SELECTION OF SPAWNING SITES BY COHO SALMON (*ONCORHYNCHUS KISUTCH*) IN FRESHWATER CREEK, CALIFORNIA

by

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in Natural Resources: Fisheries

December 2005

(Signature page)

ABSTRACT

Selection of Spawning Sites by Coho Salmon (*Onchorhynchus kisutch*) in Freshwater Creek, California

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The relative suitability of stream sites for spawning by coho salmon is related to several physical, chemical, and biological factors. The availability of high-quality spawning habitat may be much less than traditionally believed. The objectives of this study were to assess 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 to create a model of spawning habitat selection based on logistic regression analysis. I 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 in sites selected and non-selected by coho salmon during the 2004-2005 spawning season. Study results showed that coho salmon used sites with a smaller median particle diameter and a larger percentage gravel-pebble relative to sites that were not selected. Spawning sites also had higher gravel inflow rates than non-selected sites. The probability of a site being used for spawning in 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 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. Further research in Freshwater Creek is recommended to analyze the goodness-of-fit and predictive ability of this model with future datasets, as well as to assess among-tributary variation in spawning activity.

ACKNOWLEDGEMENTS

Funding for this research was provided by the California Department of Fish and Game in cooperation with Humboldt State University, the U.S. Geological Survey, and the California Cooperative Fisheries Research Unit. I am also grateful for generous scholarships provided by the Catholic Daughters of the Americas, the Alistair and Judith McCrone Graduate Fellowship, the National Fish and Wildlife Foundation Richard Guadagno Memorial Scholarship, the Marin Rod and Gun Club, and the Rotary Club of Eureka Woolford Fellowship.

A heartfelt thanks goes to my advisor, Dr. Peggy Wilzbach, for always being available to give scientific advice, answer questions, and offer encouragement. Dr. Bret Harvey and Dr. Margaret Lang guided my study methods and statistical analyses, and Dr. Howard Stauffer assisted with logistic modeling techniques. Dr. Paul DeVries and Dr. Christine May provided useful comments on the study proposal and generously loaned sampling equipment. Seth Ricker graciously shared Freshwater Creek redd survey data, and Kate Sullivan and the Pacific Lumber Company offered watershed maps and road access to stream sites. Marty Reed and Lewis McCrigler designed and repaired field equipment throughout the study. I am also grateful to all of the student technicians who worked long days in the field, braving high flows and the damp cold.

I would especially like to thank Jeremy for taking so much time out of his own work and surf schedule to ensure the success of this project. His endless optimism and encouragement made even the wettest field days seem bright and warm.

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INTRODUCTION

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; Lorenz and Eiler 1989; Bernier-Bourgault and Magnan 2002; McHugh and Budy 2004). However, some studies have suggested that depth, velocity, and substrate alone may not be sufficient to describe spawning site selection, 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, and other variables may be involved. Geist and Dauble (1998) proposed that the distribution of redds in a stream may be a function of the interaction of surface water and ground water via the hyporheic zone. They recommended incorporating additional variables in studies of spawning site selection, including temperature, dissolved oxygen, and conductivity of hyporheic water, vertical hydraulic gradient, substrate permeability, and channel morphology.

Bernier-Bourgault and Magnan (2002) found that high water velocity was a cue to brook trout (*Salvelinus fontinalis*) to select a particular site for spawning. Decreased water velocity may limit the supply of oxygen to redds and prevent the clearing of metabolic wastes from egg pockets in redds, resulting in reduced incubation success (Chapman 1988). Thus, there is a selective disadvantage to spawning in low velocities, but the energy costs associated with spawning in very high water velocities might also create significant disadvantages for spawning adults (Geist and Dauble 1998). Briggs (1953) found that the average water velocity over coho salmon redds in a coastal California stream was 0.6 m/sec. Water depths selected by spawning salmonids are often related to fish size (Hendry et al. 2001). Minimum depth criteria for coho salmon redds have been reported to vary from 0.12-0.18 m (Briggs 1953; Smith 1973; Bjornn and Reiser 1991).

In addition to stream flow and depth, substrate composition is commonly held to be an important factor in the selection of spawning sites. Salmonids tend to select substrate that is coarse and contains few fine particles (Burner 1951; McNeil and Ahnell 1964; Hoopes 1972; Curry and Noakes 1995; Bernier-Bourgault and Magnan 2002). The size of fish and water velocity constrain the maximum substrate size used by salmonids (Kondolf and Wolman 1993). Coho salmon typically spawn in gravel and pebble substrates (Platts et al. 1979; Reiser and Bjornn 1979). Burner (1951) found that coho salmon redds in the Columbia River were composed of 85% medium and small particles less than 152 mm in diameter, 10% large particles larger than 152 mm, and 5% fine particles. The presence of fine sediments in redds reduces the flow of oxygenated water to embryos and may form an armor, preventing emergence and thereby decreasing survival rates (Witzel and MacCrimmon 1983). Several studies have shown a strong inverse relationship between percentage fines and survival to emergence of coho salmon fry (McNeil and Ahnell 1964; Koski 1966; Phillips et al. 1975; Cederholm and Salo 1979; Tagart 1984).

Substrate permeability is related to the distribution of substrate sizes, percentage of fine sediments, and degree of embeddedness (McNeil and Ahnell 1964; Chapman 1988). McNeil and Ahnell (1964) found that more productive spawning streams have more permeable spawning beds, and Baxter and Hauer (2000) showed that bull trout (*Salvelinus confluentus*) redds were associated with areas of high intragravel flow. Chapman (1988) found that the permeability in egg pockets was higher than in areas adjacent to spawning activity. A possible explanation for these findings is that the conditions for embryonic development may be improved by increased inflow rates (Reiser and Wesche 1977). The detection of gravel inflow rates may be one mechanism by which spawning salmonids select redd sites that provide the greatest chance for reproductive success. However, whether salmonids have the ability to detect differences in intragravel permeability is unknown.

Vertical hydraulic gradient (VHG), which describes potential surface water-ground water exchange, is positive where upwelling occurs and negative where downwelling occurs. VHG is related to channel topography, substrate permeability, and depth of substrate, and is calculated as

$$VHG = \frac{dh}{dl}$$

where *dh* is the hydraulic head differential and *dl* is the elevation head differential. The hydraulic head differential is the difference between the water surface elevation inside a standpipe and water surface elevation of the stream, and the elevation head differential is the distance below the streambed to the first opening in the standpipe. Geist and Dauble (1998) found that upwelling hyporheic flow was associated with spawning locations of Chinook salmon and suggested that upwelling creates gradients that may provide chemical, flow pattern, and temperature cues for homing by spawning adults. Witzel and MacCrimmon (1983) found the preference of brook trout for upwelling to be so strong that redds were built in areas of upwelling even when the substrate was covered with 3 cm of silt and organic matter. Other studies have also indicated an association between upwelling and spawning locations of brook trout, bull trout, rainbow trout (*Oncorhynchus mykiss*), and sockeye salmon (*Oncorhynchus nerka*) (Webster and Eiriksdottir 1976; Sowden and Power 1985; Lorenz and Eiler 1989; Curry and Noakes 1995; Baxter and Hauer 2000).

