Influence of abiotic and biotic factors on occurrence of resident bull trout in fragmented habitats, western Montana

by Cecil Frank Rich, Jr

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
Many populations of bull trout have become isolated in small headwater drainages throughout their range. Current ecological theories suggest these small populations may be at increased risk of extinction. While many researchers have suggested that large-scale factors such as basin size and spatial arrangement of habitats may influence population persistence, there are few studies providing evidence for the importance of large-scale factors. In this study, 112 tributary streams in 5 subbasins of the Bitterroot River basin were surveyed for presence/absence of bull trout, westslope cutthroat trout, brook trout, and tailed frogs. Habitat characteristics were measured in the lower 500 meters of each tributary stream. Of 112 tributaries sampled, 67 contained bull trout, 109 had westslope cutthroat trout, 25 had brook trout, and tailed frogs were found in 71 streams. Patterns of bull trout occurrence were analyzed in relation to site and watershed scale variables and occurrence of brook trout using a combination of univariate and multiple logistic regression analyses. Elevation, basin area, and the relative abundance of bull trout in nearby larger streams were positively correlated, and tributary slope was negatively correlated, with the presence of bull trout. Site variables of stream width and woody debris were positively correlated, and channel gradient negatively . correlated, with the presence of bull trout. There was also a strong negative correlation between brook trout and bull trout presence. In comparisons of habitat variables in streams where each species was present, brook trout used habitats generally avoided by bull trout. Comparisons of the relative predictive power of bull trout occupancy from models constructed from map derived variables versus site derived variables indicated that in small streams, occupancy by bull trout was correctly predicted in 77% of cases using watershed variables and 82% of cases using site derived variables. The results suggest that in addition to local habitat, strong populations in larger mainstems are important in influencing bull trout distribution over large areas. This research supports recommendations by the Montana Bull Trout Scientific Group that protection of remaining strong bull trout populations in “core” habitats may be important in preventing regional extinction.

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ABSTRACT

Many populations of bull trout have become isolated in small headwater drainages throughout their range. Current ecological theories suggest these small populations may be at increased risk of extinction. While many researchers have suggested that large-scale factors such as basin size and spatial arrangement of habitats may influence population persistence, there are few studies providing evidence for the importance of large-scale factors. In this study, 112 tributary streams in 5 subbasins of the Bitterroot River basin were surveyed for presence/absence of bull trout, westslope cutthroat trout, brook trout, and tailed frogs. Habitat characteristics were measured in the lower 500 meters of each tributary stream. Of 112 tributaries sampled, 67 contained bull trout , 109 had westslope cutthroat trout, 25 had brook trout, and tailed frogs were found in 71 streams. Patterns of bull trout occurrence were analyzed in relation to site and watershed scale variables and occurrence of brook trout using a combination of univariate and multiple logistic regression analyses. Elevation, basin area, and the relative abundance of bull trout in nearby larger streams were positively correlated, and tributary slope was negatively correlated, with the presence of bull trout. Site variables of stream width and woody debris were positively correlated, and channel gradient negatively correlated, with the presence of bull trout. There was also a strong negative correlation between brook trout and bull trout presence. In comparisons of habitat variables in streams where each species was present, brook trout used habitats generally avoided by bull trout. Comparisons of the relative predictive power of bull trout occupancy from models constructed from map derived variables versus site derived variables indicated that in small streams, occupancy by bull trout was correctly predicted in 77% of cases using watershed variables and 82% of cases using site derived variables. The results suggest that in addition to local habitat, strong populations in larger mainstems are important in influencing bull trout distribution over large areas. This research supports recommendations by the Montana Bull Trout Scientific Group that protection of remaining strong bull trout populations in "core" habitats may be important in preventing regional extinction.

INTRODUCTION

Bull trout (*Salvelinus confluentus*), a native salmonid of the interior Pacific northwest, has declined substantially throughout its native range. It has been classified as a Category 1 species by the U.S. Fish and Wildlife Service (Federal Register, June 10, 1994), indicating that listing as a threatened or endangered species under the Endangered Species Act is warranted but precluded due to higher priority listings. Declines can be attributed to a variety of factors including degradation and loss of spawning and rearing habitat, overharvest, habitat fragmentation (Fraley and Shepard 1989, Howell and Buchanan 1992; Rieman and McIntyre 1993), and displacement by introduced salmonids (Leary et al. 1993). Although bull trout were likely distributed throughout most major drainages west of the continental divide south of latitude 49°N, as well as both sides of the continental divide between latitude 50°N and 60°N, distribution and abundance has declined substantially over the last century (Howell and Buchanan 1992, Thomas 1992). In Montana, bull trout are currently found in 42% of river and lake reaches surveyed representing a loss of 58% of their native range (Thomas 1992). Thus, many local populations of bull trout are believed to be extinct, and many remaining remnant populations are isolated in

shrinking patches of suitable habitat (Howell and Buchanan 1992; Rieman and McIntyre 1993; Thomas 1995). Current ecological theory suggests these small, isolated populations are at increased risk of extinction due to deterministic and stochastic processes (Rieman and McIntyre 1993). In order to effectively manage bull trout populations and prevent further declines, it is important to better understand factors important in governing their persistence.

