Bull Trout

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Factors Affecting the Distribution and Abundance of Bull Trout: An Investigation at Hierarchical Scales

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Abstract.—The reported declines of many stocks of bull trout *Salvelinus confluentus* in the Pacific Northwest has generated much interest in developing conservation and management plans to protect and rebuild populations. These plans require knowledge of the specific requirements of bull trout throughout their range. We describe the relationships between distribution and abundance of bull trout and physical and biotic factors across a large portion of their historical range. We surveyed 1,057 randomly selected sites from 93 streams within 18 major drainages throughout Washington, Idaho, and Montana for the presence of bull trout. We used logistic regression to assess the relationship between the occurrence of bull trout and several physical and biotic factors at site and habitat scales of analysis. Robust regression assessed relationships between densities of bull trout and physical parameters at site, stream, and basin scales of analysis. Bull trout occurred significantly more often in sites within alluviated lowlands and valleys and in sites with undercut banks, large substrates, pools, and where trees and shrubs were the dominant riparian vegetation. Bull trout occurrence at the site scale was inversely related to the percentage of canopy cover and vegetation overhang and the presence of brook trout *S. fontinalis* and rainbow trout *Oncorhynchus mykiss*. At the habitat scale, bull trout most often used large, deep pools that lacked extensive canopy cover. They rarely used fast-water habitats with fine sediments, extensive canopy cover, and brook trout. Bull trout densities correlated positively with pool depth, undercut banks, and diverse gradients, and indirectly with fine sediments at both the stream and site scales of analysis. In addition, high densities of bull trout correlated with less vegetation overhang and greater, but variable, percentages of wood and boulder cover at the site scale. The combinations of variables that correlated significantly with bull trout densities varied considerably among different basins. Additionally, the amount of variation in bull trout densities explained by significant variables decreased at finer scales of analysis. These results indicate a hierarchical relationship between the distribution and density of bull trout and physical variables. Thus, land management for bull trout enhancement or protection should be site-specific and tailored within a similar hierarchical framework.

Because of the reported decline of many stocks of bull trout *Salvelinus confluentus* within the Pacific Northwest (Goetz 1989), interest has increased in developing conservation or management plans to protect and rebuild existing populations. For example, the state of Idaho, in cooperation with several agencies, recently proposed a strategy that would reverse the decline of bull trout

and restore their habitat (IDFG 1994). Others have proposed similar plans to protect bull trout in their respective states. Plans to protect bull trout populations will require information on the distribution and habitat requirements of bull trout populations within and across their existing range. Without adequate knowledge of bull trout requirements throughout their range, these plans may be too restrictive in some areas and provide insufficient protection in others. Acquisition of data on habitat needs is a priority for researchers (Platts et al. 1993; Rieman and McIntyre 1993). Although several studies (e.g., Pratt 1984; Fraley and Shepard 1989; Buckman et al. 1992; Dambacher et al. 1992; Goetz 1994) describe the habitats of bull trout, most research in localized areas may not apply to other regions, where biotic and abiotic factors may differ.

Rieman and McIntyre (1995) reported that large-scale spatial processes affect the persistence of bull trout in the Boise River basin, Idaho. They showed that the area of available habitat above 1,600 m in elevation influences the distribution of bull trout populations. They also noted that stream width partially explained occurrence of bull trout, but they could not assess its effects because of collinearity. Because of the presumed restriction of populations by water temperature, Rieman and McIntyre (1995) defined watersheds above 1,600 m in elevation as areas of potential bull trout habitat. Others (e.g., Pratt 1984; Fraley and Shepard 1989) have also noted the importance of water temperature as a factor influencing distribution of bull trout. In addition, percent fine sediment, cover, and hydraulic complexity may also affect bull trout distribution (Pratt 1984; Weaver and White 1985). Hence, both large- and small-scale physical processes may determine distribution and density of bull trout. A hierarchical approach that relates physical processes at various landscape scales to bull trout populations may be useful. Past studies have related salmonid populations to basin geology (Fraley and Graham 1982; Nelson et al. 1992) and to physical features of aquatic habitat (Goetz 1989; Weaver and Fraley 1991; Buckman et al. 1992). Therefore, a methodology that integrates landform and fluvial processes may permit determination of bull trout habitat associations within varied geologic types.

Biotic components such as competition, predation, and hybridization can also influence distribution of bull trout. Relative densities of other salmonid species, native and introduced, are needed to evaluate the potential for interaction with, or displacement of, bull trout. Several investigators (Buckman et al. 1992; Dambacher et al. 1992; Zillner 1992; Clancy 1993) have noted the likelihood of competitive displacement or hybridization between bull trout and introduced salmonids. Hence, one should consider biotic components as potential determinants of the presence and frequency of bull trout in a watershed.

In this report we describe the relationship between the occurrence of bull trout and several physical and biological variables. Our purpose was twofold: to identify the physical and biological variables that are important in discriminating between streams with and without bull trout and to identify those variables important in discriminating among bull trout densities within occupied streams. To ascertain if bull trout populations in various watersheds respond similarly to habitat parameters, we examined relationships at various scales. We also tested interspecific associations (i.e., how often two species are found together in the same location) between all possible salmonid pairs. Populations may respond to habitat complexes differently because of interspecific competition, habitat availability, or stock- or basin-specific processes of habitat selection. If differential responses do occur, it is requisite for scientists and managers to understand these differences so they can fine-tune research and management programs.

Study Area

We selected study streams on or adjacent to lands owned by Plum Creek Timber Company in Washington, Idaho, and Montana. Because juvenile bull trout typically occupy small watersheds (Rieman and McIntyre 1993), we selected second-, third-, or fourth-order streams from watersheds with varied land uses. Most of the watersheds we sampled had little to no information on the presence of bull trout, but all lay within the historic bull trout range and upstream from known bull trout populations. Most of the streams that we surveyed were located in the Cascades or Northern Rockies ecoregions. Portions of some streams were also located in the Eastern Cascade Slopes and Foothills, and Montana Valley and Foothill Prairies ecoregions.