Salmonids often spawn in areas of transition between pools and riffles, where the variability in streambed slope creates a hydraulic gradient that results in upwelling and downwelling (Bjornn and Reiser 1991). Hoopes (1972) found that spawning sockeye salmon preferred the downstream end or tail of pools where the transition from pool to riffle induces downwelling. The structure of the redd itself also creates downwelling, increasing the flow of stream water into the tailspill where egg pockets are located (Kondolf 2000). While Chinook salmon have been observed spawning in areas of upwelling (Geist and Dauble 1998), they may also select areas of downwelling (Vronskii and Leman 1991). Whether salmonids prefer areas of upwelling or downwelling, or if they simply require a significant exchange of water between subsurface and surface flows is unknown (Baxter and Hauer 2000), and preferences may vary with species and location.

The physicochemical characteristics of the hyporheic zone are related to the degree of upwelling or downwelling flow and may provide a set of cues potentially used by spawning salmonids to detect suitable spawning sites. In general, upwelling flows tend to have lower dissolved oxygen levels, but higher temperature, conductivity, and nutrients than downwelling flows (Bjornn and Reiser 1991). The availability of dissolved oxygen to embryos in the egg pocket is also determined by the relationships between gravel permeability, water velocity, and dissolved oxygen concentration (McMahon 1983). The percentage saturation of dissolved oxygen in egg pockets has been shown to limit the survival to emergence of salmonid fry (Koski 1966; Chapman 1988). Several studies have investigated the relative importance of dissolved oxygen, conductivity, and temperature in the selection of redd sites by salmonids. Bernier-Bourgault and Magnan (2002) observed no significant differences in these variables between sites selected and non-selected for spawning by brook trout. However, Baxter and McPhail (1999) found that areas selected for spawning by bull trout in a British Columbia stream had higher water temperatures than non-selected locations. Differences in dissolved oxygen, conductivity, and temperature between redd sites and non-selected sites might be expected if coho salmon prefer sites with high VHG or intragravel permeability.

Habitat complexity, including the presence of woody debris and vegetative cover, may also be important to spawning salmonids. Brook trout redds are often located near riparian cover (Witzel and MacCrimmon 1983), Chinook salmon may prefer sites associated with large woody debris (Merz 2001), and sockeye salmon spawning habitat is frequently near undercut banks, banks with overhanging vegetation, and log jams (Hoopes 1972). Instream structures, such as wood, log jams, and boulders, create areas of increased velocity that are suitable for spawning, as well as areas of decreased velocity in back eddies that provide a resting place adjacent to redds (Merz 2001). The currents created by large woody debris may also sweep fine sediments away from the spawning bed (Sedell and Swanson 1984). Merz (2001) suggested that the presence of woody debris may make less desirable habitat more suitable for spawning and may permit an increased concentration of redds in favorable stream reaches.

In addition to these microhabitat parameters, interactions with other salmon may affect redd site selection. Coho salmon redds average 2.8 m^2 in size, and a single coho salmon spawning pair may occupy and defend a territory of 11.7 m^2 (Burner 1951). High densities of spawners occupying the same areas in a stream may result in the superimposition or reuse of redds and cause increased mortality of previously deposited eggs. Hoopes (1972) questioned whether the tendency of salmonids to choose sites near other spawners is a result of social behavior or a preference for certain physical characteristics of the habitat. Witzel and MacCrimmon (1983) found that female brook trout may have a behavioral preference to spawn on existing redd sites. In another study, the presence of existing redds was an important component of redd site selection for brook trout and brown trout (*Salmo trutta*) (Essington et al. 1998).

The relative suitability of stream sites for spawning by coho salmon is thus 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). This study sought to explain why salmonids build redds in some areas of such reaches, but not in others that appear equally suitable. Due to the complexity of redd site selection and the possible involvement of many interacting variables, there is a need for models tailored to specific river systems that may more accurately predict spawning habitat use (Shirvell 1989; Geist and Dauble 1998; McHugh and Budy 2004). Much of the effort to rehabilitate populations of coho salmon and other salmonids has focused on enhancing habitat suitability for juveniles and spawning adults. Spawning site selection studies have been used to predict spawning habitat use and to suggest strategies for restoring habitat (e.g., Keeley and Slaney 1996).

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 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 water velocity, depth, and substrate criteria. I 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 non-selected by spawning coho salmon. I predicted that (i) microhabitat factors would differ between used and unused sites and (ii) the best-fitting model of spawning site selection in Freshwater Creek would be a better predictor of habitat use than a traditional model based solely on velocity, depth, and substrate.

MATERIALS AND METHODS

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 km^2 in area. The major tributaries to the mainstem Freshwater Creek are McCready Gulch, Little Freshwater Creek, Cloney Gulch, Graham Gulch, and South Fork Freshwater Creek (Figure 1). Approximately three quarters of the watershed is owned and managed for timber production by the Pacific Lumber Company. The lower watershed is zoned for small private residences and ranches.

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 6.1-9.9 ºC with a mean of 7.8 ºC between 15 December 2004 and 05 February 2005, and stream flow in the mainstem Freshwater Creek averaged 42.0 cfs during this study. The highest peak flows were 332 cfs and 305 cfs on 31 December 2004 and 7 January 2005, respectively. Based on prorating these flows with an adjacent watershed for which 30 years data are available (Bigelow 2003), these flows are estimated to occur with a recurrence interval of less than one year. The three study reaches have low gradients ranging from 1.0-1.4%.

Riparian vegetation includes alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*) willow (*Salix spp.*), blackberry (*Rubus ursinus*), and salmonberry (*Rubus*