Bull trout exhibit three general life history patterns: (1) fish reside in large rivers and migrate up smaller tributaries to spawn (fluvial); (2) fish reside in lakes or reservoirs and migrate up smaller tributaries to spawn (adfluvial); and (3) fish migrate little and spend their entire lives in headwater streams (resident). Diversity in life history strategies is thought to be important to the stability and persistence of populations inhabiting variable environments (Northcote 1992). Migratory populations may be important in recolonizing vacant habitats, providing support to populations in marginal habitat, and providing gene flow between populations. However, in some areas, remaining populations appear to persist only as the resident form due to disruption of migratory corridors and habitat loss (Ratliff and Howell 1992; Thomas 1995). The vast majority of literature available for bull trout is based on studies of migratory (fluvial and adfluvial) populations (Fraley and Shepard 1989; Goetz 1989), while information on resident populations is relatively limited (Howell and Buchanan 1992). Thus, loss of the component of populations which follow a migratory life history due to disruption of migratory corridors has caused concern that remaining resident

populations may be at increased likelihood of extinction due to deterministic, stochastic, and genetic risks (Rieman and McIntyre 1993; Thomas 1995).

Recent studies suggest that large-scale spatial processes such as spatial arrangement, size, and connection between habitats strongly influence species distribution and persistence over large areas (Rieman and McIntyre 1995). For example, when Fausch et al. (1994) examined the importance of altitude and elevation on distributions of two charr species on a Japanese island, relationships at the scale of a single watershed were imprecise, while patterns of distribution over the entire island indicated the primary importance of these factors in influencing distribution over a large scale. Lanka et al. (1987) found large-scale geomorphic variables predicted trout standing crop as accurately as site habitat variables in Wyoming streams. Bozek and Hubert (1992) found that three dimensions of stream habitat (gradient, stream width, and elevation) adequately described large-scale patterns of segregation of salmonid species in the central Rocky Mountains. Rieman and McIntyre (1995) demonstrated that area of available habitat fragments influences the distribution of bull trout at a large scale, an effect consistent with the predictions of island biogeography and metapopulation theory (Wilson and McArthur 1967; Hanski and Gilpin 1991). Smogor et al. (1995) found densities of American eels (*Anguilla rostrata*) best explained by large-scale variables while densities were not strongly or consistently predicted by local habitat features in Virginia streams. Despite these recent studies of large-scale influences on fish distribution, the majority of

studies of salmonid habitat use and requirements have focused on relationships with channel structure and spatial scales at the stream reach and habitat unit scale (Salo and Cundy 1987; Fausch et al. 1988; Meehan and Bjornn 1991). Because models constructed at these smaller scales may mask differences between streams or watersheds, they often lack the generality to be applied over larger scales. Thus, investigators believe that larger-scale factors may be equally as important as local habitat in defining species needs by accounting for population-level processes such as extinction and colonization (Rieman and McIntyre 1995; Smogor et al. 1995).

Patterns of species presence/absence over large areas have been used to test indirectly for the importance of these larger-scale "spatial processes" in influencing species distribution (Harrison et al. 1988; Thomas et al. 1992; Rieman and McIntyre 1995). Rieman and McIntyre (1995) used presence/absence data for bull trout over a large area to examine the importance of habitat patch size on occurrence. Beauchamp et al. (1992) used presence/absence surveys of brook trout (*Salvelinus fontinalis*) in a large number of Adirondack Mountain lakes to develop models to predict changes in fish distributions as a result of acidification. The occurrence of multiple species assemblages of salmonids also has been examined in relation to physical habitat, geomorphic, and climatic variables to describe limits of each species distribution in multiple species assemblages at a regional scale (Bozek and Hubert 1992; Fausch et al. 1994). Ross et al. (1990) used occurrence data to

examine the interaction of geographic position and microhabitat availability on the longitudinal distribution of the bayou darter (*Etheostoma rubrum*) in Mississippi streams.

Patterns of presence/absence can thus help elucidate factors associated with persistence over a large area. For bull trout, declining distribution and abundance is thought to be due to their very specific habitat requirements and intolerance to habitat degradation (Rieman and McIntyre 1993). Most remaining bull trout populations in the Bitterroot National Forest, Montana, are in watersheds least disrupted by road building and timber harvest (Clancy 1993). Bull trout abundance is strongly correlated with levels of fine sediments (Shepard et al. 1984a; Leathe and Enk 1985; Weaver and Fraley 1991). High levels of fine sediments in the substrate decrease bull trout abundance by limiting egg-to-fry emergence survival and by filling of streambed interstices used as winter habitat for juveniles (Rieman and McIntyre 1993). Woody debris is also an important habitat component for bull trout in many streams as it provides habitat complexity, creates pool habitat, provides a long term food source for stream invertebrates, and is an important component of winter habitat for salmonids (Goetz 1991; Jakober 1995). Bull trout density correlated significantly with woody debris density on the Bitterroot National Forest (Clancy 1993). Removal of woody debris by logging activities has also been found to reduce population density of *S. malma*, a close relative of bull trout (Bryant 1983; Elliot 1986; Murphy et al. 1986).

