respectively. Based on prorating these flows with an adjacent watershed for which 30 years of data are available (Bigelow 2003), these flows are estimated to occur with a recurrence interval of less than 1 year. The three study reaches have low gradients ranging from 1.0 to 1.4%.

The salmonids present in the study reaches included coho salmon, Chinook salmon, steelhead *Oncorhynchus mykiss*, and cutthroat trout *O. clarkii*. Based on

mark-recapture of tagged adults intercepted at a permanent weir, the California Department of Fish and Game estimated that the escapement of adult coho salmon into Freshwater Creek in 2005 was 974 ± 72 (95% confidence interval) individuals (Ricker 2006).

Methods

Study design.—Three 500-m study reaches in the middle main stem (from river meter [rm] 3,200 to rm 3,700), upper main stem (from rm 400 to rm 900), and south fork (from rm 100 to rm 600) of Freshwater Creek were selected for sampling based on accessibility and observed spawning activity during the 2003–2004 season (California Department of Fish and Game, unpublished data). The rm 0 point for the middle main stem was the confluence with Graham Gulch, and the rm 0 point for the other two study reaches was the confluence of the upper main stem with the south fork. Areas within each reach that were unsuitable for spawning coho salmon were eliminated from sampling. Unsuitable habitat was defined as habitat having substrate consisting primarily of sand or silt less than 4 mm in diameter or depths greater than 30 cm. These criteria are based on habitat suitability indices indicating that coho salmon spawn in substrates ranging in particle size from 13 to 150 mm (Hassler 1987) and on the finding of Regnart (1991) that the range of depths

of coho salmon redds in Freshwater Creek was 6–21 cm. The total lengths of stream habitat characterized as suitable in the study reaches were 292, 290, and 348 m in the middle main stem, upper main stem, and south fork, respectively.

During the December 2004–February 2005 spawning season, we sampled all coho salmon redds and a random sample of 4-m² unused sites in the study reaches. Approximately equal numbers of redds and unused sites were sampled within each reach. Over the course of the spawning season, a total of 53 redds and 52 unused sites were sampled and the location of each unit was recorded on maps of the study reaches. Redds were identified by the direct observation of coho salmon spawning activity and the presence of fish on successive days. Test digs, which were identified by the absence of coho salmon on subsequent days, were not considered completed redds and were not sampled for this study. To avoid disturbing the fish, redds were sampled as soon as coho salmon stopped defending the nest site and were no longer nearby.

Microhabitat sampling.—Water depth and velocity were measured at the center of the unused units and at the upstream edge of redds during winter base-flow conditions. This point most closely approximates conditions before redd construction and gives more accurate measurements of the depth and velocity selected by the female (Bjornn and Reiser 1991). Depth (cm) was measured with a stadia rod, and velocity (m/s) was measured with a Marsh-McBirney Flo-Mate velocity meter at 60% of the total depth. Surface water temperature (°C) and dissolved oxygen (mg/L) were measured with a YSI 55 dissolved oxygen meter, and conductivity (µS/cm) was measured with a YSI 30 conductivity meter.

The size-classes of substrate particles found in the sample unit were measured using Wolman pebble counts. We used grid sampling as described by Bunte and Abt (2001) to perform the pebble count. Sampling points were established using a 12 × 12 grid with intersections spaced approximately 15 cm apart. We systematically selected 144 particles at the intersections and recorded size-classes according to the Wentworth scale. Particles sampled in this way can be accurately measured to 4 mm (Kondolf and Li 1992). Thus, any streambed materials finer than 4 mm were recorded as fines. While the process of redd construction by salmonids reduces fine sediments within redds (Kondolf 2000), we sampled nest sites 3–10 d after construction when small particles had probably moved back into the disturbed gravel of the redd (Chapman 1988; Grost et al. 1991). We assumed that the substrate sampled beside or within redds was representative of substrate before spawning and created cumulative size

distribution curves from the pebble counts for selected and unused units. In evaluating differences in substrate composition between selected and unused sites, we compared the median particle diameter (d_{50} , i.e., the size at which 50% of the particles are finer), the percentage of gravel and pebble substrate, and the percentage of fines less than 4 mm. Gravel and pebble with low fines is optimum for survival, growth, and development of coho salmon embryos, and for emergence of alevins (Platts et al. 1979). Based on published ranges of substrate sizes used by coho salmon, percentage gravel–pebble substrate was used in logistic regression modeling.