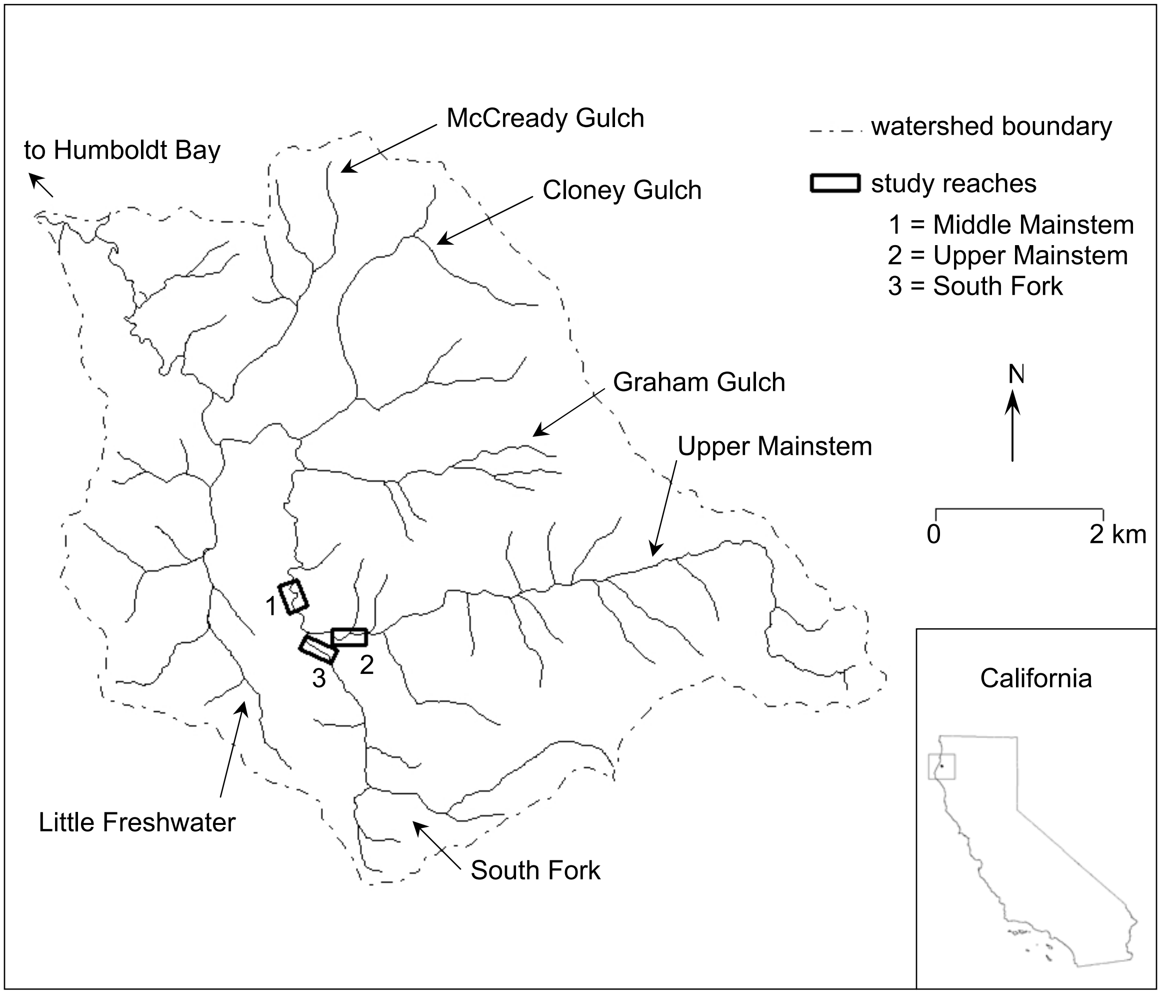

Figure 1. Location of Freshwater Creek (latitude 40°44’, longitude 124°02’) in northern California (inset) and a watershed map showing the primary coho salmon spawning tributaries and locations of the three 500-m study reaches.

spectabilis). Upslope forests are dominated by second-growth coastal redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*). Salmonids present in the study reaches include coho salmon, Chinook salmon, steelhead trout (*Oncorhynchus mykiss*), and cutthroat trout (*Oncorhynchus clarki*). Other fish species found in the basin include coast range sculpin (*Cottus aleuticus*), prickly sculpin (*Cottus asper*), Pacific lamprey (*Lampetra tridentata*), and three-spine stickleback (*Gasterosteus aculeatus*). The coastal giant salamander (*Dicamptodon tenebrosus*), southern torrent salamander (*Rhyacotriton variegatus*), northern red-legged frog (*Rana aurora*), and tailed frog (*Ascaphus truei*) complete the aquatic vertebrate assemblage.

Study Design

Three 500-m study reaches in the Middle Mainstem (3200-3700 river m), Upper Mainstem (400-900 river m), and South Fork (100-600 river m) were selected for sampling based on accessibility and observed spawning activity during the 2003-2004 season (California Department of Fish and Game, unpublished data). Areas within each reach that were unsuitable for spawning coho salmon were eliminated from sampling. Unsuitable habitat was defined as having substrate comprised 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 which indicate that coho salmon spawn in substrates ranging in size from 13-150 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 Mainstem, Upper Mainstem, and South Fork, respectively.

During the December 2004-February 2005 spawning season, I sampled all coho salmon redds and a random sample of 4-m^2 non-selected sites in the study reaches. Approximately equal numbers of redds and non-selected 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 the redds 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. Redds were sampled as soon as coho salmon stopped defending the nest site and were no longer present nearby in order to avoid disturbing the fish.

Microhabitat Sampling

I measured water depth and velocity at the center of non-selected units and at the upstream edge of redds during winter base flow conditions. This point most closely approximates conditions prior to 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 0.6 times the total depth. Surface water temperature and dissolved oxygen were measured with a YSI model 55 dissolved oxygen meter. Conductivity was measured with a YSI model 30 conductivity meter.

A Wolman pebble count was used to select and record the size classes of substrate particles found in the sample unit. This method has been shown to be more precise and reproducible than visual estimates of the percentage of sediment size classes appearing in an area (Kondolf and Li 1992). I used grid sampling as described by Bunte and Abt (2001) to perform the pebble count. A portion of a soccer net served as a 12x12 grid with intersections spaced approximately 15 cm apart. I systematically selected 144 particles with a pin flag at the intersections in the net 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 stream bed materials finer than 4 mm were recorded as fines. While the process of redd construction by salmonids has been shown to reduce fine sediments within redds (Kondolf 2000), I sampled nest sites 3-10 days after construction when small particles had likely moved back into the worked gravel of the redd (Chapman 1988; Grost et al. 1991). I 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 non-selected units.

Several researchers have debated the usefulness of a single metric to describe stream substrate. The geometric mean diameter, d_g, and the fredle index are two metrics commonly used as indices of gravel quality. However, the usefulness of these metrics may be limited because gravel mixtures with the same geometric mean diameter or fredle index can have very different size compositions. Kondolf (2000) proposed the use of d_{50}, the median particle diameter, or size at which 50 percent of particles are finer. Median particle diameter was used in this study to evaluate differences between redds and non-selected sites. Tappel and Bjornn (1983) recommended that redd particles should be characterized by the proportion within a specified size range. 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 was used in logistic regression modeling.

I inserted a modified Terhune Mark VI standpipe to a depth of 20 cm in the substrate to measure gravel inflow rate (ml/sec), which is an index of intragravel permeability (cm/hr). This depth corresponds to the mean depth of coho salmon egg pockets below the original level (i.e. before redd construction) of the stream bed (DeVries 1997). The standpipe was inserted at the upstream edge of redds in order to avoid disturbance to developing embryos in the mound. Gravel inflow rates were measured following the protocol of Barnard and McBain (1994). A vacuum pump was used to apply suction 2.5 cm below the surface of the water inside the standpipe. While maintaining this constant pressure head, water was drawn through the perforated standpipe buried in the substrate, and a stopwatch was used to measure the time required to collect a volume of water. Five replicates were recorded for each sample point.

Physicochemical factors associated with the hyporheic water were sampled by inserting the dissolved oxygen and conductivity meter probes into the standpipe. Similarity between conductivity at the surface and in the standpipe may indicate that the hyporheic zone water is comprised largely of stream surface water, while elevated conductivity values suggest a higher proportion of groundwater. However, the relative proportion of groundwater and surface water does not necessarily indicate whether the sample point is in a zone of upwelling or downwelling (Geist et al. 1998). These hydraulic variables were measured using a device described by Wanty and Winter (2000). I 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 difference between the height of the hyporheic water inside the tubing and the stream surface water outside the tubing. VHG was calculated by dividing this difference by 14 cm, which is the distance between the streambed and the first opening in the buried standpipe.

In order to quantify other attributes of the physical habitat, I described both selected and non-selected units in relation to the presence or absence of existing redds within a distance of 10 m, and presence or absence of riparian or instream cover within 2 m. Cover types included overhanging riparian vegetation, instream woody debris, boulders, or 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. Kruskal-Wallis non-parameteric rank sum tests were used to compare microhabitat variables between selected and non-selected sites (Zar 1999). To avoid the compounding of error associated with testing substrate particle sizes that were mutually dependent within samples, I used the Bonferroni procedure (Neter et al. 1985) 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 Inc. 2000).