We surveyed 93 streams within 18 major drainages throughout Washington, Idaho, and Montana (Table 1). Washington systems generally consisted of mixed volcanics, igneous materials, and basalt. Some sedimentary types also occurred in the Yakima and Naches systems. Granites constituted the

TABLE 1.—Streams surveyed for the presence of bull trout in Washington, Idaho, and Montana. An asterisk (*) indicates streams with bull trout.[a]

Basin	Stream surveyed
	Washington
Pend Oreille River	*Winchester, *West Branch LeClerc, *East Branch LeClerc, Middle Branch LeClerc, S.F. Tacoma, Calispell, Cee Cee Ah
Green River	Intake, Sawmill, upper Green, Twin Camp, Pioneer, Tacoma
Yakima River	*Box Canyon, *Gold, Domerie, French Cabin, Little, Big, N.F. Taneum, S.F. Taneum, W.F. Teanaway, N.F. Teanaway
Naches River	*Indian, *Crow, N.F. Little Naches, M.F. Little Naches
	Idaho
Lochsa River	*Rock, *Twin, *Walton, Pack, Upper Brushy, N.F. Spruce, Parachute
St. Joe River	*Mosquito, *Medicine, *Beaver, *Simmons, *Fly, E.F. Bluff, Allen, Burton, Kelly, Red Raven, Alpine, Sisters, Lick, Fishook, Boulder
Little N.F. Clearwater River	*Rutledge, *Adair, *Jungle, Spotted Louis, *Lost Lake, *Montana
Priest Lake	Caribou, Sema
	Montana
Swan River	*Lion, *Elk, *Squeezer, *Cold, *Goat, Beaver
Thompson River	*Jungle, *Deerhorn, *Little Thompson, *Schroeder, Murr, Meadow, Lazer
Fisher River	Trail, Little Wolf, Richards, Elk, McGinnis, East Fisher, Owl–Himes
Kootenai River	Ruby, Dunn, Shaffer
Flathead Lake	Dayton
Whitefish Lake	Lazy
Little Bitteroot River	Tamarack
Clark Fork River	Mill, Bear, Buffalo Bill, Lynch, W.F. Petty
Blackfoot River	*Belmont, East Twin, Fawn, Finley, Bear
Bull Lake	*Stanley

[a] E.F., M.F., N.F., S.F., W.F. are East, Middle, North, South and West forks, respectively.

rock types in the Pend Oreille system. Varied degrees of timber management and agriculture occurred in all systems surveyed in Washington. Idaho systems, commonly affected by logging, were mostly in granitics, although belt geology also occurred in the St. Joe system. Montana systems generally occurred in belt geology or belt metasediments. Glacial till, moraines, and outwash filled many of the valley bottoms. Timber management, agriculture, and mining occurred in these systems.

Methods

Sampling Design

We selected sampling sites by the procedures described in Hillman and Platts (1993). We divided each stream into 10-km reaches. The number of reaches that we sampled within each watershed represented at least 60% of the drainage length. Within each reach, we randomly selected 12 sites, each 100 m long. This sampling intensity was sufficient to provide a reasonable probability of detecting bull trout. For example, if we assume a minimum population of 25 bull trout in 10 km of stream and a Poisson sampling distribution, the probability of detection would be 95% (Hillman and Platts 1993). It is unlikely, however, that the detection efficiency of our sampling equipment is 1.0, thus the overall probability of detection would be less than 95%. Sampling began in the most downstream reach and progressed upstream. If we found no bull trout in the first reach, we sampled the next upstream reach. We continued upstream until we found bull trout or until we had sampled all reaches.

To maintain the highest sampling efficiency possible, we used both snorkeling and electrofishing to verify the presence of bull trout. We first searched the sites by snorkeling. During the daytime, two observers moved upstream through each site. Because juvenile bull trout tend to conceal themselves during daylight hours (Pratt 1984; Goetz 1989), snorkelers searched carefully under banks and in cover, such as woody debris and rock crevices. This often involved moving or disturbing the cover to locate concealed fish. If no bull trout were found, we made a single pass upstream through the sites with backpack electrofishers. We used no barrier nets during electrofishing. We fished slowly and extensively through all possible cover and recorded the size and relative abundance of all salmonids encountered. To increase the accuracy of our density estimates, we snorkeled at night in streams known to have bull trout (Goetz 1994). We also snorkeled at night in streams in which we found bull trout during daytime observations but that were previously not considered bull trout streams.

We divided each fish species into five size-classes, each 7.6 cm long, from less than 7.6 cm to larger than 30.5 cm. We estimated total length of each fish and assigned it to a size-class. Because census methods currently used to estimate bull trout numbers have wide-ranging and usually unknown efficiencies (Goetz 1994), we reported relative densities for each species and size-class encountered as "none" (0/100 m), "sparse" (1–9/100 m), "many" (10–50/100 m), or "numerous" (>50/100 m).

In addition to population surveys, we described the physical characteristics of each site with the

TABLE 2.—Physical variables determined or measured at each site during bull trout presence–absence surveys in Washington, Idaho, and Montana (from Hillman and Platts 1993).

Variable[a]	Description
Valley width (m)	The distance across a valley bottom between the valley bottom boundaries
Valley bottom type (VBT)	Distinguished by average channel gradient, valley form, and the geomorphic processes that shaped the valley (Naiman et al. 1992)
Channel width (m)	Width of the bank-full channel
Stream state type	Description of the present condition of the stream and banks (see Table 3)
Channel type	Description of channel gradient, incision, and sinuosity (Rosgen 1993)
Dominant and subdominant substrate type	Description of the particles that constitute the streambed (Platts et al. 1983)
Gradient (%)	Drop in water surface elevation per unit length of channel
Temperature (°C)	Measured at midchannel
Riparian vegetation	Description of the dominant vegetation along the banks (Platts et al. 1987)
Habitat type	Description of the morphologic and hydraulic properties of channel geomorphic units (Hawkins et al. 1993)
Habitat length (m)	Length of each habitat unit measured at the center of the wetted channel
Habitat width (m)	Mean width of the habitat unit measured across the wetted channel perpendicular to the flow
Tailcrest depth (cm)	Deepest point where the tail of the channel forming the pool reaches its highest elevation
Maximum depth (cm)	Deepest point in a habitat unit
Sediment depth (cm)	Depth of sediment materials <2 mm in diameter in pool habitats
Surface fines (%)	Percentage of the wetted streambed surface area within a habitat unit that is covered with materials <2 mm in diameter
Number LWD jams	Count of log clusters (two or more) with log diameters >10 cm
Number logs	Count of individually spaced logs with diameters >10 cm
LWD (wood) cover (%)	Percentage of the wetted surface area of a habitat unit that is covered with LWD
Boulder cover (%)	Percentage of the wetted surface area of a habitat unit that has boulder cover
Undercut banks (%)	Percentage of the water surface area in a habitat unit that is covered by undercut banks
Vegetation overhang (%)	Percentage of the water surface area in a habitat unit that is shaded by vegetation within 30.5 cm of the water surface
Canopy cover (%)	Percentage of the water surface area in a habitat unit shaded by trees and shrubs that hang over the stream at >30.5 cm above the stream surface

[a] LWD is large woody debris.