To measure gravel inflow rate (mL/s), which is an index of intragravel permeability, we inserted a modified Terhune (1958) Mark VI standpipe to a depth of 20 cm in the substrate. This depth corresponds to the mean depth of coho salmon egg pockets below the original level (i.e., before redd construction) of the streambed (DeVries 1997). The standpipe was inserted at the upstream edge of redds to avoid disturbing developing embryos in the mound. Gravel inflow rates were measured following the protocol of Barnard and McBain (1994), with five replicates recorded for each sample point.

Physicochemical factors associated with the hyporheic water were sampled by inserting dissolved oxygen and conductivity meter probes into the standpipe. Vertical hydraulic gradient (VHG), which describes potential surface water–groundwater exchange, was measured using a device described by Wanty and Winter (2000). We inserted Tygon tubing into the standpipe, created a large loop that fell below the level of the surface water, drew hyporheic water from the standpipe into the tubing with a 60-mL syringe, and measured the hydraulic head differential as the difference between the height of the hyporheic water inside the tubing and the stream surface water outside the tubing. We calculated VHG by dividing this difference by an elevation head differential of 14 cm, which was the distance between the streambed and the first opening in the buried standpipe. The VHG is positive where upwelling occurs and negative where downwelling occurs.

To quantify other attributes of the physical habitat, we described both the selected and unused units in relation to the presence or absence of existing redds within a distance of 10 m and the presence or absence of riparian or instream cover within 2 m. These distances were chosen based on findings of Burner (1951), who reported that coho salmon redds average 2.8 m² and that a single coho salmon spawning pair may occupy and defend a territory of 11.7 m². Cover types included overhanging riparian vegetation, in-

stream woody debris, boulders, and undercut banks. The presence of any cover was scored as 1 and the absence of cover was scored as 0. Study units were given a binary code of 1 if they were located in a pool tail or run tail and 0 if they were in any other habitat type.

Statistical analyses.—Paired *t*-tests were used to compare water physicochemistry between surface water and hyporheic water. To compare microhabitat variables between selected and unused sites the Wilcoxon rank-sum test was used for continuous variables, and the chi-square test for equality of proportions with a Yates correction for continuity was used for binary variables (Zar 1999). To avoid compounding the error associated with testing substrate particle sizes that were mutually dependent within samples, we used the Bonferroni procedure (Kuehl 2000) to test hypotheses at an experimentwise error rate of 0.05. Five particle size classes were evaluated simultaneously, so null hypotheses for individual particle sizes were rejected at $P < 0.01$. A significance level of 0.05 was used for all other statistical tests. The evaluation of microhabitat characteristics was performed with S-PLUS 2000 software (MathSoft 2000).

We used multivariate logistic regression to model the selection of spawning habitat in the study reaches by coho salmon. The presence of a redd was assumed to imply suitability, and the presence or absence of redds at sampling sites was modeled as a function of the various continuous and categorical microhabitat variables sampled (McHugh and Budy 2004). The response variable was the presence or absence of a coho salmon redd in a given sample unit. The linear logit function, which was estimated using standard statistical techniques, was used to generate estimates for \hat{p} ranging from 0 to 1, the probability that a given stream site will be selected by spawning coho salmon. This relationship is given by the equation

$$\hat{p} = e^{\text{logit}} / (1 + e^{\text{logit}}).$$

Using the approach of Burnham and Anderson (2002) we developed a set of 16 models for spawning site selection in Freshwater Creek. The first two models tested the hypothesis that depth, velocity, and substrate (percentage of gravel–pebble alone and together with percentage of fine sediments) represented the best model of site selection by spawning coho salmon. A second set of models tested whether addition of gravel inflow rates and surface–groundwater exchange improved the fit of the traditional model, and whether the model improved if velocity was replaced by these variables. The next model tested whether the inclusion of physicochemical variables enhanced the fit of the traditional model. A fourth

set of models tested hypotheses that habitat unit type and cover improved the traditional model and that proximity to other spawners played a role in site selection. Remaining candidate models included varying combinations of variables. All candidate models were tested for plausibility with the data and ranked using the Akaike information criterion corrected for small sample sizes (AIC_c). We examined the variance inflation factors of independent variables to ensure that there was no multicollinearity between variables.