I used multivariate logistic regression to model the selection of spawning habitat in the study reaches by coho salmon. With this method, the presence of a redd is taken to imply suitability, and the presence or absence of redds at a range of sites is modeled as a function of the various continuous and categorical microhabitat variables sampled (McHugh and Budy 2004). In this study, the response variable is 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 between the linear domain and the finite response domain is given by the equation

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

Using the approach of Burnham and Anderson (2002), I developed a set of 20 models for spawning site selection in Freshwater Creek. The models tested the hypotheses that inflow rates and upwelling and downwelling are better predictors of redd site selection than the traditional model, and that interactions with other spawners play a role in site selection. Candidate models were also developed to test whether habitat unit type (i.e. pool tail or run tail) might better explain the data than gravel inflow rates or VHG, and whether percentage fines explains more of the variability in the data than percentage gravel-pebble. I also included models with and without the variables dissolved oxygen, temperature, and conductivity to evaluate the importance of these physicochemical factors. All candidate models were tested for plausibility with the data and ranked using the Akaike information criterion corrected for small sample sizes (AIC_c). *A posteriori* exploratory model selection was used in order not to overlook any potentially good-fitting models. Subsets of the best-fitting model were also analyzed to estimate the contributions of each separate variable to explaining the data. Using Kruskal-Wallis non-parametric rank sum tests, I examined relationships among independent variables in the best-fitting model in order to ensure that multicollinearity between variables did not exist.

To determine how well the best-fitting model fit the data, I used a χ^2 goodness-of-fit test (Hosmer and Lemeshow 1989) and a classification table. The latter approach simulates responses (1 for selected; 0 for non-selected) 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. 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 dataset, 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 Inc. 2003). Data were pooled among stream study reaches to improve statistical power and robustness.

RESULTS

A total of 53 selected redd sites and 52 non-selected sites were sampled in the three study reaches between 15 December 2004 and 05 February 2005. No coho salmon spawning activity was observed in the study reaches after this period. Of the sites sampled, 20 were in the Middle Mainstem (7 selected and 13 non-selected), 6 were in the Upper Mainstem (3 selected and 3 non-selected), and 79 were in the South Fork (43 selected and 36 non-selected) (Figure 2).

The positioning of redds with respect to water depth, velocity, and substrate was in agreement with values reported in the literature. Coho salmon redds in Freshwater Creek were located at depths ranging from 4 cm to 30 cm, with a mean 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 mm to 45 mm, averaging 25 mm.

Surface water velocity ($\chi^2 = 2.16$, df = 1, $p = 0.141$) and depth ($\chi^2 = 0.87$, df = 1, $p = 0.350$) were not significantly different between selected and non-selected sites (Figure 3). Coho salmon used sites with a smaller d_{50} (Kruskal-Wallis rank sum test: $\chi^2 = 12.07$, df = 1, $p < 0.001$) and a larger percentage gravel-pebble ($\chi^2 = 17.74$, df = 1, $p < 0.001$) relative to sites that were not selected (Table 1). The fraction of substrate composed of cobble was significantly lower at redd sites than at non-selected sites ($\chi^2 = 12.01$, df = 1, $p < 0.001$; Figure 4). Spawning sites had higher gravel inflow rates than non-selected sites ($\chi^2 = 9.82$, df = 1, $p = 0.002$; Figure 3). The percentage

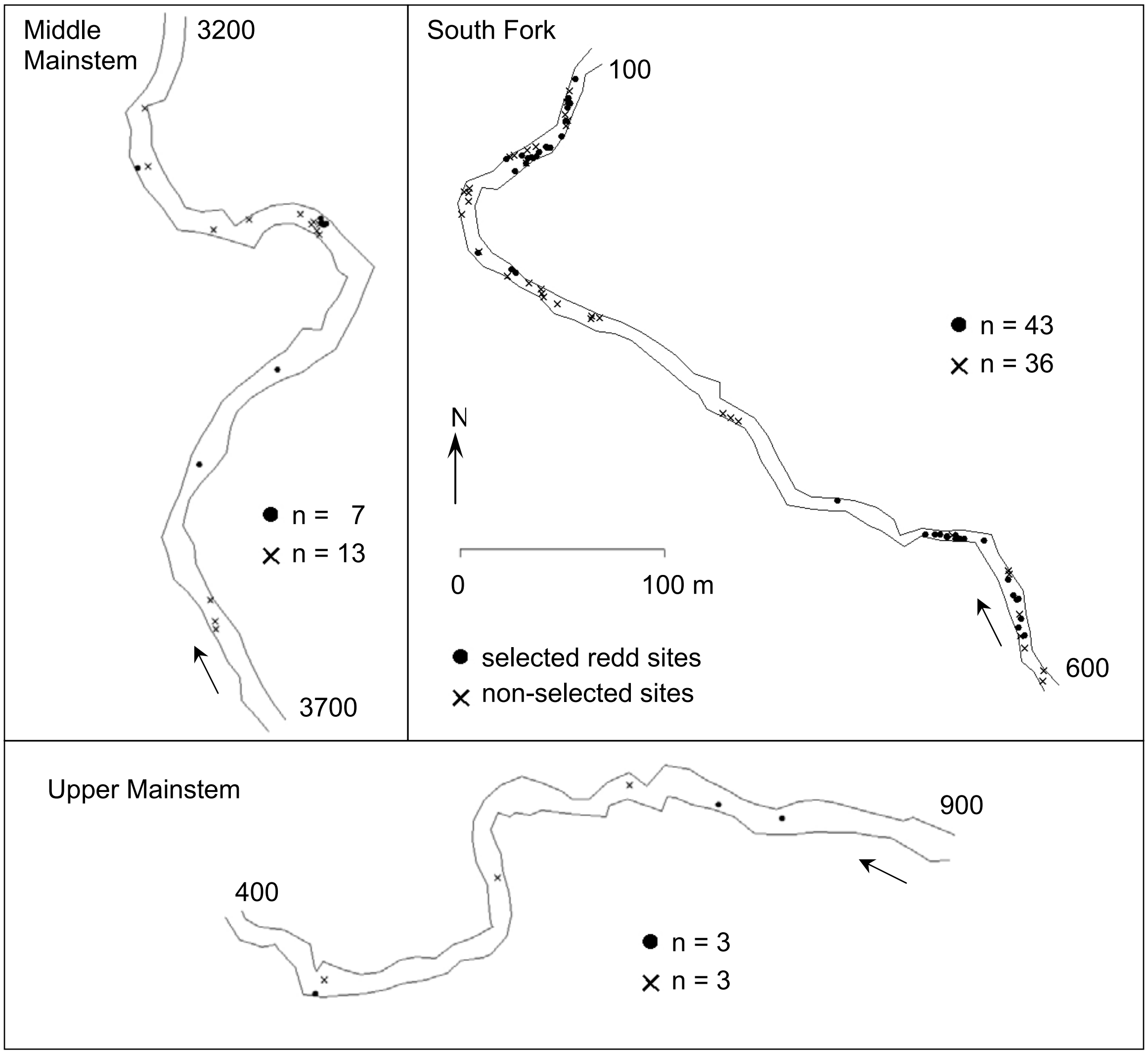

Figure 2. Maps of stream study sections in the Freshwater Creek watershed showing sample locations of coho salmon redds and non-selected sites. Numbers at the beginning and end of the Middle Mainstem reach indicate stream distance in meters upstream of the confluence of Graham Gulch with the mainstem, while numbers on the South Fork and Upper Mainstem reaches represent stream distance in meters upstream of the confluence of the South Fork and Upper Mainstem. Arrows indicate the direction of stream flow.