In addition to physical habitat factors, metapopulation connectivity and interactions with brook trout also appear to influence bull trout distribution. The importance of movement is well established for migratory populations of bull trout (Shepard et al. 1984b; Fraley and Shepard 1989), and may also be important in resident populations (Bonneau 1994; Jakober 1995). Migration links summering or foraging habitats to safe wintering areas. Dispersal is thought to be important in providing demographic support to weak local populations, reestablishing locally extinct populations, and providing gene flow between populations (Rieman and McIntyre 1993). Remnant bull trout populations residing in headwater streams with harsher and more variable environmental conditions are likely to have more frequent extinction events than downstream sections (Horowitz 1978). Thus, strong populations of bull trout in the mainstem of a watershed may be important in providing support to smaller tributaries that serve as seasonal habitat or that have small populations in marginal habitats (Osborne and Wiley 1992). Brook trout may also influence the large-scale distribution of bull trout. Brook trout commonly hybridize with bull trout producing sterile offspring where their distributions overlap leading to eventual loss of bull trout populations (Cavender 1978; Leary et al. 1983; Markle 1992). Leary et al. (1983, 1993) documented a shift from a community dominated by bull trout to one dominated by brook trout in Lolo Creek, a tributary of the Bitterroot River. Habitat conditions appear to play a role in the interactions between bull trout and brook trout. In the Bitterroot River basin,

overlap of bull trout and brook trout is minimal, with bull trout predominating in watersheds with low disturbance, whereas brook trout occur primarily in highly disrupted basins (Clancy 1993).

Although a migratory life form of bull trout was once common in the Bitterroot River, most remaining populations now exist as isolated, headwater resident populations (Thomas 1995). Population fragmentation has resulted from a number of causes. The valley bottom is heavily irrigated during summer months when water withdrawals leave many tributary streams severely dewatered in their lower sections (Good et al. 1984; Spoon 1987; Clancy 1993). Water diversion structures in both the mainstem of the Bitterroot River as well as lower sections of tributary streams likely form seasonal barriers to upstream migration of bull trout and downstream migrants may be trapped in irrigation diversions, preventing them from reaching the river (Thomas 1995). Portions of the lower Bitterroot River and some tributaries are likely unsuitable during summer months as water temperatures commonly exceed 21 °C (Spoon 1987), higher than commonly reported maximum summer temperatures for bull trout of 10.0 to 15.0 °C (Fraley and Shepard 1989; Buckman et al. 1992). The probable causes of high water temperature include tributary dewatering, loss of riparian vegetation to shade streams, warm irrigation return flows, and warm water releases from reservoirs (Thomas 1995).

Biological factors have also been important in fragmentation of bull trout populations. Nonnative species such as brown trout (*Salmo trutta*), rainbow

trout (*Oncorhynchus mykiss*), and brook trout are now common through much of the mainstem of the Bitterroot River and many tributaries and may lead to more restricted migratory movements by bull trout (Fraser et al. 1995). Brown trout are thought to have adverse effects on bull trout (Moyle 1976), although whether the mechanism is competition or predation is not known. As mentioned, brook trout hybridize with bull trout producing sterile progeny (Leary et al. 1993). Studies on the Bitterroot National Forest indicate that brook trout may be replacing bull trout populations in some streams (Leary et al. 1983, 1993; Clancy 1993).

Clearly the distribution and abundance of bull trout are correlated with a variety of habitat characteristics and the patchy distribution of bull trout relative to other species suggests that bull trout have relatively specific habitat requirements (Rieman and McIntyre 1993). Although these specific requirements make bull trout populations vulnerable to habitat fragmentation and disruption, there have been no limits defined in the literature describing the range of habitat conditions where bull trout populations are likely to persist. Species conservation plans require information at both local habitat and watershed scales. In this study, potential habitat was defined for bull trout from relationships between patterns of occurrence and physical habitat at local (site) and watershed scales. The central question addressed in this study was: what is the relative importance of physical habitat, connection between habitats, and nonnative species in affecting large-scale distributions of bull trout? Specifically,

my objectives included: (1) determining the distribution and relative abundance of bull trout and other species over a large portion of the Bitterroot River basin; (2) relating patterns of presence and absence of bull trout to site and watershed scale habitat variables, and occurrence of brook trout; (3) and developing statistical models to predict the occurrence of bull trout.

STUDY AREA

The upper Bitterroot River in western Montana is composed of two major forks (East and West Forks) that join to form the main river at Conner, Montana, which then flows 135 km to the confluence with the Clark Fork of the Columbia River (Figure 1). The Bitterroot River drains an area of 7298 km^2 with a mean annual flow of 68 m^3/s (U.S. Geological Survey 1995). The valley bottom is dry with precipitation averaging 30 - 40 cm per year while higher elevations are moist with 75 - 125 cm of precipitation per year. Most of the higher elevation forested lands form the Bitterroot National Forest, while most of the unforested valley bottom land is in private ownership. The geology of the western and southern parts of the basin is dominated by granitic rock of the Idaho batholith and the eastern side of the basin is composed of sedimentary rock. Elevation ranges from about 1,000 m to 2,200 m above sea level.