To determine how well the best-fitting model fit the data, we used a chi-square goodness-of-fit test (Hosmer and Lemeshow 1989) and a classification table. The latter approach simulates responses (1 for selected; 0 for unused) on the basis of the \hat{p} prediction function, provides the number of correct predictions, and returns specificity and sensitivity values for various cutoff values of p . Specificity describes the ability to predict a nonevent (unused sites) correctly, while sensitivity describes the ability to predict an event (selected sites) correctly. The best-fitting model was also analyzed for goodness of fit using a cross-validation procedure (Breiman et al. 1984). With this method a single sample is removed from the data set, a new model containing the same parameters as the best-fitting model is estimated based on the remaining samples, and the response is predicted for the deleted sample from the refitted model. This process is iterated for all sample points, and the percentage correctly classified provides a measure of the goodness of fit of the model. Logistic regression analyses were carried out using SAS version 9.1 software (SAS Institute 2003). Data were pooled among stream study reaches to improve statistical power and robustness.

Results

Of the 53 redd sites and 52 unused sites we sampled, 20 were in the middle main stem (7 selected and 13 unused), 6 were in the upper main stem (3 selected and 3 unused), and 79 were in the south fork (43 selected and 36 unused) (Figure 2). All redds found in the study reaches between 15 December 2004 and 5 February 2005 were sampled. Coho salmon spawning activity was not observed in the study reaches after this period.

Coho salmon redds in Freshwater Creek were located at depths ranging from 4 to 30 cm, with a mean depth of 15 cm (Table 1). Surface water velocity at redd sites ranged from 0.01 to 1.01 m/s, averaging 0.25 m/s, and the median diameter of substrate particles ranged from 9 to 45 mm, averaging 25 mm.

Surface water velocity (Wilcoxon rank-sum statistic [W] = -1.47, $df = 1$, $P = 0.142$) and depth ($W = -0.93$, $df = 1$, $P = 0.352$) did not differ between selected and unused sites (Table 1). Coho salmon used sites with a

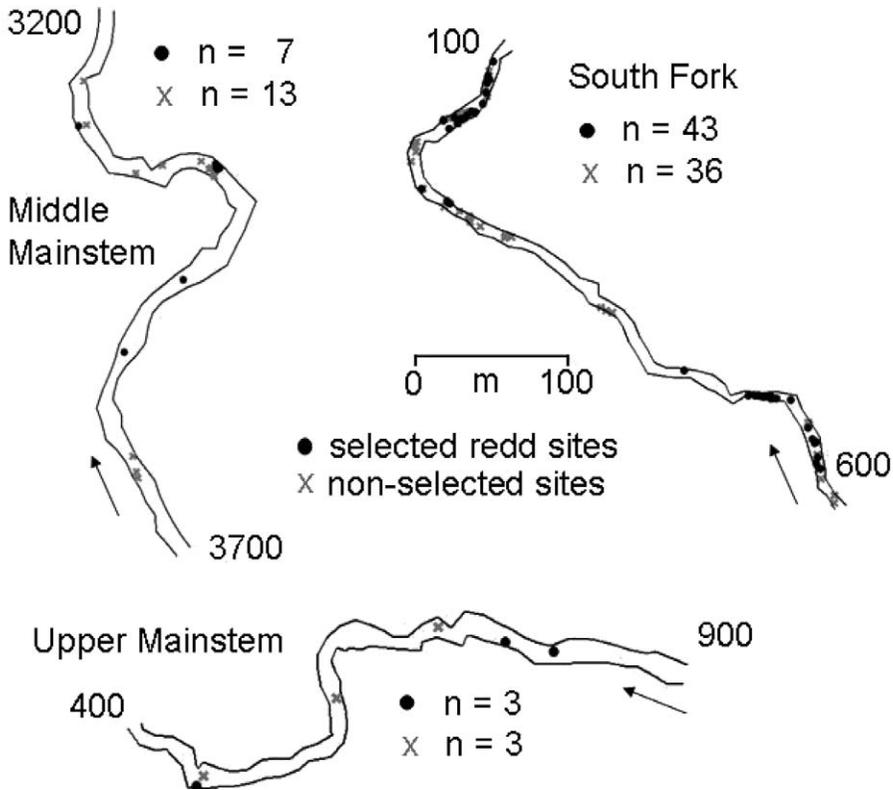


FIGURE 2.—Maps of the study sections in the Freshwater Creek watershed showing the locations of the coho salmon redds and unused sites sampled. The numbers at the beginning and end of the middle main-stem reach indicate stream distance in meters upstream of the confluence of Graham Gulch with the main stem, while those on the south fork and upper main-stem reaches represent stream distance in meters upstream of the confluence of the south fork and upper main stem. Arrows indicate the direction of stream flow.

smaller d_{50} ($W = 3.47$, $df = 1$, $P < 0.001$) and a larger percentage gravel-pebble ($W = -4.21$, $df = 1$, $P < 0.001$) relative to sites that were not selected. The fraction of substrate composed of cobble was lower at redd sites than at unused sites ($W = 3.46$, $df = 1$, $P < 0.001$; Figure 3). Spawning sites had higher gravel inflow rates than unused sites ($W = -3.13$, $df = 1$, $P = 0.002$; Table 1). The percentage gravel-pebble within the substrate was positively correlated with gravel inflow rates ($R^2 = 0.13$; Figure 4), but the percentage of fine particles less than 4 mm was not related to gravel inflow rates. The potential for upwelling or downwelling surface water, VHG, did not differ between selected and unused sites ($W = 1.10$, $df = 1$, $P = 0.271$; Table 1).