Table 1. Means and standard deviations of microhabitat characteristics at selected coho salmon redd sites and non-selected sites in the Freshwater Creek watershed. D_{50} is the median diameter of substrate particles. Cover is a binary variable indicating the presence or absence of riparian cover or instream woody debris, boulders, or undercut banks within 2 m of the sample unit. Proximity to other redds represents the presence or absence of existing 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 as determined by a non-parametric Kruskal-Wallis test ($p < 0.05$).

	Selected sites		Non-selected 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

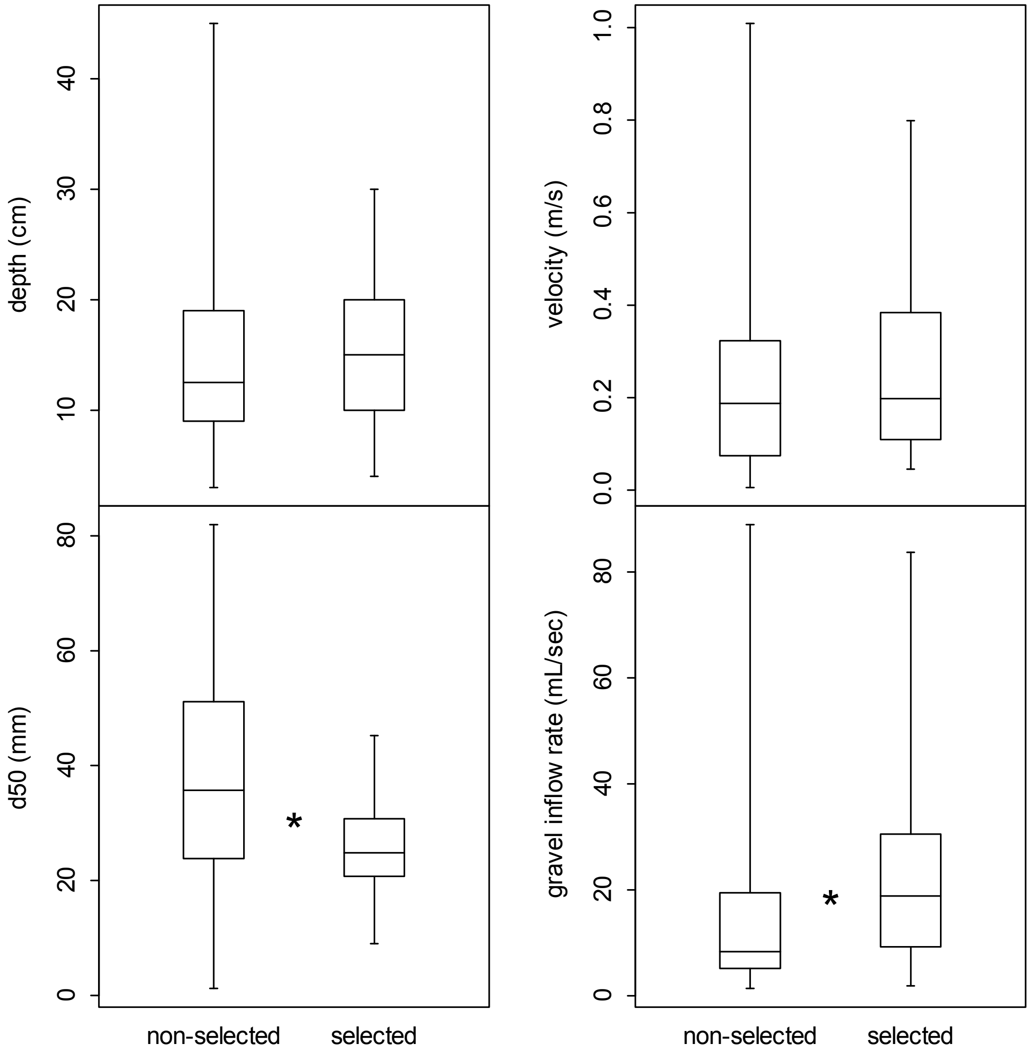

Figure 3. Box-and-whisker plots representing depth, velocity, gravel size (represented by median diameter, d_{50}), and gravel inflow rates at sites selected and non-selected for coho salmon spawning in Freshwater Creek. The lower and upper whiskers correspond to the minimum and maximum of the range of data, respectively. The lower and upper bounds of each box represent quartiles, and the middle line represents the median. Asterisks indicate statistically significant differences between means based on a Kruskal-Wallis test ($p < 0.05$).

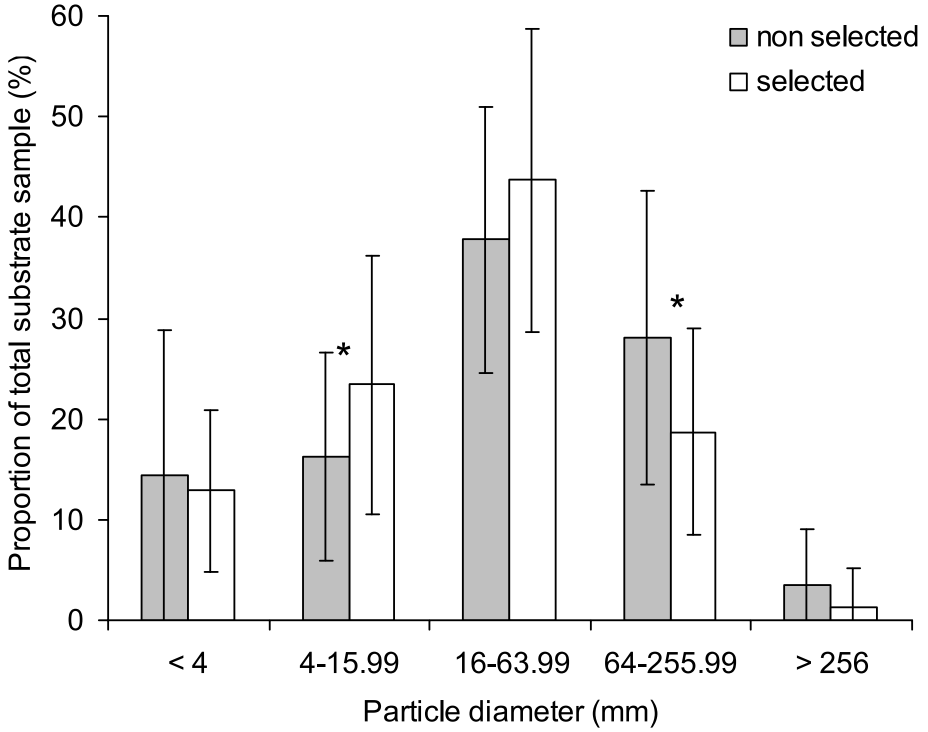

Figure 4. Mean proportion of particle size classes at sites selected and non-selected for coho salmon spawning in Freshwater Creek. Bars are means ± standard deviation. For each particle size class, asterisks indicate that data are significantly different as determined by a Kruskal-Wallis test ($p < 0.01$).

gravel-pebble within the substrate was positively correlated with gravel inflow rates ($R^2 = 0.13$; Figure 5), but the percentage fine particles less than 4 mm was not related to gravel inflow rates. VHG, the potential for upwelling or downwelling surface water, did not vary significantly between selected and non-selected sites ($\chi^2 = 1.22$, df = 1, $p = 0.269$; Table 1).