TABLE 3.—Description of stream state types observed during bull trout presence–absence surveys in Washington, Idaho, and Montana.

State type	Description of state type
Natural	Banks in straight reaches are stable and overhanging; point bars are vegetated; cut banks are vegetated, stable, and usually overhanging
Eroded banks	Banks in straight reaches are mostly eroded and unstable; point bars are mostly vegetated; cut banks are eroded and nearly vertical; bank-full width is less than twice base flow width at bends
Laid-back banks	Banks in straight reaches are eroded; point-bars are mostly nonvegetated; point bars may be cut off during high flows; cut banks are eroded or laid back; bank-full width is greater than twice base flow width at bends
Channelized	Stream sinuosity has been diminished to protect roads, railroads, urban development, industrial facilities, and other anthropogenic features
Cutoff point bars	Laid-back point bars have been cut off, forming backwaters and islands at base flow
Mine tailings	Mine tailings are the dominant substrate and bank-forming material; most tailings are not vegetated
Braided	Braided channels result from deposition of sediments (channel aggradation)
Impounded	Tailwaters of reservoirs
Multiple channel	Multiple channels result from erosion of substrates
Straight	Similar to channelized but not restricted to anthropogenic features; natural features restrict lateral movement of the channel
Entrenched	Channel has cut the base of high terraces or residual slopes on at least one bank; high banks are unstable and constitute sediment sources to the stream

procedures of Hillman and Platts (1993). After completing the fish survey, we measured 24 habitat variables (Table 2). We classified the variables into two categories: those that described the site and those that described the conditions of each habitat type within a site. Site variables included valley width, valley bottom type (Naiman et al. 1992), channel width, stream state type (Table 3), channel type (Rosgen 1993), dominant and subdominant substrate types, gradient, water temperature, riparian vegetation, and habitat types.

We classified habitat types with the level-2 system in Hawkins et al. (1993). That is, a habitat unit was an area of the stream with relatively homogenous depth and flow that was bounded by sharp gradients in both depth and flow (turbulent fast water, nonturbulent fast water, scour pool, and dammed pool). A recorded habitat unit had to be

equal to or longer than the average width of the wetted channel. For each habitat type within a site, we measured length and width, maximum depth, percent surface fines, number of large-woody-debris (LWD) jams, number of individually spaced logs, percent wood (LWD) cover, percent boulder cover, percent bank undercut, percent vegetation overhang, and percent canopy cover. We measured tailcrest and fine sediment depths only in slow-water habitats. We also recorded the number of habitat units within each 100-m site and calculated their wetted areas.

Statistical Analyses

We tested the association between the occurrence of bull trout and the physical and biological variables that we measured. We hoped to identify those variables that discriminated between streams or sites with and without bull trout. To identify those factors that most influenced bull trout densities, we assessed the relationship between the physical parameters and the relative densities of bull trout.

Presence–absence analyses.—We analyzed presence–absence at two levels of resolution: sites and habitats. In the first level, we tested for differences between sites with and without bull trout. Specifically, we tested the hypothesis that site conditions did not differ between sites with and without bull trout. At this level we pooled data across habitat types. In the second level we pooled data across sampling sites and tested for differences between specific habitat types with and without bull trout. Here, we tested the hypotheses that the physical characteristics of specific habitat types did not differ between sites with and without bull trout. For example, we tested the hypothesis that the physical conditions of scour pools did not differ between sites with and without bull trout. We examined relationships at the finer scale to see if microhabitat characteristics influenced bull trout distributions. We included both site and habitat variables at all levels of analysis.

Before testing statistical hypotheses, we screened all data for normality assumptions and for patterns of missing values and variance. After screening the data, we calculated descriptive statistics (i.e., mean, range, standard deviation, and 95% confidence limit) for each continuous variable at both the site and habitat levels. Because the data did not always meet normality and homogeneity of variance assumptions, we used the Mann–Whitney *U*-test to assess if continuous variables differed significantly between sites with and without bull trout at both levels of analysis. The Kolmogorov–Smirnov two-sample test assessed if discrete variables (valley bottom type, state type, channel type, substrate type, riparian vegetation, and habitat type) differed significantly between sites with and without bull trout. Because we ran 115 two sample tests, the probability of a type I error, assuming $\alpha = 0.05$, was $1 - (1 - 0.05)^{115} = 0.997$ (Hays 1988). That is, there was a 99.7% chance of rejecting a true hypothesis of no difference. To reduce this error, we accepted significance at $\alpha = 0.001$. Thus, the maximum probability of a type I error in our two-sample analysis is 0.108.

Because several variables differed significantly between sites with and without bull trout at both scales of analysis, we used stepwise logistic regression (logit analysis) to assess which variables were statistically most important in determining bull trout presence. Unlike stepwise discriminant analysis, logit analysis does not require multivariate normality and equal variance–covariance matrices across groups. Logit analysis accepts discrete independent variables and provides a probabilistic prediction that may reflect environmental effects. We first calculated Pearson and Spearman rank correlation matrices to test for multicollinearity among variables. We used this information to select an array of independent variables for use in logistic regression. At the site level of analysis, we excluded gradient because it correlated with channel type. We excluded fine sediment depth and maximum water depth from analysis because they correlated with habitat type. We removed boulder cover and number of individually spaced LWD because they correlated with dominant substrate and percent instream wood cover, respectively. At the habitat level, we removed channel width because it correlated with maximum depth and habitat area. We excluded gradient because it correlated with channel type.

We used SYSTAT LOGIT (Steinberg and Colla 1991) for all stepwise analyses. We used both untransformed and log-transformed ($\log_e[x + 1]$) variables. Both sets of variables produced similar results, but the untransformed data produced better-fitting models and are the only results presented here. We modeled discrete independent variables with dummy variables (Hosmer and Lemeshow 1989). We first fit models using independent variables without interactions. Later, because valley bottom type entered all models, we tested its interaction with the other independent variables. We tested only first-order interactions. We used the maximum-likelihood method to fit the models and

then evaluated the significance ($P \leq 0.05$) of each of the independent variables that entered the model with the t-ratio (Wald's test) and the 95% confidence interval for the odds ratio (Hosmer and Lemeshow 1989). Because logit accepts significance at $P \leq 0.05$ and we accepted significance at $P \leq 0.001$ in the two-sample test, some variables entered the logit model that were not significantly different in the two-sample analysis. We evaluated the goodness-of-fit of each model by the magnitude of McFadden's rho^2 and by the likelihood ratio statistic (Hosmer and Lemeshow 1989). Rho^2 values between 0.20 and 0.40 indicate very satisfactory fits (Hensher and Johnson 1981).