Mean temperature, dissolved oxygen, and conductivity did not vary between selected and unused sites ($P > 0.05$). However, hyporheic water was warmer than surface water at both selected sites (paired t -test: $t = 4.07$, $df = 52$, $P < 0.001$) and unused sites ($t = 3.63$, $df = 51$, $P < 0.001$; Table 2). Dissolved oxygen was lower

in interstitial water (selected sites: $t = 5.15$, $df = 52$, $P < 0.001$; unused sites: $t = 5.07$, $df = 51$, $P < 0.001$), and conductivity was higher in interstitial water than surface water (selected sites: $t = 3.99$, $df = 52$, $P < 0.001$; unused sites: $t = 2.76$, $df = 51$, $P = 0.008$; Table 2).

A total of 16 different logistic regression models were applied to the pooled data set. Candidate models included the covariates depth (DEP), velocity (VEL), percent gravel-pebble (GRAVPEB), percent fines (FIN), gravel inflow rates (INF), location at a pool or run tail (TAIL), upwelling or downwelling (VHG), presence of cover (COV), presence of existing redds within 10 m (PROX), hyporheic dissolved oxygen (DO), hyporheic temperature (TEMP), and hyporheic conductivity (COND). The best-fitting model from this set of candidate models contained the variables GRAVPEB, TAIL, and PROX (Table 3). This model explained 38% of the variation in the data, and had an Akaike weight of 0.48, indicating a 48% chance that this model is the best-fitting given the data set and

TABLE 1.—Means ± SDs of microhabitat characteristics at selected coho salmon redd sites and unused sites in the Freshwater Creek watershed. The variable d_{50} is the median diameter of substrate particles. Presence of cover, presence of existing redds, and location at tails of pools or runs are binary variables (1 = present, 0 = absent); the data are the proportions of sites that had a value of 1. Cover indicates the presence or absence of riparian cover or instream woody debris, boulders, or undercut banks within 2 m of the sample unit. The presence of existing redds represents the presence or absence of coho salmon redds within 10 m of the sample unit. Habitat units were scored as 1 for pool or run tails and 0 for all other habitat types. Asterisks indicate statistically significant differences between selected and unused sites as determined by a Wilcoxon test for continuous variables and a χ^2 test of proportions for binary variables ($P < 0.05$).

Variable	Selected sites	Unused sites
Velocity (m/s)	0.27 ± 0.19	0.23 ± 0.21
Depth (cm)	15 ± 6	15 ± 8
d_{50} (mm)	25 ± 9	38 ± 19*
Fraction gravel-pebble	0.67 ± 0.13	0.54 ± 0.17*
Fraction fines <4 mm	0.13 ± 0.08	0.14 ± 0.14
Gravel inflow rate (mL/s)	25.0 ± 21.9	16.4 ± 19.5*
Vertical hydraulic gradient	<0.0 ± 0.1	<0.0 ± 0.1
Presence of cover	0.42 ± 0.50	0.38 ± 0.49
Presence of existing redds	0.77 ± 0.42	0.48 ± 0.50*
Location at a pool or run tail	0.34 ± 0.48	0.12 ± 0.32*

collection of candidate models ($AIC_c = 119.2$, $R^2 = 0.38$). Based on this model, the linear logit function was estimated as (Table 4)

$$\text{logit} = -4.8586 + 6.0490 \times \text{GRAVPEB} + 1.7386 \times \text{TAIL} + 1.3287 \times \text{PROX.}$$

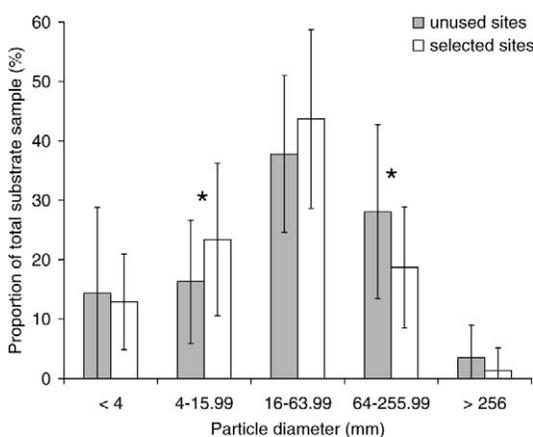


FIGURE 3.—Mean proportions of particle size-classes at selected and unused sites for coho salmon spawning in Freshwater Creek. The thin vertical lines indicate SDs. For each particle size-class, asterisks indicate proportions that are significantly different as determined by a Wilcoxon rank-sum test ($P < 0.01$).