Mean temperature, dissolved oxygen, and conductivity did not vary significantly between selected and non-selected sites ($p > 0.05$). However, hyporheic water was significantly warmer than surface water at both selected sites (paired *t*-test: $t = 4.07$, df = 52, $p < 0.001$) and non-selected sites ($t = 3.63$, df = 51, $p < 0.001$; Table 2). Dissolved oxygen was significantly lower in interstitial water (selected sites: $t = 5.15$, df = 52, $p < 0.001$; non-selected sites: $t = 5.07$, df = 51, $p < 0.001$), and conductivity was significantly higher in interstitial water than surface water (selected sites: $t = 3.99$, df = 52, $p < 0.001$; non-selected sites: $t = 2.76$, df = 51, $p = 0.008$; Table 2).

A total of twenty 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 0.42, indicating a 42% chance that this model is the best-fitting given

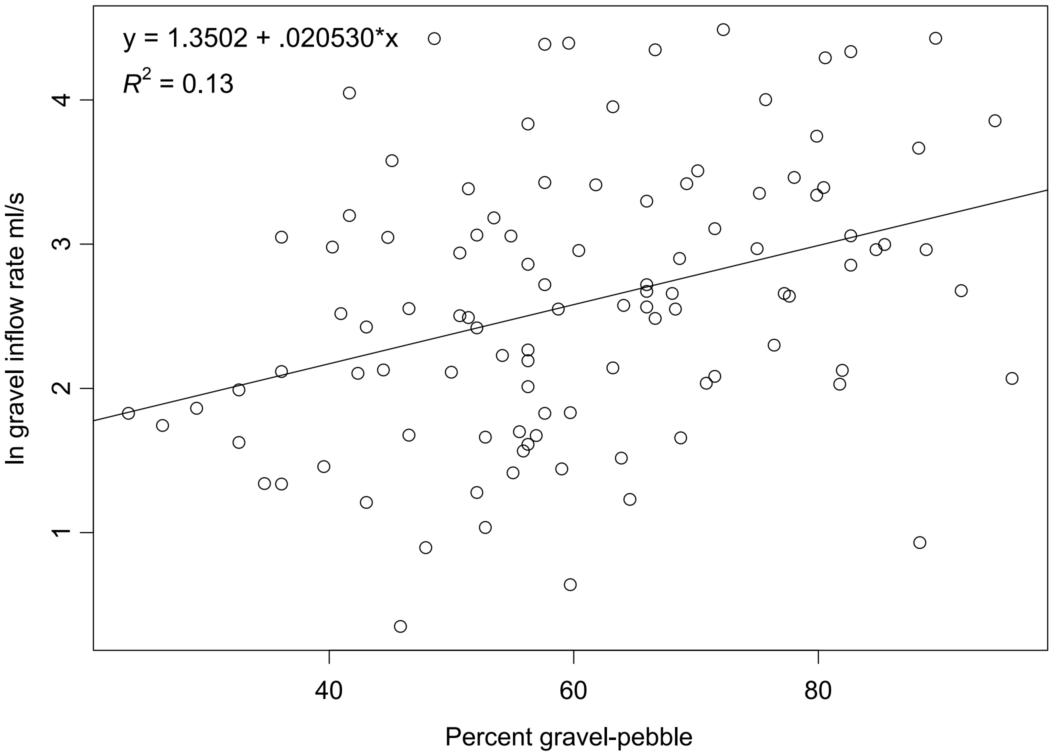

Figure 5. Plot of log gravel inflow rates vs. percent gravel-pebble in Freshwater Creek during winter 2004-2005. Points represent data from both selected and non-selected sites for coho salmon spawning. The regression is significant at α = 0.05 (F =14.88, df = 1, 103, $p < 0.001$).

Table 2. Physicochemical characteristics of surface and hyporheic water at sites selected and non-selected for coho salmon spawning in Freshwater Creek during the 2004-2005 winter. Asterisks indicate statistically significant differences as determined by paired *t*-tests ($p < 0.05$).

	Selected sites			Non-selected sites		
	Surface		Hyporheic	Surface		Hyporheic
Temperature (°C)	7.8 ± 0.9	*	7.8 ± 0.9	7.9 ± 0.9	*	8.0 ± 0.8
Dissolved oxygen (mg/l)	11.6 ± 0.4	*	10.9 ± 1.1	11.5 ± 0.5	*	10.5 ± 1.7
Conductivity (µS/cm)	82.1 ± 13.5	*	86.1 ± 14.6	86.4 ± 13.8	*	91.0 ± 16.1

Table 3. Model selection results describing the selection of stream sites for spawning by coho salmon in the Freshwater Creek watershed. The abbreviations for model covariates are as follows: INF = gravel inflow rate, GRAVPEB = percent gravel-pebble, FIN = percent fines less than 4 mm, VHG = upwelling or downwelling, VEL = surface water velocity, PROX = presence of existing redds nearby, DEP = surface water depth, TAIL = location at a pool-riffle or run-riffle transition, COV = presence of riparian or instream cover, DO = hyporheic dissolved oxygen, TEMP = hyporheic temperature, and COND = hyporheic conductivity. The best-fitting model with the lowest AIC_c and the competing model are highlighted in bold print.

Model covariates	k	AIC_c	$\Delta\ AIC_c$	Akaike weight	R^2
1 (null model)	1	147.6	28.4	0.000	x
INF	2	145.0	25.8	0.000	0.06
GRAVPEB FIN	3	131.2	12.0	0.001	0.24
FIN INF	3	146.7	27.5	0.000	0.06
INF VHG	3	147.1	27.9	0.000	0.06
GRAVPEB TAIL PROX	**4**	**119.2**	**0.0**	**0.423**	**0.38**
DEP VEL GRAVPEB	4	132.7	13.5	0.000	0.24
GRAVPEB FIN INF	4	132.8	13.6	0.000	0.24
INF VHG PROX	4	141.8	22.6	0.000	0.15
VEL INF VHG	4	148.5	29.3	0.000	0.07
DEP GRAVPEB TAIL PROX	**5**	**120.0**	**0.8**	**0.280**	**0.39**
GRAVPEB FIN INF TAIL	5	126.2	7.0	0.013	0.33
GRAVPEB FIN INF PROX	5	129.5	10.3	0.002	0.30
VEL GRAVPEB FIN INF	5	134.7	15.5	0.000	0.25
INF VHG COV PROX	5	142.8	23.6	0.000	0.16
DEP GRAVPEB INF TAIL PROX	6	121.3	2.1	0.146	0.40
DEP GRAVPEB FIN TAIL PROX	6	122.0	2.8	0.102	0.39
DEP VEL GRAVPEB FIN INF TAIL PROX	8	124.7	5.5	0.027	0.41
DEP VEL GRAVPEB FIN INF TAIL VHG COV PROX	10	128.2	9.0	0.005	0.42
DEP VEL GRAVPEB FIN INF TAIL VHG COV PROX DO TEMP COND	13	134.0	14.8	0.000	0.44