In addition to bull trout, native fishes in the Bitterrroot basin include several cyprinids, westslope cutthroat trout (*Oncorhynchus clarki lewisi*), slimy sculpin (*Cottus cognatus*), mountain whitefish (*Prosopium williamsoni*), and longnose sucker (*Catostomus catostomus*). Brown trout, brook trout, rainbow trout, and Yellowstone cutthroat trout (*Oncorhychus mykiss bouvieri*) have been introduced in the upper basin. Brown trout and rainbow trout are common in the mainstem of the Bitterroot River and the lower sections of most tributaries

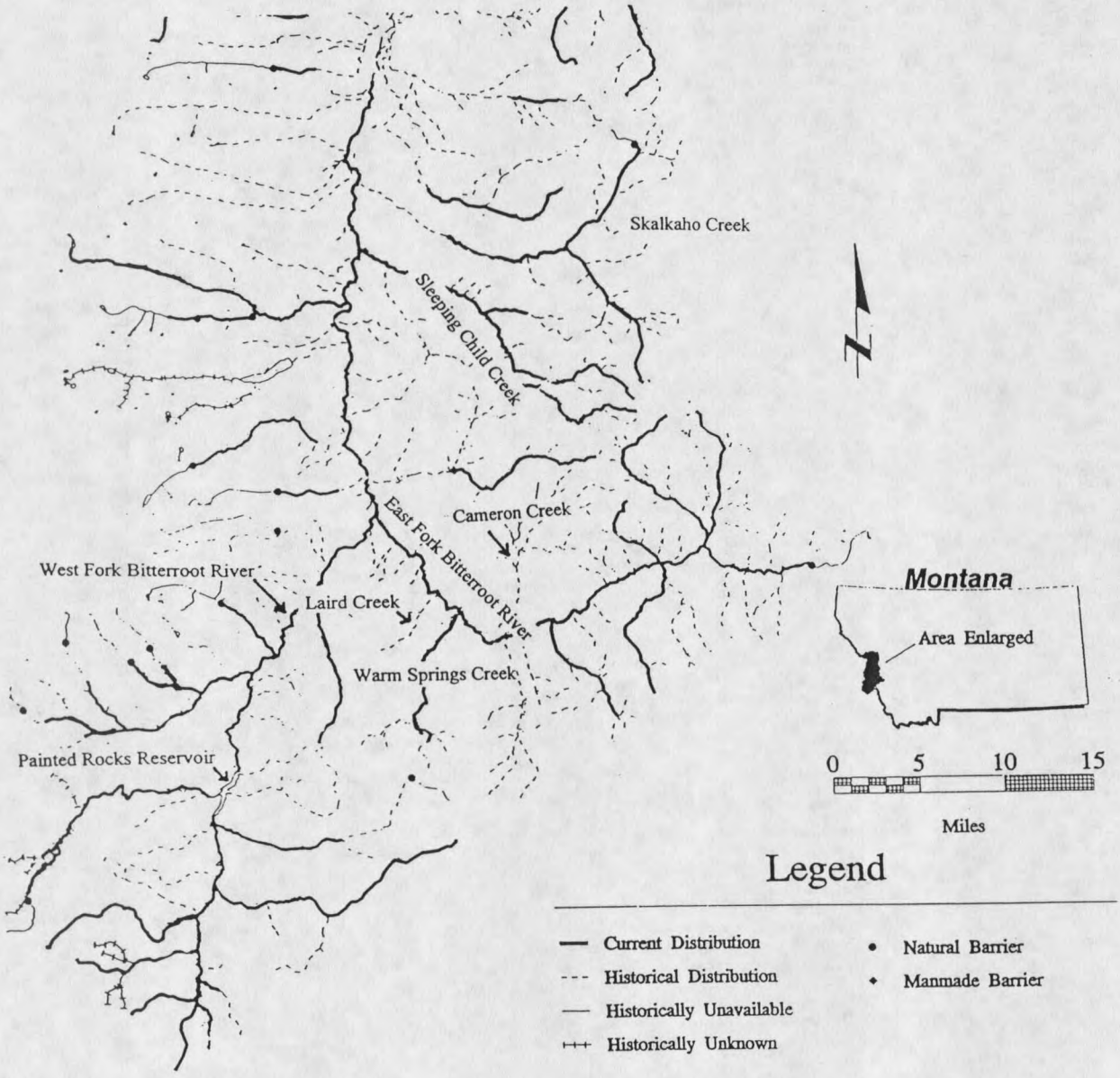

Figure 1. Bull trout distribution in the upper 2/3 of the Bitterroot River basin from survey data collected by the Montana Department of Fish, Wildlife, and Parks.

entering the main river. Brook trout are common in lower elevation streams and have been found in 75% of watersheds containing bull trout, although often not in the same stream reaches as bull trout (Clancy 1993).