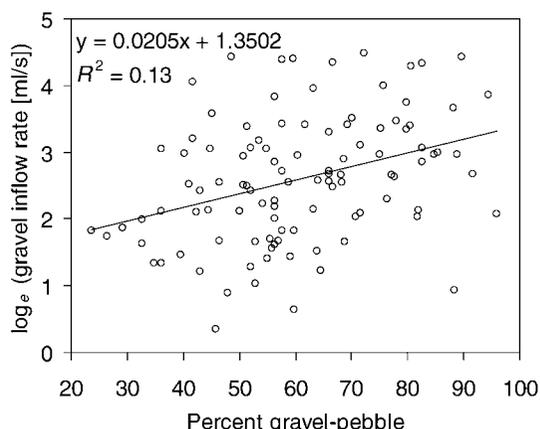


FIGURE 4.—Log_e transformed values of gravel inflow rates as a function of percent gravel-pebble in Freshwater Creek during winter 2004–2005 ($F = 14.88$, $df = 1, 103$, $P < 0.001$). The data points represent data from unused sites as well as those selected by coho salmon for spawning.

Examination of variance inflation factors indicated that multicollinearity did not exist between predictor variables in the best-fitting model or any other model.

The next best model overall contained the same three variables, with the added covariate depth ($\Delta AIC_c = 0.8$, Akaike weight = 0.32). While this model explained slightly more of the variation in the data ($R^2 = 0.39$), penalization for the added covariate resulted in a higher AIC_c than the best-fitting model. In this study the best-fitting model was a better predictor of spawning habitat use than the traditional depth-velocity-substrate model, which explained just 24% of the variation in the data ($\Delta AIC_c = 13.5$, Akaike weight < 0.001).

A Hosmer and Lemeshow goodness-of-fit test on the best-fitting model indicated that there was no evidence

TABLE 2.—Physicochemical characteristics of surface and hyporheic water at sites selected by coho salmon for spawning and unused sites in Freshwater Creek during winter 2004–2005. Surface and hyporheic water differed in all characteristics at both selected and unused sites, as determined by paired *t*-tests ($P < 0.05$). Confidence limits (95% CLs) for the differences between means (surface – hyporheic) are given.

Variable	Temperature (°C)	Dissolved oxygen (mg/L)	Conductivity (µS/cm)
Selected sites			
Surface water	7.8	11.6	82.1
Hyporheic water	7.8	10.9	86.1
95% CLs for difference	-0.09, -0.03	0.44, 1.01	-5.96, -1.98
Unused sites			
Surface water	7.9	11.5	86.4
Hyporheic water	8.0	10.5	91.0
95% CLs for difference	-0.10, -0.03	0.63, 1.47	-7.94, -1.26

TABLE 3.—Results for models describing the selection of stream sites for spawning by coho salmon in the Freshwater Creek watershed. See text for abbreviations of model covariates; *k* is the number of parameters estimated, AIC_c the Akaike information criterion corrected for small sample size, and ΔAIC_c the difference between the value of AIC_c for the model in question and that for the model with the lowest value. The best-fitting model is indicated by bold italics.

Model covariates	<i>k</i>	AIC_c	ΔAIC_c	Akaike weight	R^2
<i>GRAVPEB, TAIL, PROX</i>	4	119.2	0.0	0.478	0.38
DEP, GRAVPEB, TAIL, PROX	5	120.0	0.8	0.317	0.39
DEP, GRAVPEB, COV, TAIL, PROX	6	121.6	2.4	0.142	0.39
DEP, GRAVPEB, PROX	4	124.9	5.7	0.027	0.32
DEP, GRAVPEB, TAIL	4	125.6	6.4	0.019	0.32
DEP, VEL, GRAVPEB, PROX	5	126.9	7.7	0.010	0.32
DEP, VEL, GRAVPEB, COV, TAIL	6	129.1	9.9	0.003	0.32
DEP, VEL, GRAVPEB, FIN	5	132.7	13.5	0.001	0.27
DEP, VEL, GRAVPEB	4	132.7	13.5	0.001	0.24
DEP, GRAVPEB, COV	4	132.8	13.6	0.001	0.24
DEP, GRAVPEB, INF, VHG	5	132.9	13.7	0.001	0.26
DEP, VEL, GRAVPEB, INF	5	133.3	14.1	0.000	0.26
DEP, VEL, GRAVPEB, VHG	5	134.5	15.3	0.000	0.25
DEP, VEL, GRAVPEB, COND, TEMP, DO	7	134.7	15.5	0.000	0.29
DEP, TAIL, PROX	4	136.2	17.0	0.000	0.21
1 (null model)	1	147.6	28.4	0.000	0.00