the dataset and collection of candidate models ($AIC_c = 119.2$, $R^2 = 0.38$). Examination of the subsets of the best-fitting model showed that the individual covariates GRAVPEB, TAIL, and PROX explained 21%, 10%, and 12% of the variation in the data, respectively (Table 4). None of the subset models performed as well as the best-fitting 3-covariate model. Based on this model, the linear *logit* function was estimated as (Table 5):

$$logit = -4.8586 + 6.0490*GRAVPEB + 1.7386*TAIL + 1.3287*PROX$$

There was no indication of multicollinearity between the variables GRAVPEB and TAIL or GRAVPEB and PROX (Kruskal-Wallis rank sum test: $\chi^2 = 0.02$, df = 1, $p = 0.882$, and $\chi^2 = 2.87$, df = 1, $p = 0.090$, respectively). Similarly, there was no significant relationship between pool or run tails and proximity to existing redds ($\chi^2 = 0.19$, df = 1, $p = 0.662$)

The next best model overall contained the same three variables, with the added covariate depth ($\Delta AIC_c = 0.8$, Akaike weight = 0.28). 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. The full model containing all 13 covariates explained just 6 percent more of the variation in the data than the best-fitting model with 3 covariates, and had a very low Akaike weight of <0.001 (Table 3). In this study, the best-fitting model was a better predictor of spawning habitat use than the

Table 4. Subsets of the best-fitting logistic regression model for spawning site selection by coho salmon in Freshwater Creek during the 2004-2005 winter. The abbreviations for model covariates are as follows: GRAVPEB = percent gravel-pebble, PROX = presence of existing redds nearby, and TAIL = location at a pool-riffle or run-riffle transition.

Model covariates	k	AIC_c	Δ AIC_c	Akaike weight	R^2
GRAVPEB	2	131.9	12.7	0.002	0.21
TAIL	2	141.9	22.7	0.000	0.10
PROX	2	139.8	20.6	0.000	0.12
GRAVPEB TAIL	3	124.7	5.5	0.059	0.30
GRAVPEB PROX	3	126.4	7.2	0.026	0.29
TAIL PROX	3	134.2	15.0	0.001	0.21
GRAVPEB TAIL PROX	4	119.2	0.0	0.914	0.38

Table 5. Intercept and covariate coefficient estimates for the best-fitting models of coho salmon spawning site selection in Freshwater Creek during the 2004-2005 spawning season.

Model	Parameter	df	Estimate	SE	χ^2	*p*
Pooled 1	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
Pooled 2	Intercept	1	-5.9538	1.5053	15.64	< 0.001
	DEP	1	0.0460	0.0389	1.40	0.237
	GRAVPEB	1	6.7836	1.7645	14.78	< 0.001
	TAIL	1	1.5741	0.6251	6.34	0.012
	PROX	1	1.3507	0.5011	7.27	0.007

traditional depth, velocity, and 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 statistical evidence to reject the null hypothesis that the model fits the data well ($\chi^2 = 7.56$, df = 7, $p = 0.373$). This model classified sites well, with 71.4% correctly classified by resubstitution (Table 6), and 73.3% correctly classified 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.

Table 6. 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. 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.

	Percentages				
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

DISCUSSION

The probability of a site being used for spawning in the Middle Mainstem, Upper Mainstem, and South Fork 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 other variables may be important in the suitability of habitat for spawning, the inclusion of these variables in models did not improve the classification of sites. The mean depth at redd sites was above the minimum depth criteria 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 are commonly used in PHABSIM models of spawning habitat, they did not explain much of the variation of the data in this study, perhaps owing to the relative homogeneity of these measurements in the study reaches. Since deep pools were not included in the population of sampling sites, slow-moving, deep waters were not encountered. However, Bernier-Bourgault and Magnan (2002) also found that depth was not a significant variable in the selection of redd sites by brook trout.

In this study, hyporheic dissolved oxygen and conductivity were not significantly different between selected sites and non-selected sites. While some studies have shown dissolved oxygen and conductivity to be significantly different between redd sites and unused sites (Geist 2000), others have shown that oxygen gradients and ion concentrations were not involved in homing to spawning areas (Curry and Noakes 1995; Bernier-Bourgault and Magnan 2002). The range of surface water temperatures at redd sites was within the range at which coho salmon spawning was observed by Burner (1951), and the range of hyporheic temperatures was within the optimum range suggested for egg incubation (Bell 1973). Geist (2000) found that water temperature was not significantly different between selected and non-selected Chinook salmon spawning sites, and temperature was not a significant variable in the selection of redd sites by coho salmon in Freshwater Creek.

The results of this study suggest that coho salmon may be more likely to use substrate particle sizes as cues in the selection of spawning sites than characteristics of stream flow or physicochemistry. Curry and Noakes (1995) proposed that brook trout redd sites may be selected using visual or tactile stimuli such as substrate composition if minimum physical, thermal, and chemical thresholds were satisfied. This may have been the case in this study because depth, velocity, temperature, dissolved oxygen, and conductivity did not appear to limit the availability of spawning habitat. 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 non-selected sites as I had expected. Because pools where fines typically accumulate were eliminated from the sampling area, substrate particles in non-selected 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 utilized 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 66.2 cm (Seth Ricker, California Department of Fish and Game, 50 Ericson

Court, Arcata, CA 95521, 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 selected sites than in non-selected 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 fine particles less than 4 mm was not significantly different between selected and non-selected 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 have been shown to be 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 non-selected sites may explain why fines did not play a role in spawning site selection, but the fraction gravel-pebble (4-64 mm) did. Gravel inflow rates were significantly higher in selected redd sites than in non-selected sites, but were not in the top models of spawning site selection. One possible reason for this is the fact that inflow rates were highly variable, and accounted for only 6% of the variation in the data. Since inflow rates varied directly with percentage 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).

Vertical hydraulic gradient did not vary significantly between selected and non-selected sites. This may be due in part to the imprecision of the measurement technique (Wanty and Winter 2000), or to a lack of range of VHG in the study reaches. The structure of the redd itself may create localized downwelling into the redd mound (Kondolf 2000). Inserting the standpipe upstream of the redd pot may have prevented detection of this downwelling. If VHG had been measured instead in the redd mound, stronger downwelling currents may have been encountered at selected sites. Hyporheic exchange at the channel bedform scale also varies with discharge and water surface slope (Vaux 1968), and this variability may have led to the finding of insignificance. Although the difference in VHG was not significant in this study, coho salmon may prefer sites with a potential for downwelling. Upwelling ground water 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 (Baxter and Hauer 2000). However, at the southern end of the distribution of coho salmon, dissolved oxygen may be relatively more important than temperature to the development of alevins.

In Freshwater Creek, coho salmon may favor redd sites where downwelling surface water brings oxygenated water to the egg pocket. Female coho salmon showed a significant preference for spawning in pool to riffle and run to riffle transitions, where convex bedforms induce downwelling. 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.