Sampling focused on the upper basin near and within the East and West Forks of the Bitterroot River (Figure 1). These drainages were chosen due to their similar geology and because bull trout were known to be present in each basin over a relatively wide range of abundance. Prior to this study, knowledge of bull trout distribution in the Bitterroot River basin was primarily limited to larger systems including the Bitterroot River and the lower section of subbasins (Figure 1). Occurrence information in each drainage was based primarily on surveys of larger tributaries. There was little data on distribution of bull trout in smaller tributaries (first to third order; stream order determined using method of Strahler [1957]).

METHODS

Tributary streams (first to fourth order) were surveyed for presence/absence of bull trout and other species including cutthroat trout, brook trout, and tailed frog (*Ascaphus truei*). Here I focus on factors associated with bull trout occurrence. Habitat variables were estimated at two different scales. Watershed variables were derived from large-scale topographic maps and site variables were measured in study reaches. Sampled subbasins included Skalkaho and Sleeping Child Creeks, the East Fork of the Bitterroot River from Laird Creek to the headwaters (excluding Cameron Creek), and the West Fork of the Bitterroot River above Painted Rocks Reservoir (Figure 1). Known bull trout abundance in larger (fourth order) streams varied widely in this area (Figure 1).

Fish sampling

Presence/absence sampling for bull trout was conducted from early June through August of 1993-95 during low flow. In each subbasin, sampling was conducted in all streams defined on 1:24,000 scale USGS topographic maps. Additional streams were added if they were deemed capable of supporting fish upon field examination. Sampling was confined to streams that were small enough (first to fourth order) to effectively sample using a backpack electrofisher.

Because my objective was to determine bull trout occurrence over a large area rather than accurately estimate abundance, my sampling protocol attempted to maximize the number of streams surveyed while ensuring that no significant populations went undetected. This was accomplished by adopting a hierarchical sampling design, similar to that described by Rieman and McIntyre (1995), to increase the probability of detecting bull trout presence. Sampling occurred within 500 m long study reaches spaced evenly over estimated suitable habitat in each stream. The first study reach was located near the mouth of each stream. Study reaches were divided into five 100 m sections. In order to facilitate detection, I sampled 30 m of habitat in each 100 m section judged most likely to contain bull trout (pools, accumulations of woody debris, and boulders; Pratt 1984; Jakober 1995; see also Rieman and McIntyre 1995). If a strong bull trout population was found in the first reach (presence of multiple age classes), bull trout were considered present and sampling was ended. If none or very few bull trout were found, additional 500 m study reaches were sampled. If no bull trout were found in the second reach, a third reach was sampled. Bull trout were considered absent if none were collected in the three reaches. In some streams the second or third reaches were not sampled if the likelihood of bull trout presence was considered very low (i.e., very steep gradients, lack of pool/riffle development, very low water flow, and absence of cutthroat trout). Rieman and McIntyre (1995) found that the theoretical probability of correctly detecting

presence of bull trout was 0.82 using a similar sampling design.

Fish were captured by single pass electrofishing. Care was taken to electroshock slowly and extensively through all areas of cover during an upstream pass. A two person crew used a Smith-Root Model 12A backpack electrofisher operated at a DC pulse frequency of 30 - 50 hertz, 500 μs pulse duration, and 500 - 1000 V depending on water conductivity (range 20 - 220 μS). Capture efficiency was probably reduced in the few streams sampled draining highly resistant geology with low conductivity (20 - 50 μS), but the majority of streams surveyed had conductivity suitable for effective electrofishing (> 50 μS). In low conductivity waters, voltage gradient was increased before pulse frequency to increase shocking efficiency. Studies of the impacts of pulsed DC current on spinal injury rates in salmonid fish have shown high pulse frequency rather than voltage level to be the primary cause of spinal injury (W. Fredenberg, U.S. Fish and Wildlife Service, personal communication; Sharber 1994).

To determine detection probability for single pass electrofishing, I compared relative sampling efficiency between single pass and three-pass population estimates (White et al. 1978) in eight 100 m sections blocknetted at each end. On average, 69 % of the total number of bull trout captured in three pass removals were captured in the first pass ($R^2 = 0.60$; $P = 0.024$; Figure 2). These data further suggest that my sampling design had a high probability of detecting fish when they were present.