to reject the null hypothesis that the model fit the data well ($\chi^2 = 7.56$, $df = 7$, $P = 0.373$). This model classified sites well, 71.4% being correctly classified by resubstitution (Table 5) and 73.3% by cross-validation. In general, this model was better at predicting the probability that a site would be selected than not selected. The highest level of correct classification was achieved at a cutoff probability value of 0.35, which corresponds to 86.8% sensitivity and 55.8% specificity. The second-best model, containing the covariates DEPTH, GRAVPEB, TAIL, and PROX, also performed reasonably well, correctly classifying 72.4% and 73.3% of used and unused sites by resubstitution and cross-validation, respectively.

Discussion

The probability of a site’s being used for spawning by coho salmon within suitable habitat in the middle main stem, upper main stem, and south fork reaches of Freshwater Creek was best modeled as a positive function of the gravel–pebble fraction of the substrate, location at a pool or run tail, and presence of existing redds in proximity to the site. While the other variables

we considered may be important in site selection, their inclusion in models did not improve the classification of sites. The mean depth at redd sites was above the minimum depth criterion for coho salmon spawning suggested by Smith (1973) of 12 cm, and the surface water velocity at redd sites was within the suggested range of 0.19–0.69 m/s. While depth and velocity represent two of the three major habitat variables used in traditional models of spawning habitat, they did not contribute predictive power in this study after slow-moving, deep waters were excluded from the population of sampling sites.

Substrate composition was the only one of the three traditional habitat variables retained in the best model. Substrate particle size was an important component of site selection in Freshwater Creek, but the median diameter of particles was not greater in selected sites than in unused sites as we had expected. Because pools where fines typically accumulate were eliminated from the sampling area, substrate particles in unused sites were probably larger than they would have been otherwise. On the other hand, fish size does limit the size of particles that can be moved and used for redds. Kondolf (2000) suggested that spawning females can move gravels with a median diameter up to 10% of their body length. The average size of female coho salmon in Freshwater Creek during the 2004–2005 spawning season was 66.4 cm ($SD = 58.3$, $n = 254$) (S. J. Ricker, California Department of Fish and Game, personal communication), corresponding to a movable particle diameter of 66 mm. Thus, it is not surprising that coho salmon selected substrate particles classified as gravel and pebble for redd construction, and the percentage gravel–pebble was significantly higher in

TABLE 4.—Intercept and covariate coefficient estimates for the best-fitting model of coho salmon spawning site selection in Freshwater Creek during the 2004–2005 spawning season. See text for covariate abbreviations.

Variable	df	Estimate	SE	χ^2	<i>P</i>
Intercept	1	−4.8586	1.1186	18.87	<0.001
GRAVPEB	1	6.0490	1.6167	14.00	<0.001
TAIL	1	1.7386	0.6127	8.05	0.005
PROX	1	1.3287	0.4967	7.16	0.008

TABLE 5.—Classification table for the best-fitting model of coho salmon redd site selection, which contains the covariates percent gravel–pebble, location at a pool or run tail, and presence of existing redds nearby. The percentage correct is the rate of correct classification. Sensitivity is the proportion of selected sites that were predicted to be selected, and specificity is the proportion of unused sites that were predicted to be unused. False positive is the proportion of sites that were predicted to be selected but that were actually unused, and false negative is the proportion of sites that were predicted to be unused but that were actually selected. As the cutoff probability level increases, the probability of correctly classifying a selected site decreases and the probability of correctly classifying an unused site increases. The best percent correct classification overall, 71.4%, occurs at a probability level of 0.35.