The proximity of potential spawning sites to other redds was another significant factor in redd site selection in Freshwater Creek. This suggests that social interactions may be important to spawning coho salmon. Female coho salmon in Freshwater Creek often select existing redd sites on which to spawn (Seth Ricker, California Department of Fish and Game, 50 Ericson Court, Arcata, CA 95521, 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 Mainstem and Upper Mainstem, 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 and brown trout could not be explained by habitat availability alone, and females have a behavioral preference to spawn on existing redd sites. They argue that the presence of existing redds makes potential sites more attractive to females than they would be otherwise.

Information about coho salmon carrying capacity and spawning habitat availability in Freshwater Creek was insufficient to allow me to make conclusions regarding the possible effects of fish density. However, in this study, redds tended to occur close to other redds even in the Middle Mainstem and Upper Mainstem reaches where fish densities were low. Logistic regression analysis of selected and non-selected sites in these two reaches revealed that the best-fitting model of spawning site selection contained the same variables as the model resulting from analysis of the pooled data from all three reaches. Proximity to existing redds alone accounted for 11.9% of the variation in the data in this study. Nevertheless, further study in Freshwater Creek is required to determine 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.

The results of multivariate logistic regression analysis indicated that spawning site selection in 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 6)

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

If $\hat{p}$ is greater than a threshold p, then the site is predicted to be selected for spawning, and if $\hat{p}$ is less than the threshold 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

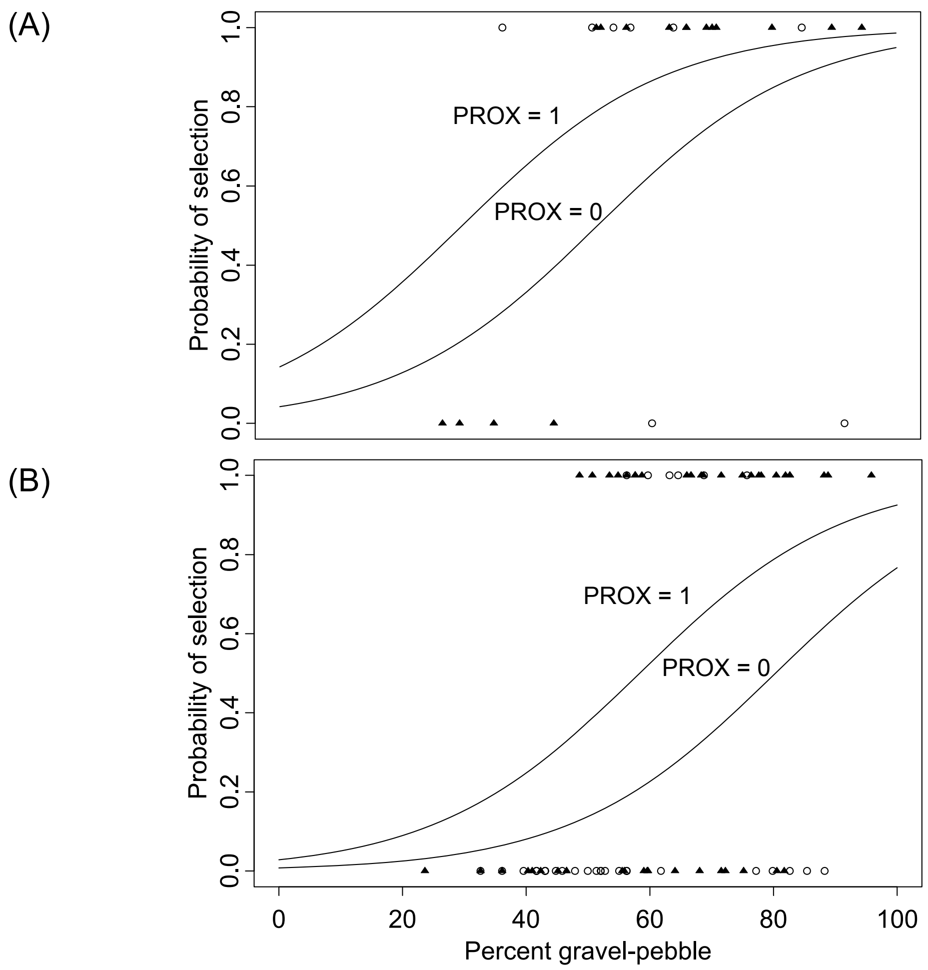

Figure 6. Plots of predicted probabilities of site selection for coho salmon spawning vs. percent gravel-pebble in Freshwater Creek. The plots represent sites located at pool-riffle or run-riffle transitions (A) and sites not located at pool or run tails (B). The upper curve in each plot corresponds to sites within 10 m of existing redds (PROX = 1), and the lower curve corresponds to sites not in proximity to other redds (PROX = 0). Observed values of the percent gravel-pebble at selected (*p* = 1) and non-selected (*p* = 0) sites are superimposed on each plot. Filled triangles and open circles represent sites at which existing redds were and were not observed within 10 m, respectively.

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 threshold p of 0.30 would be recommended (Table 6). 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. It should be noted that the Freshwater Creek basin has been actively managed for timber harvest and should not be considered a pristine watershed. Further research is needed to determine the applicability of this study to other watersheds.

One goal of salmonid recovery is to increase the abundance of fish by improving the various habitats that are utilized at different life history stages. The limited availability of good spawning habitat in any watershed directly impacts the reproductive success of salmonid populations. The traditional habitat model, PHABSIM, may overestimate the true availability of suitable spawning habitat if other variables are involved in redd site selection (Geist and Dauble 1998). The results of this study indicate that other variables may indeed be involved in redd site selection in Freshwater Creek, as the best-fitting model clearly out-performed the model containing water depth, velocity, and substrate variables.

Understanding the parameters that make one stream more productive than another is especially important for coho salmon populations that are threatened by habitat alteration. By identifying the habitat features that attract spawning coho salmon, managers may be better able to develop spawning habitat enhancement projects that improve their reproductive success. For example, knowledge of the habitat preferences of salmonids has been used to select potential areas for the creation of artificial spawning habitat in natural stream systems (e.g., Kondolf et al. 1996; Bernier-Bourgault and Magnan 2002). Redd site selection models may also be used to quickly and efficiently assess the availability of suitable spawning habitat in stream systems.

Many fisheries managers have cited the need for a more holistic, ecosystem-based approach to habitat enhancement (Waters 1995). At a larger spatial scale, the overall availability of suitable habitat for spawning in a given stream may be influenced by land management history. Several studies have documented the increased siltation of streams resulting from logging operations (McNeil and Ahnell 1964; Burns 1972; Cederholm and Salo 1979). Landslides are also responsible for a large amount of fine sediments in the spawning gravels of coho salmon (Cederholm and Reid 1987). Logging near streams may reduce natural sources of woody debris in streams, which may further compound these sedimentation effects. Further research is needed in Freshwater Creek to assess among-tributary variation in spawning activity. In this study, the South Fork reach had over 4 times as many coho salmon redds as the Middle Mainstem and Upper Mainstem reaches combined. Land management history, geology, gradient, drainage area, or other factors may explain some variation in the availability of preferred redd sites between subbasins.

In conclusion, the best model of spawning site selection in Freshwater Creek explains habitat use based on substrate, geomorphic channel unit, and proximity to existing redds. Further research is recommended to analyze the goodness-of-fit and predictive ability of this model with future datasets. Coho salmon also selected sites with significantly higher gravel inflow rates, and future studies may help determine the ability of coho salmon to detect inflow rates and how permeability may change through time from the period preceding redd construction to the emergence of fry.

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