Density–habitat analyses.—To assess relationships between densities of bull trout and habitat parameters, we used only data from the 31 streams that contained bull trout. We tested relationships at three different scales: site, stream, and site within basins or subbasins. At the site scale of analysis, data from each site represented one data point ($N = 358$); at the stream scale, data from each stream constituted one data point ($N = 31$). In the final level of analysis, we analyzed relationships between bull trout densities and habitat parameters within each basin separately. Although we found bull trout in 12 basins or subbasins, small sample sizes precluded us from analyzing relationships in all but the Swan ($N = 66$), Lochsa ($N = 28$), and St. Joe ($N = 55$) river basins. We assumed that populations of bull trout within these basins represented separate demes or metapopulations.

For each stream and sampling site, we calculated two scores for each independent variable; one represented central tendency and the other variability. We used the latter as a measure of diversity. For each continuous independent variable, we calculated the mean and coefficient of variation (CV = 100·SD/mean). The CV offers a surrogate for variability because it is independent of the magnitude of the mean. For discrete independent variables, we calculated the mode and number of levels of each discrete variable that occurred within the stream or site. For example, if the dominant substrate along the length of a stream ranged from gravel to cobble to boulders, but cobbles occurred most frequently, we calculated the mode as 3 (code for cobble) and the number of levels as three, because three of the six dominant substrate types occurred throughout the length of the stream. These calculations produced a new data matrix with 46 independent variables.

We calculated mean densities of bull trout for each stream as the sum of total abundance in each site (including sites with densities of zero), divided by the total number of sites sampled. We recorded a relative density of none as 0 fish/100 m, sparse as 5 fish/100 m, many as 25 fish/100 m, and numerous as 51 fish/100 m. We summed relative abundance values for each size-class of bull trout to calculate total bull trout abundance for each site. For example, if we observed three different size-classes at a site, with two sparse and the other numerous, the total abundance for the site would equal 61 fish/100 m. We recognize that these are rough estimates of bull trout densities; however, given that no single method can effectively census bull trout across the range of conditions that we sampled, a relative density estimate suffices for our level of analyses. That is, in this study we were not concerned with predicting densities accurately from an array of physical habitat variables but wanted to assess general associations between relative densities and habitat variables across a wide range of landscapes.

Before testing associations between relative densities and habitat parameters, we screened all data for variance patterns and linearity. Bivariate plots tested linearity of untransformed and transformed ($\log_e[x + 1]$; $x^{0.5}$; x^2; x^3) variables. For most variables, linearity improved when we log-transformed densities and continuous independent variables. Transformation did not improve linearity of discrete variables. We removed from further analyses those independent variables not related to density. We then calculated Pearson and Spearman rank correlation matrices to test for multicollinearity among independent variables. If two independent variables correlated, we removed the one that had the poorest linear relationship with relative density. McHenry's variable selection algorithm (McHenry 1978) selected the final array of independent variables that we used in multiple regression. This stepping procedure selected a subset of variables that provided a minimum Wilk's lambda. We then used robust multiple regression (Hamilton 1991) to assess the relationships between bull trout densities and the final array of habitat variables. We used robust regression because it is less sensitive to outliers than is least-squares regression.

Results

Presence–Absence Analyses

We found bull trout in 31 of the 93 streams surveyed (Table 1). Of the 5,021 bull trout we found, 29.3% were less than 75 mm long, 36.5%

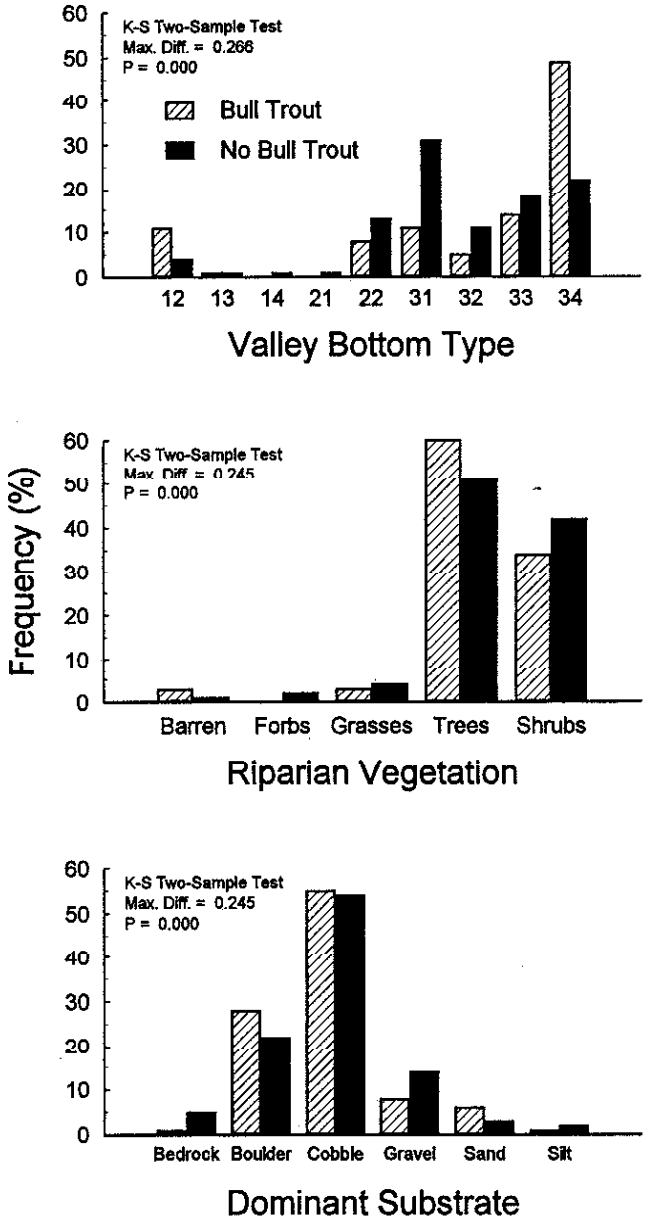

FIGURE 1.—Relative frequency of valley bottom types, riparian vegetation, and dominant substrate types in sites with and without bull trout in Washington, Idaho, and Montana. Kolmogorov–Smirnov two-sample tests (K–S) assessed differences between sites with and without bull trout. Valley bottom types (from Naiman et al. 1992) are 12 = alluviated lowlands; 13 = wide mainstream valley; 14 = mainstream valley; 21 = moderate sloping plateaux and terraces; 22 = alluviated moderate slope bound; 31 = V-shaped moderate gradient bottom; 32 = V-shaped high gradient bottom; 33 = V-shaped bedrock canyon; 34 = alluviated mountain valley.

were 75–150 mm, 23.4% were 150–225 mm, 8.9% were 225–300 mm, and 1.9% were larger than 300 mm. We observed bull trout in seven different valley bottom types (Figure 1), in streams with valley widths that ranged from 4 to 3,810 m, and channel widths and gradients that ranged from 0.3 to 26 m and from 0 to 23%, respectively (Table 4). We found bull trout in streams with varying degrees

TABLE 4.—Descriptive statistics of continuous variables measured in stream sites with and without bull trout. Probability values of the Mann–Whitney *U*-test are given.