Cutoff probability level	Correct (%)	Sensitivity (%)	Specificity (%)	False positive (%)	False negative (%)
0.00	50.5	100.0	0.0	49.5	
0.05	50.5	100.0	0.0	49.5	
0.10	57.1	100.0	13.5	45.9	0.0
0.15	61.9	100.0	23.1	43.0	0.0
0.20	68.6	96.2	40.4	37.8	8.7
0.25	67.6	92.5	42.3	38.0	15.4
0.30	70.5	90.6	50.0	35.1	16.1
0.35	71.4	86.8	55.8	33.3	19.4
0.40	69.5	83.0	55.8	34.3	23.7
0.45	66.7	77.4	55.8	35.9	29.3
0.50	61.9	62.3	61.5	37.7	38.5
0.55	65.7	60.4	71.2	31.9	36.2
0.60	68.6	60.4	76.9	27.3	34.4
0.65	63.8	47.2	80.8	28.6	40.0
0.70	65.7	45.3	86.5	22.6	39.2
0.75	65.7	41.5	90.4	18.5	39.7
0.80	62.9	32.1	94.2	15.0	42.4
0.85	61.0	24.5	98.1	7.1	44.0
0.90	55.2	13.2	98.1	12.5	47.4
0.95	51.4	5.7	98.1	25.0	49.5
1.00	49.5	0.0	100.0		50.5

selected sites than in unused sites, while larger cobbles were avoided.

Whereas percentage gravel–pebble was an important component of redd site selection in Freshwater Creek, the fraction of substrate composed of particles less than 4 mm was not significantly different between selected and unused sites. The pebble count method used to classify substrate particles may have underestimated the fraction of fines present in the substrate, because the surface layer is typically deficient in fines (Kondolf 2000). While several studies have demonstrated a significant decrease in the survival to emergence of coho salmon fry with an increasing fraction of fine particles (Koski 1966; Phillips et al. 1975; Cederholm and Salo 1979; Tagart 1984), intragravel permeability and survival to emergence are positively correlated with the fraction of particles 3.35–26.9 mm in diameter (Tagart 1984). The relatively low percentage of fine sediment found in both selected and unused sites may explain why fines did not play a role in spawning site selection, but the fraction gravel–pebble (4–64 mm) did.

Our hypothesis that the addition of gravel inflow rates and vertical hydraulic gradient would capture more fully the influence of velocity in habitat selection by spawning coho salmon was not supported in our analysis, nor did model status improve when velocity

was replaced by the hyporheic variables. Gravel inflow rates were highly variable and higher in selected than in unused sites, but accounted for only 6% of the variation in the data. As inflow rates varied directly with percentage of gravel–pebble, fish may rely more on the tactile stimuli of substrate composition in choosing a redd site than on permeability and groundwater velocity, which adults may not be able to detect (Sowden and Power 1985). The range in values of vertical hydraulic gradient in our study was small, which may have contributed to its insignificance. Although the difference in VHG between selected and unused sites was not significant, we believe that coho salmon in California are likely to prefer sites with a potential for downwelling. Upwelling groundwater is typically warmer than surface water during temperate winters and may be preferred by salmonids spawning in cold streams where temperature is limiting to embryonic growth. In contrast, at the southern limit of the distribution of coho salmon, dissolved oxygen may be relatively more important than temperature to alevin development.

The importance of downwelling to California coho salmon was reflected in the preference of females for spawning in the pool-to-riffle and run-to-riffle transitions, where convex bedforms induce downwelling that brings oxygenated water to the egg pocket. While

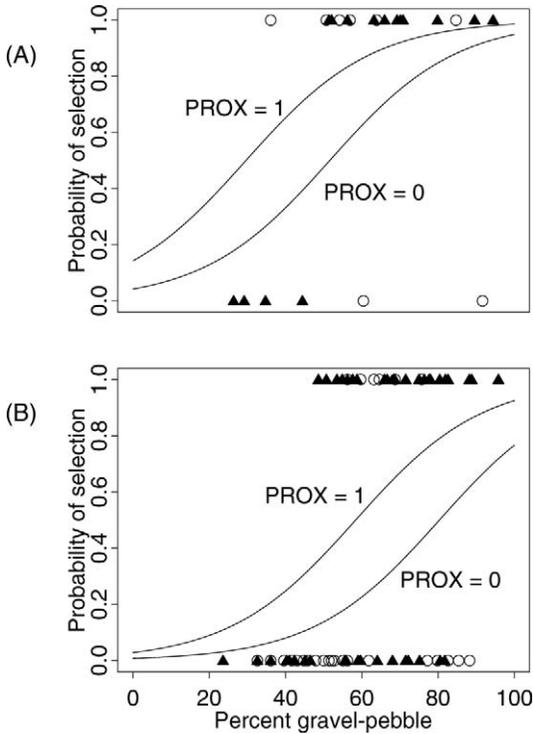


FIGURE 5.—Predicted probabilities of site selection by coho salmon for spawning versus percent gravel-*pebble* in Freshwater Creek. The plots represent (A) sites located at pool-riffle or run-riffle transitions and (B) sites not located at pool or run tails. The upper curve in each plot (PROX = 1) pertains to sites within 10 m of existing redds, the lower curve (PROX = 0) to sites not in proximity to other redds. Observed values of the percent gravel-*pebble* at selected ($p = 1$) and unused ($p = 0$) sites are superimposed on each plot; triangles represent sites at which existing redds were observed within 10 m, circles sites at which redds were not observed within 10 m.