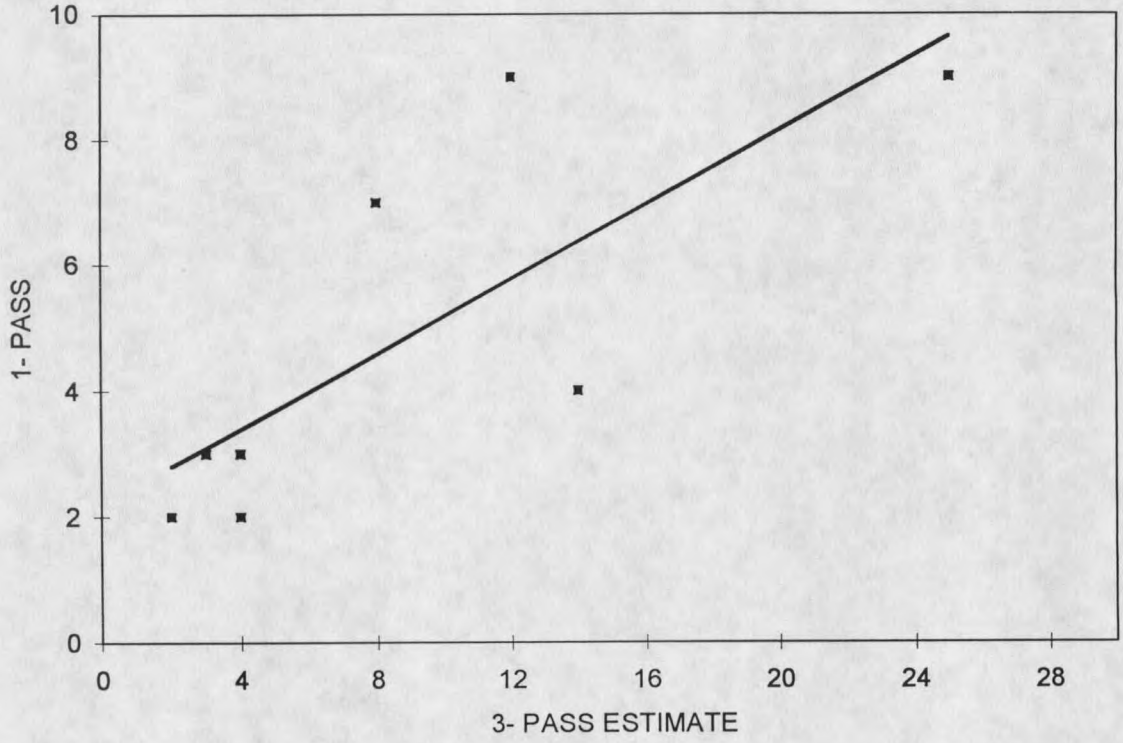

Figure 2. Relative bull trout electrofishing efficiency for 1 - pass versus a 3 - pass population estimate ($y = 2.192 + 0.298(x)$; $R^2 = 0.60$; $P = 0.024$; $n = 8$).

Site habitat variables

I examined relations between bull trout occurrence and site habitat features measured in the portions of each 100-m section where fish were sampled. Methods for measuring habitat variables are listed in Table 1. Values for site habitat variables were averaged to determine habitat characteristics of each sampling reach. Because the number of sites sampled in a stream varied from 1 to 3 depending on bull trout occurrence, I used site habitat data derived only from the first reach for each stream to minimize bias. To test the assumption that habitat variables measured in the first reach reflected stream habitat conditions, I compared habitat condition of the first reach to upstream reaches with a Wilcoxon matched pairs nonparametric test (Gibbons 1985). Although there were significant differences for gradient, canopy closure, and stream width, differences in other variables were not highly significant ($P > 0.05$) over the longitudinal range of each tributary surveyed (Table 2), suggesting that the first reach reasonably represented habitat in additional reaches.

Watershed variables

Watershed variables were measured for each tributary stream from 1:24,000 USGS topographic maps (Table 3). These variables were included in the analysis to determine if large-scale geomorphic features were important in affecting bull trout occurrence.

Table 1. Methods used to estimate site habitat variables in each sampling reach.

Wetted channel width and mean depth - Measured at three evenly spaced points along the distance electrofished in each 100m section. Depth measurements were made at 1/4, 1/2, and 3/4 across the channel with a meter stick. Mean depth was obtained by dividing the three measurements by four to account for zero depth at stream margin.

Gradient (%) - Measured with a clinometer over a representative section of the study reach.

Fine sediment - Estimated visually as the average percent of substrate particles less than 6.35 mm. Categories were "low" (< 20%), moderate (20 - 40%), high (>40%).

Canopy closure - Measured at three evenly spaced points along each section electrofished using a densiometer. Recorded as low (< 25%), moderate (25 - 75%), and high (>75%).

Pool frequency (no. / 100-m) - Pools were at least as long as the stream width and greater than 15 cm in depth.

Woody debris (no. / 100-m) - Number of pieces at least three meters in length and 10 cm diameter.

Biotic factors

Occupancy of small tributary streams by bull trout may depend on "demographic support" from larger populations nearby (Pulliam 1988; Hanski 1991) and on presence or absence of brook trout (Leary et al 1983, 1993). To determine if bull trout occurrence in tributary streams was related to bull trout abundance in nearby larger ("mainstem") streams, mainstem abundance was

coded as "absent" (bull trout absent), "weak" (< 5 / 100 m stream length), or "strong" (> 5 / 100 m stream length; Montana Dept. of Fish, Wildlife, and Parks, Hamilton, MT, data files). To determine if the presence of brook trout influenced bull trout distributions, the presence/absence of brook trout at each site was included as an independent variable in the analysis.

Table 2. Wilcoxon signed-rank test for comparison of habitat features determined from streams where one reach versus multiple reaches were sampled.