Variable[a]	Sites with bull trout		Sites without bull trout		
	Mean	Range	Mean	Range	*P*-value
Valley width (m)	185.7	3.7–3,810	130.6	3.0–1,829	0.000
Channel width (m)	7.8	0.3–26.2	7.3	0.3–45.7	0.000
Gradient (%)	3.4	0–23	3.6	0–27	0.000
Temperature (°C)	10.1	4.4–21.7	9.7	3.3–17.2	0.404
Habitat area (m^2)	102.9	0.7–1,226.3	98.6	0.8–3,044.1	0.000
Tailcrest depth (cm)	13.2	0–76	12.7	0–91	0.001
Maximum depth (cm)	42.7	5–305	40.1	3–457	0.000
Sediment depth (cm)	4.3	0–79	4.6	0–91	0.000
Surface fines (%)	20.1	0–100	20.7	0–100	0.566
LWD jams	0.9	0–37	1.3	0–31	0.000
Individual logs	3.1	0–99	3.1	0–75	0.011
LWD cover (%)	6.5	0–80	6.6	0–85	0.526
Boulder cover (%)	23.7	0–100	20.4	0–100	0.001
Undercut banks (%)	21.7	0–100	13.3	0–100	0.000
Vegetation overhang (%)	5.3	0–95	8.5	0–100	0.000
Canopy cover (%)	25.9	0–100	35.5	0–100	0.000

[a] LWD = large woody debris.

of instream and overhead cover. For example, we observed bull trout in streams with little or no instream cover and very little vegetation on the banks. We also found them in streams with abundant wood and boulder cover and well-vegetated banks.

Site scale.—Most mean physical habitat variables differed significantly ($P < 0.001$) between sites with and without bull trout (Table 4). Only temperature, tailcrest depth, maximum depth, surface fines, number of individually spaced logs, LWD cover, and boulder cover did not differ significantly ($P \geq 0.001$) between sites with and without bull trout. Logit analysis indicated that bull trout most frequently occurred in sites with undercut banks and with little overhanging vegetation and canopy cover (Table 5); they also used sites with trees and shrubs along the banks (Figure 1). Bull trout less frequently used sites with grasses, forbs, or no vegetation along the banks.

TABLE 5.—Summary of variables that entered stepwise logistic regression analyses (see Table 2 for description of variables). The order of variables represents their statistical importance in the logit model. Arrows next to continuous variables indicate the relationship between the variable and the occurrence of bull trout; an up arrow indicates a direct relationship, a down arrow an inverse relationship. Discrete variables were modeled as dummy variables. The likelihood ratio statistic (LRS), degrees of freedom (df), significance (*P*), and McFadden's rho-squared (rho^2) are given for each level of analysis.

Input or statistic	Site scale[a]	Habitat scale[a]: Turbulent fast water	Nonturbulent fast water	Scour pool	Dammed pool
Input	Undercut↑	VBT	Undercut↑	VBT	Undercut↑
	Veg. overhang↓	Rainbow t.↓	Canopy↓	Rainbow t.↓	Veg. overhang↓
	Canopy↓	Surface fines↓	VBT	Canopy↓	Channel type
	VBT	Cutthroat t.↑	Riparian veg.	Maximum depth↑	Wood cover↑
	Riparian veg.	Dominant sub.	Dominant sub.	Riparian veg.	Tailcrest depth↑
	Dominant sub.	Riparian veg.	Brook t.↓	Dominant sub.	VBT
	Rainbow t.↓	Habitat area↑	Rainbow t.↓	Brook t.↓	Riparian veg.
	Brook t.↓	Valley width↑	Valley width↑	Undercut↑	
	Valley width↑	Veg. overhang↓		Habitat area↑	
	Habitat type			Veg. overhang↓	
Statistic					
LRS	1227.974	392.073	405.492	469.150	92.885
df	26	23	22	24	23
P	0.000	0.000	0.000	0.000	0.000
Rho^2	0.194	0.207	0.208	0.231	0.239

[a] VBT = valley bottom type; veg. = vegetation; t. = trout; sub. = substrate.

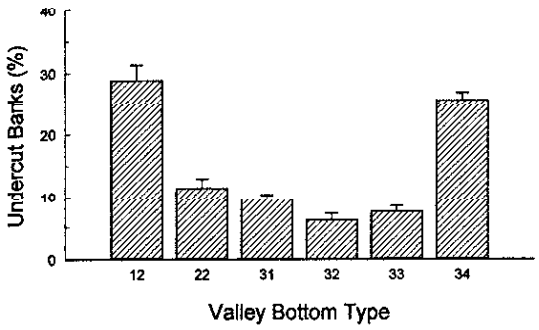

FIGURE 2.—Mean percent and 95% confidence interval of undercut banks measured within different valley bottom types as defined in Figure 1.

Bull trout used specific valley bottom types. We observed them in alluviated lowlands and mountain valleys and V-shaped valleys and canyons, but they most often used alluviated lowlands and mountain valleys (Figure 1). Bull trout frequently used sites with boulders and cobbles, although they also occupied sites with sand as the dominant substrate (Figure 1). Bull trout more often occurred in sites without rainbow trout *Oncorhynchus mykiss* and brook trout *S. fontinalis* (Table 5). On the other hand, bull trout and cutthroat trout *O. clarki* occurred together more often than bull trout and other salmonids. Valley width and habitat type entered the logit last.

Several variables did not enter the model (i.e., did not increase the predictability of the logit), although some differed significantly ($P < 0.001$) between sites with and without bull trout. For example, state type did not enter the logit model even though bull trout appeared to most often use sites with natural or laid-back bank state types (Table 3). Bull trout also occurred more often in A (entrenched, step–pool, 4–10% gradient) and C (meandering, riffle–pool, <2% gradient) channel types (Rosgen 1993). In addition, subdominant substrate, channel width, gradient, habitat area, and number of log jams differed significantly ($P < 0.001$) between sites with and without bull trout but did not enter the model.