neither water physicochemistry nor proximity to cover added to model strength, location in pool or run tails did. This finding may support the conclusion of Montgomery et al. (1999) that decreased pool spacing is associated with an increased abundance of coho salmon redds. Fukushima (2001) also found a preference of spawning salmonids for stream reaches with increased channel sinuosity, which leads to the formation of pool-riffle sequences that create ideal hydraulic conditions for egg development. Baxter and Hauer (2000), who found that bull trout spawn in upwelling areas at one spatial scale and downwelling areas at a different spatial scale, emphasized the need to consider habitat selection at multiple scales within a hierarchical geomorphic context.

That the inclusion of the proximity of sites to other redds improved model ranking suggests that social

ecology may combine with habitat features at varying scales in affecting redd site selection. Female coho salmon in Freshwater Creek often select existing redd sites on which to spawn (S. J. Ricker, California Department of Fish and Game, personal communication). At high spawner densities, redds may be superimposed or occur in close proximity to each other as a result of limited habitat availability, and site selection is likely to vary with spawner density. To some extent the south fork study reach may have had a higher density of spawning fish due to its increased proportion of suitable habitat (348 m, compared with 292 m and 290 m in the middle main stem and upper main stem, respectively). However, this does not completely explain the much greater density of fish observed in the south fork. Essington et al. (1998) concluded that the high frequency of redd superimposition by brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* could not be explained by habitat availability alone, and females have a behavioral preference to spawn on existing redd sites. They argued that the presence of existing redds makes potential sites more attractive to females than they would be otherwise. While this may reflect a shared preference for unmeasured habitat features, alternative explanations offered by Quinn (2005) are that the second female uses the site to take advantage of the labors of the first female, or that competition may be involved. For example, a female may attempt to destroy the embryos of the first female to reduce local competition for her offspring.

The information about coho salmon carrying capacity and spawning habitat availability in Freshwater Creek was insufficient to allow us to make conclusions regarding the possible effects of fish density on site selection. However, in this study, redds tended to occur close to other redds even in the middle main-stem and upper main-stem reaches where fish densities were low. Logistic regression analysis of selected and unused sites in these two reaches revealed that the best-fitting model of spawning site selection contained the same variables as the model resulting from the analysis of the pooled data from all three reaches. Proximity to existing redds alone accounted for 11.9% of the variation in the data. Nevertheless, further study is required to distinguish whether this preference for locations near other redds is indeed the result of social behavior, or whether it can be explained by habitat availability, fish density, or a precise preference for natal sites or other unmeasured habitat variables.

Multivariate logistic regression analysis suggested that spawning site selection in suitable areas of Freshwater Creek was best explained by the percentage

gravel–pebble of the substrate, whether the site was located at a pool–riffle or run–riffle transition, and whether it was in close proximity to existing redds. This model estimates the probability that a site will be selected for spawning by coho salmon as (Figure 5)

$$\hat{p} = \frac{e^{-4.8586+6.0490 \times \text{GRAVPEB}+1.7386 \times \text{TAIL}+1.3287 \times \text{PROX}}}{1 - e^{-4.8586+6.0490 \times \text{GRAVPEB}+1.7386 \times \text{TAIL}+1.3287 \times \text{PROX}}}$$

If \hat{p} is greater than a cutoff p , then the site is predicted to be selected for spawning, and if \hat{p} is less than the cutoff p , then the site is predicted to be unused. While this model fits the developmental data set well, subsequent studies are necessary to test the goodness of fit to new data sets. With sufficient testing of the predictive ability of this model, it may be used to recommend fisheries management actions. For example, if managers were interested in predicting the presence of coho salmon redds with a minimum sensitivity of 90%, a cutoff p of 0.30 would be recommended (Table 5). Any combination of GRAVPEB, TAIL, and PROX variables that results in $\hat{p} \geq 0.30$ would result in a response prediction of 1, or selection of the site for coho salmon spawning. Further research is needed to determine the applicability of the results of this study to other watersheds.

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