Site variable	Comparison[a]	Z-value	P level[b]
Canopy	1 vs 2 reaches	2.20	0.03
	1 vs 3 reaches	1.73	0.08
Depth	1 vs 2 reaches	0.17	0.87
	1 vs 3 reaches	1.74	0.08
Gradient	1 vs 2 reaches	3.34	<0.01
	1 vs 3 reaches	2.97	<0.01
Woody Debris	1 vs 2 reaches	1.38	0.17
	1 vs 3 reaches	1.88	0.06
Pool Frequency	1 vs 2 reaches	0.25	0.81
	1 vs 3 reaches	0.59	0.56
Fine Sediment	1 vs 2 reaches	0.71	0.48
	1 vs 3 reaches	1.12	0.26
Stream Width	1 vs 2 reaches	1.49	0.14
	1 vs 3 reaches	2.34	0.02

[a] 58 streams had two reaches sampled and 30 streams had three reaches sampled.
[b] P-level for two-sided test.

Table 3. Watershed variables and methods used for their measurement from 7.5' USGS topographic maps.

Aspect - Coded as either predominantly north or south facing.
Stream length (km) - Length for entire perennial stream measured by planimeter and determined as an average of three measurements.
Basin area (km^2) - Measured by planimeter and determined as an average of three measurements.
Elevation (m) - Determined at stream mouth.
Stream order - Determined using the method of Strahler (1957).
Tributary slope - Slope of stream from mouth to upper end of the highest-elevation first order stream.
Link magnitude - Number of first order tributaries in a stream basin (Scheidegger 1965).
D-link - Measure of location of tributary stream within a drainage network. Determined as a cumulative link magnitude from the headwaters of a river basin to the mouth (Osborne and Wiley 1992).

Data analysis

Relationships between the occurrence of bull trout and site, watershed, and biotic variables were first examined with univariate tests. I used Mann-Whitney nonparametric tests (Gibbons 1985) for continuous variables and chi-square tests for categorical variables (Neter et al. 1993) to test for differences in habitat and biotic variables between streams where bull trout were present versus absent. I used a similar analysis to compare values for site and

watershed variables for streams with bull trout present and brook trout absent versus those with brook trout present and bull trout absent.

Significant variables identified using univariate analyses were used in stepwise logistic regression (LR) analyses of variables affecting bull trout occurrence (Hosmer and Lemeshow 1989). Analyses were performed using the forward stepwise model-building procedures of SAS release 6.11 (Proc Logistic, SAS Institute Inc.). The stepwise procedure reduces problems associated with correlated variables by selecting one variable that produces the greatest increase in model goodness of fit from two or more correlated variables. The SAS logistic regression program uses jackknife procedures in calculating regression parameter estimates to reduce bias associated with the circularity of classifying the same observations that are used to construct the parameter estimates. Regression diagnostics were used to identify outliers and influential observations in final models.

Logistic regression was performed on three sets of variables: watershed, site, and a combination of habitat and biotic variables. The first set included watershed variables estimated from topographic maps. The second set used field site habitat variables. After controlling for the effects of physical habitat, I tested for the relative importance of habitat and biotic variables by adding mainstem abundance of bull trout and presence of brook trout to the habitat models. Addition of biotic variables to habitat models was assessed based on two indicators of improvement in model fit; (1) the log-likelihood test and (2) their

contribution to the predictive capacity of the model (classification accuracy).

I used Spearman's rank correlation to examine correlations between watershed, site, and between site variables to determine whether watershed variables might be surrogates for site level variables. To examine how bull trout occurrence varied over the range of different combinations of variables, I constructed bivariate plots. Bivariate plots give a smoothed representation of the proportion of bull trout occurrence over the range of one variable (i.e., width) for given ranges of a conditioning variable (such as low or high woody debris). Nonparametric kernal smoothing and LOWESS regression (Trexler and Travis 1993) was used initially to smooth the presence/absence data (1's and 0's), but the curves produced were too noisy. I settled on univariate LR because it produced smooth curves . Curves were generated using predicted proportions of bull trout occurrence from univariate LR output and plotting these for two or more ranges of the conditioning variable. Variables examined were those that had the best explanatory power in site level LR models.

RESULTS

I sampled a total of 204 reaches in 112 streams. Streams ranged from 0.9 m to 7.0 m in wetted width. Bull trout were found in 67 (60%) streams (Figure 3), 109 (97%) streams contained westslope cutthroat trout, and 25 (22%) streams had brook trout. When bull trout were present, they were almost always (66 of 67) found in the lowermost study reach. Approximately two-thirds of streams in the East Fork and Skalkaho basins contained bull trout while only half the streams sampled in the West Fork contained bull trout.

Univariate analysis

Watershed-level analysis indicated that bull trout were more likely to be present in higher elevation basins draining larger areas, with lower gradients, larger link magnitudes, and higher stream order (Table 4). Site-level analysis also showed that presence of bull trout was significantly related to variables reflecting preference for wider and deeper streams with lower channel gradients (Table 4). Streams which contained bull trout also had significantly higher frequency of woody debris and pool habitats (Table 4). Thus streams which contained bull trout were larger, of lower gradient, at higher elevation, contained more complex habitat in the form of pools and woody debris, and had a stronger nearby mainstem population than those streams where bull trout were absent (Table 4).