We found significant interactions between valley bottom type and several independent variables and the occurrence of bull trout. Bull trout occurred more often in alluviated lowlands and alluviated mountain valleys with undercut banks than in V-shaped valley bottom types with undercut banks. Undercut banks, however, were more common in alluviated valley bottom types than in other valley types (Figure 2). Although bull trout were less likely to use sites with extensive canopy cover, they did occur more often in V-shaped valley bottom types with canopy cover than in alluviated lowlands with canopy cover. Bull trout also occurred more frequently in V-shaped valleys of moderate gradient with LWD cover than in alluviated lowlands with LWD cover. Finally, bull trout more often occupied sites in alluviated lowlands with boulder cover than in alluviated valleys of moderate slope with boulder cover.

Habitat scale.—We observed bull trout in all types of habitat, although we most often found them in the slow-water habitats. In all habitat types, several physical variables differed significantly between habitats with and without bull trout (Table 5). For example, in both turbulent and nonturbulent fast-water habitats, bull trout occurred most often in alluviated lowlands and valleys and in sites where trees and shrubs dominated riparian vegetation. They also occurred most often in fast-water habitats with boulders and cobbles that lacked fine sediments and rainbow trout. We observed bull trout in turbulent fast-water habitat with little overhanging vegetation. In nonturbulent fast-water habitat they most often used sites with less canopy cover and no brook trout. Of the variables that did not enter the models, channel width and number of log jams differed significantly ($P < 0.001$) between fast-water habitat with and without bull trout.

Bull trout most often occupied slow-water habitats (scour and dam pools) within alluviated lowlands and valleys (Table 5). The dominant riparian vegetation in these sites consisted of trees and shrubs. We often found bull trout in slow-water habitats with undercut banks that lacked extensive overhanging vegetation. Bull trout frequently occupied scour pools with boulders or cobbles, but not with brook trout or rainbow trout. In contrast, we found bull trout more often in dammed pools with instream wood cover than in dammed pools without wood cover. Bull trout also frequently used dammed pools in A and C channel types. Of the variables that did not enter the logit, maximum depth and boulder cover differed significantly ($P < 0.001$) between dammed pools with and without bull trout. State type, channel type, subdominant substrate, valley width, gradient, and number of log jams did not enter the logit but differed significantly ($P < 0.001$) between scour pools with and without bull trout.

As at the site scale, the occurrence of bull trout in both fast- and slow-water habitats was related to the interaction of undercut banks and canopy

TABLE 6.—Results of robust multiple regression that assessed relationships between densities of bull trout and physical habitat conditions at three different scales. At the site scale the model was significant (F = 49.281; P = 0.000; R^2 = 0.530); at the stream scale the model was significant (F = 41.211; P = 0.000; R^2 = 0.899). Models were significant for the Swan (F = 4.851; P = 0.031; R^2 = 0.070), the Lochsa (F = 16.063; P = 0.000; R^2 = 0.668), and the St. Joe (F = 12.016; P = 0.000; R^2 = 0.462) basins.

Variable[a]	Coefficient	SE	T-value	P-value	Bivariate r^2
		Site scale			
Constant	−5.639	0.483	−11.677	0.000	
Maximum depth	1.423	0.138	10.344	0.000	0.219
Wood cover CV	0.612	0.191	3.203	0.001	0.170
Maximum depth CV	0.860	0.316	2.717	0.007	0.108
Valley width	0.229	0.046	5.785	0.000	0.060
Vegetation overhang	−0.313	0.077	−4.078	0.000	0.045
Undercut banks	0.225	0.043	5.261	0.000	0.018
Boulder cover	0.169	0.039	4.400	0.000	0.016
Wood cover	0.245	0.076	3.226	0.001	0.015
		Stream scale			
Constant	0.269	0.844	0.318	0.753	
Gradient CV	1.696	0.405	4.193	0.000	0.336
Sediment depth CV	−2.246	0.269	−8.347	0.000	0.314
Maximum depth	1.744	0.243	7.171	0.000	0.253
Surface fines	−0.689	0.094	−7.367	0.000	0.116
Undercut banks	0.197	0.064	3.076	0.005	0.109
		Swan Basin			
Constant	2.476	0.526	4.708	0.000	
Number of habitat types	0.607	0.276	2.203	0.031	0.070
		Lochsa Basin			
Constant	4.749	0.625	7.600	0.000	
Vegetation overhang	−1.362	0.268	−5.080	0.000	0.335
LWD jams CV	1.094	0.382	2.860	0.008	0.071
Canopy cover CV	−4.893	1.315	−3.722	0.001	0.030
		St. Joe Basin			
Constant	1.104	0.595	1.855	0.071	
Undercut banks CV	2.699	0.554	4.876	0.000	0.543
Gradient	−1.272	0.365	−3.482	0.001	0.095
Tailcrest depth CV	2.650	0.960	2.759	0.009	0.083

[a] CV = coefficient of variation; LWD = large woody debris.

cover with valley bottom type. In both types of habitat, bull trout more often used alluviated valley bottom types with undercut banks than V-shaped valley bottom types with undercut banks. In contrast, bull trout occurred more often in V-shaped valley bottom types with canopy cover than in alluviated valleys with canopy cover.

Density–Habitat Analyses

Site scale.—The first level of analysis assessed the relationships between bull trout relative density and physical habitat variables measured within all sites in the 31 streams that contained bull trout (N = 358). Robust multiple regression identified eight variables that explained 53% of the variation in bull trout densities among sampling sites (Table 6). The analysis indicated a direct relationship between bull trout density and maximum pool depth, wood cover CV, maximum depth CV, valley width, percent undercut banks, percent boulders, and percent wood cover. Bull trout densities related inversely to the percentage overhanging vegetation along the streambanks.

Stream scale.—The second level of our analysis compared bull trout relative densities to physical habitat variables at the stream scale (N = 31). At this scale, robust multiple regression identified five variables that explained 89% of the variation in bull trout densities (Table 6). Bull trout densities correlated directly with stream gradient CV, maximum pool depth, and percentage of undercut banks. There was an inverse relationship between bull trout densities and fine sediment and sediment depth CV.

Basin scale.—The final level of our analysis described relationships between bull trout densities and physical variables within three separate river basins. These analyses allowed us to assess if bull

trout in separate basins responded differently to habitat assemblages. We regressed bull trout relative densities against physical variables measured in the Swan (N = 66), Lochsa (N = 28), and the St. Joe (N = 55) river basins. We assumed bull trout from these basins represented separate metapopulations. We believe this assumption is justified because each basin drains to a different major basin and barriers block upstream migration into the Swan and St. Joe rivers. No known barriers block migration of bull trout among tributaries within each of the basins.

Physical variables that correlated significantly with bull trout densities differed among the three river basins (Table 6). In the Swan River basin, only the number of habitat types per 100 m correlated with relative densities of bull trout, and explained only 7% of the variation in densities. Robust regression identified three variables that explained 67% of the variation in relative densities of bull trout in the Lochsa River basin. Both percent overhanging vegetation and canopy cover CV related inversely to bull trout densities, whereas log jams CV correlated directly with relative densities. In the St. Joe River basin, undercut banks CV and tailcrest depths correlated directly with bull trout densities, whereas gradient was inversely related with relative densities. These three variables explained 46% of the variation in bull trout densities in the St. Joe River basin.

Discussion

In this study we described the relationships between bull trout distribution and relative abundance and several physical variables in watersheds across a large portion of bull trout range in the Pacific Northwest. Others have investigated the influence of physical variables on bull trout distribution and density (McPhail and Murray 1979; Pratt 1984; Shepard et al 1984; Buckman et al. 1992; Dambacher et al. 1992; Ziller 1992; Goetz 1994; Saffel and Scarnecchia 1995; Underwood et al. 1995). However, those studies had limited geographic scope and generally involved small watersheds within the drainage area of a single river or lake. We sought to ascertain stream habitat variables that defined bull trout distribution and abundance across a large portion of the bull trout range.

Presence–Absence Analyses

Bull trout occurred most often within alluviated lowland and valley streams with undercut banks, large substrate, trees and shrubs as the dominant riparian vegetation, and slow-water habitat. They less frequently used sites with extensive canopy cover and overhanging vegetation. Bull trout often occupied sites that lacked brook trout and rainbow trout, but they often occurred together with cutthroat trout. At the habitat scale, bull trout rarely used turbulent fast-water habitat where fine sediment covered the streambed. They also occurred rarely in nonturbulent fast water with extensive canopy cover and brook trout. In scour pools, bull trout most often used the deepest and largest pools that lacked abundant canopy cover. They often used dammed pools in A and C channel types with instream wood cover. We found no difference in water temperatures between sites with and without bull trout. We measured temperatures only once at a given site, so these temperatures probably did not represent the true longer-term temperature regime of the bull trout streams.

Valley bottom type distinguished bull trout streams at both the site and habitat scales. Alluviated lowlands and mountain valleys are probably important to bull trout because they tend to produce low-gradient meandering channels, which have lower water velocities and greater potential for habitat complexity. In addition, groundwater input probably affects streams in these valley bottom types. Several studies indicate that bull trout select spawning locations in low-gradient, low-velocity areas (McPhail and Murray 1979; Oliver 1979; Fraley and Shepard 1989) and where groundwater upwells (Allan 1980; Shepard et al. 1984; Ratliff 1987). In addition to maintaining colder water temperatures for spawning, groundwater input may also maintain migratory corridors in aggraded stream reaches by augmenting late-summer instream flows, prevent anchor ice formation and maintain overwinter habitat, and moderate water temperature fluctuations, which provides a stable incubation and rearing environment. Other factors may also explain the association between the presence of bull trout and alluviated valley bottom types. For example, these bottom types may attract bull trout because they provide relatively high prey availability, low water velocities, and adequate cover. In addition, it is possible that some of the mature bull trout that we observed between June and November in alluviated valley bottom types were holding there before moving to spawning locations. Fraley and Shepard (1989) noted that adult bull trout may hold at the mouths of spawning tributaries for up to 1 or 2 months before moving to spawning sites.

Although riparian trees and shrubs were an important component of bull trout streams at both the

site and habitat scales, bull trout occurred less frequently in sites with extensive overhanging vegetation and canopy cover. Reduced vegetative cover may increase primary productivity and ultimately fish productivity (Murphy et al. 1981; Bisson et al. 1992). The importance of vegetative cover for moderating stream temperatures may also be reduced in areas with substantial groundwater input.

Occurrence of bull trout was related significantly to the presence of undercut banks and large substrate. These factors provide cover for bull trout. McPhail and Murray (1979), Ptolemy (1979), and Shepard et al. (1984) reported that bull trout frequently used undercut banks as cover. Our observation that bull trout occurred more frequently in sites with boulder and cobble substrate than in sites with bedrock and finer bed materials comports with the findings of Oliver (1979), McPhail and Murray (1979), and Shepard et al. (1984). Because bull trout are highly substrate oriented and territorial, large substrates provide the habitat complexity, velocity breaks, concealment cover, and visual isolation necessary for foraging and evading predators. Fine sediments in turbulent fast-water habitat negatively correlated with bull trout presence. Excessive inputs of fine sediments could be detrimental to bull trout.

At the site and habitat scale, the occurrence of bull trout was inversely related to the presence of brook and rainbow trout. Competition may explain this association. However, we can find no evidence that bull trout and rainbow trout compete for food or space. Boag (1987) examined rainbow trout and bull trout populations in a northern Alberta stream and found no interaction for food between the two species. Allan (1980) also suggested that rainbow trout did not compete with bull trout for space and food. In the Upper Arrow Lakes of British Columbia, juvenile rainbow trout and bull trout may partition habitat (McPhail and Murray 1979). The inverse relationship that we observed may simply reflect the spatial segregation between the two species; rainbow trout most often occurred in the V-shaped valley bottom types, and bull trout most often occurred in alluviated valley bottom types. In contrast, bull trout are less likely to coexist with brook trout. In areas in Montana where bull trout and brook trout occur together, bull trout populations have declined (Goetz 1989). Wallis (1948) noted that the feeding habits of brook trout and bull trout were similar. Both species used similar habitat in Sun Creek, Crater Lake National Park, Oregon (Dambacher et al. 1992). Competition and hybridization threaten the bull trout with extinction in that system.

Our analysis of first-order interactions suggested that valley bottom type is not only an important factor related to bull trout distribution in and of itself but that interactions between valley bottom type and other variables increase the probability that bull trout will occupy a given location. For example, bull trout occurred more often in alluviated valley bottom types with undercut banks than in other valley bottom types with undercut banks. Bull trout also occurred more often in V-shaped valley bottom types with canopy cover than in alluviated valley bottom types with canopy cover. Indeed, valley bottom type was one of the most important variables describing the distribution of bull trout.

Recent work by Rieman and McIntyre (1995) also suggests that large-scale processes are important to the distribution of bull trout. Their work in the Boise River basin, Idaho, shows that watershed size and stream width are important factors explaining the occurrence of bull trout. They postulate that larger patch sizes favor increased probability of recolonization and decreased risk of extirpation from environmental catastrophe. Our work indicates that watershed-scale physical processes are probably the most important factors that determine bull trout distribution and occurrence in third- and fourth-order watersheds. Watershed size, geology, and the percentages of specific valley bottom types probably function in concert to provide the flow regimes, channel size, water temperatures, gradient, and substrate compositions that bull trout require for rearing, spawning, and migration. These processes and habitat features are not ubiquitous. Thus, tributary watersheds must exhibit a specific array of physical characteristics, independent of management history, that provide spawning, rearing, and migratory habitat necessary for colonization and persistence of bull trout. Hence, it is inappropriate to assume that bull trout used all tributary watersheds, at least as natal streams, within a river basin.

Density–Habitat Analyses

Regardless of the scale of analysis, the highest relative densities of bull trout occurred in stream areas with the deepest pools. Others have noted the affinity of bull trout for pool habitats (McPhail and Murray 1979; Oliver 1979; Pratt 1984; Goetz 1991; Martin et al. 1992; Saffel and Scarnecchia 1995). In our analysis, greater relative densities were more closely associated with pool depth than

with the frequency of pools. We would expect that as pool depth increases, the ability of the stream to provide habitat for more bull trout increases. Deeper pools also provide more of the microhabitat features important to bull trout, such as cooler water temperatures, lower water velocities, and cover.

Many of the other variables that correlated significantly with bull trout density have also been described by other researchers. As we indicated earlier, variables such as undercut banks, woody debris, and boulders, which correlated positively with relative density, provide concealment cover and possibly increase carrying capacities (Goetz 1989; Martin et al. 1992). We, like Shepard et al. (1984) and Leathe and Enk (1985), observed an inverse relationship between relative densities of bull trout and fine sediments in the substrate. Important variables such as gradient CV, wood cover CV, and pool depth CV represent habitat diversity. Mullan et al. (1992) suggested that habitat complexity in any form is important to bull trout abundance. The relationship between bull trout relative density and valley width is probably indicative of greater channel complexity. Wider valleys tend to contain channels with higher sinuosity and braiding, which indicates increased habitat complexity. The inverse relationship between bull trout densities and overhanging vegetation may be related to the presence of shrubs and trees. That is, shade from trees and shrubs, which correlated directly with bull trout occurrence, may prevent the establishment of grasses and forbs that typically form overhanging vegetation.

We found little consistency in density–habitat relationships across various scales. There was no agreement between significant variables at the basin scale of analysis and there was little agreement between significant variables at the basin and stream scales of analysis. Furthermore, the amount of variation in bull trout densities explained by the significant independent variables decreased at finer scales of resolution. These findings suggest that assemblages of habitat conditions at finer scales may be more important than the habitat patterns that we measured. Bisson et al. (1982) stated that the preferred habitat of juvenile salmonids may be unique for each tributary. On the other hand, it is possible that at finer scales of resolution, habitat preferences could be similar but be expressed at a scale too small to be measured in a repeatable manner, at least with the methodologies currently available.

Study Limitations

Certainly, we have not described all the factors that affect the distribution and abundance of bull trout. Because we collected data during summer and early fall, the relationships explained here may not reflect habitat used by bull trout during other periods of the year, especially during times of different temperature and flow regimes. Because we measured water temperature only once at each site, we may have underestimated the true relationship between bull trout occurrence and temperature regimes. About 90% of all the bull trout we observed were smaller than 225 mm. Results may differ for larger bull trout. Our use of relative rather than absolute densities may increase the amount of unexplained variability at finer scales of analysis. We did not evaluate interactions between available habitat and interspecific or intraspecific competition. Thus, our results may be confounded by various seeding levels relative to habitat capacity and by displacement from preferred habitats by other fish, especially introduced species. For example, past fishing pressure and the introduction of brook trout may have reduced bull trout populations beyond the effects of any habitat limitations. Lastly, our results may not apply outside the ecoregions, geologies, or even river basins that we sampled.

Management Implications

Based on the results of this study, we recommend that land management activities be tailored to various geomorphic valley bottom types. Watershed analysis nested within a hierarchical framework of physical processes and management standards is the logical choice for protecting and maintaining bull trout habitat. Because watershed analysis can be both costly and time consumptive, managers may wish to consider implementation of some interim habitat protection measures until such analyses can be completed.

Our study indicates that bull trout occurred most often in lower-gradient alluvial lowlands and mountain valleys, which tend to be sensitive to increased sediment supply and loss of channel roughness (Montgomery and Buffington 1993). Large woody debris, which is important for complex arrangements of bars, pools, and riffles (Lisle 1986); large channel substrate; and streambank armoring from roots, cobbles, and boulders increase channel roughness. Management activities in alluviated valley bottom types should maintain rooting strength from trees and shrubs near streambanks to preserve undercut banks and stable chan-

nels. Although not strongly correlated with bull trout distribution or abundance, riparian canopy coverage may be important for temperature modulation, at least in areas without groundwater influences. Activities that can potentially modify flow regimes or coarse sediment loading need to maintain pool depths and channel complexity. Land management in other, higher-gradient valley bottom types should minimize sediment input and temperature effects on bull trout habitat.

Future research should explore the interaction between basin geomorphology, habitat, and bull trout assemblages. That is, it is important to assess how basin geomorphology, especially valley bottom type, affects water temperature fluctuations, flow regimes, channel complexity, and the occurrence of bull trout. With such information, it may be possible to develop a model that predicts bull trout distribution as well as delineates specific areas of habitat assemblages critical to their survival.

Conclusions

Our study indicates that there is a high degree of variability in the habitat factors that contribute to the distribution and abundance of bull trout. This variability tends to increase indirectly with the scale of resolution. That is, there is a greater consistency among significant independent variables at coarser scales of resolution (e.g., the influence of valley bottom type on bull trout distribution) than at finer scales (e.g., bull trout density and microhabitat relationships within specific basins). This suggests that physical conditions influence bull trout distribution and density in a hierarchical fashion. We postulate that bull trout use resources hierarchically from the geographic range (e.g., ecoregion, geologic district, elevation) to home ranges (e.g., watersheds with minimum patch sizes and specific valley bottom types), then to habitat conditions within the home range (e.g., stream reaches with diverse habitat types and deep pools). Ultimately, bull trout occupy specific locations within the habitat (e.g., undercut banks, boulder cover).

We suggest that life history requirements and spatial landscape patterns drive bull trout distribution. Bull trout density and habitat selection, on the other hand, adaptively respond to the specific ways in which habitat diversity is expressed within any given watershed. With the exception of a few, well-documented bull trout habitat requirements (i.e., temperature and fine sediment), our work suggests that it is inappropriate to develop and implement regionwide management standards for bull trout habitat without considering hierarchical and site-specific processes that define that habitat. We agree with Johnson (1980), who stated that the criteria for resource use may be different at each level so that, when making inferences, researchers studying resource use must consider the level being studied.

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