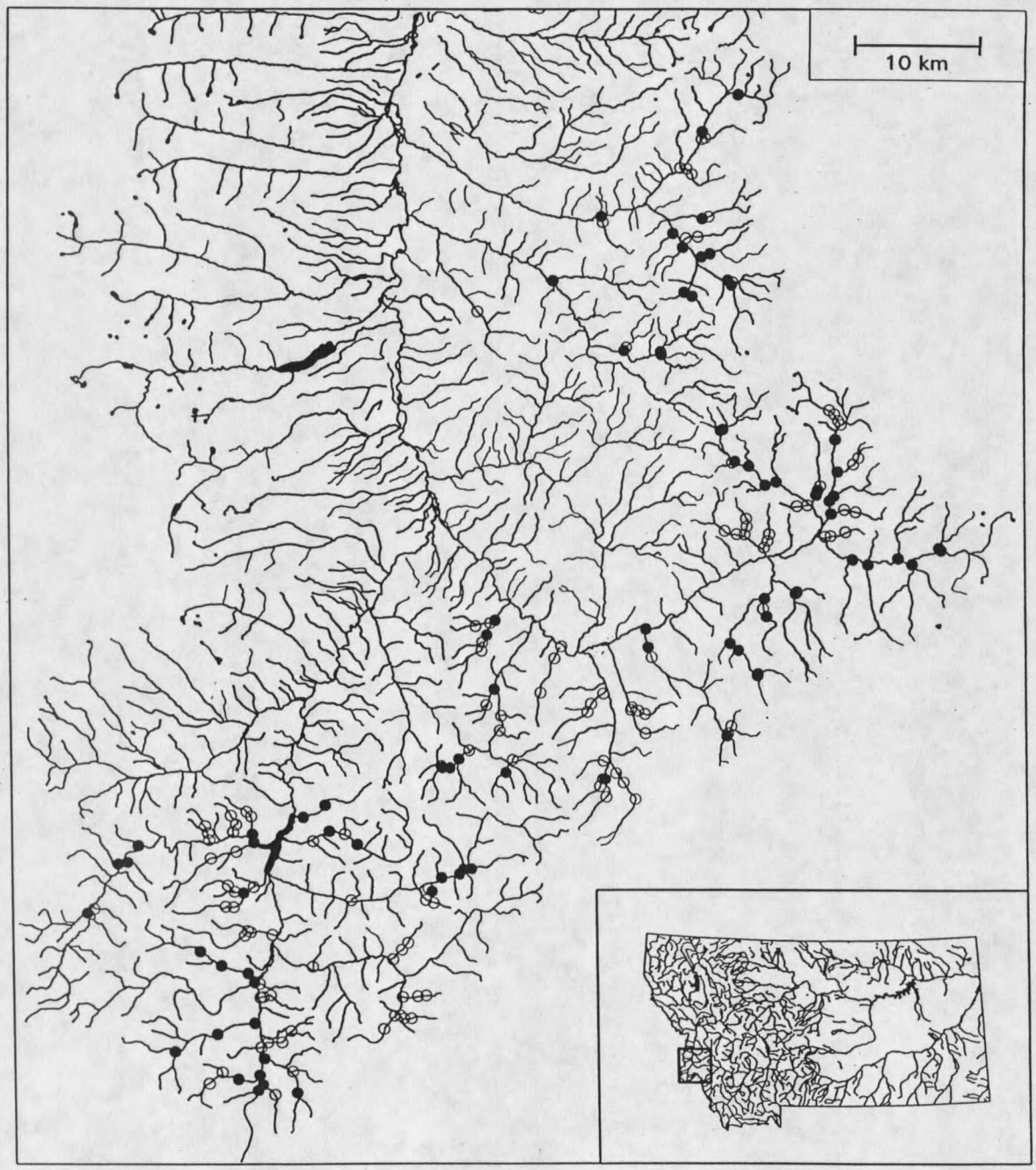

Figure 3. Results of presence/absence sampling for 204 reaches in the upper 2/3 of the Bitterroot River basin. Closed circles represent reaches with bull trout present while open circles represent reaches with bull trout absent.

Table 4. Summary of results of median, Mann-Whitney, and chi-square contingency table analysis to test for differences between watershed, site, and biotic variables for tributary streams with bull trout present versus absent in the Bitterroot River basin, Montana.

Variables [a]	Bull trout present [b]	Bull trout absent [b]	Test [c]	*P*
Watershed				
Basin aspect	(30 south, 37 north)	(17 north, 28 south)	X^2 = 3.28	0.070
D-link	18.0 (2 - 471)	22.0 (2 - 343)	Z = 0.29	0.773
Basin area (km^2)	11.7 (2.0 - 129.7)	5.0 (1.72 - 32.0)	Z = 4.43	<0.001
Tributary slope (%)	8.0 (2.7 - 17.7)	12.9 (4.8 - 22.7)	Z = 4.64	<0.001
Elevation (m)	1725 (1353 - 1945)	1573 (1341- 1914)	Z = 3.35	0.001
Link magnitude	4.0 (1 - 89)	2.0 (1 - 20)	Z = 3.72	<0.001
Stream length (km)	5.6 (0.9 - 31.5)	3.7 (1.6 - 12.5)	Z = 2.59	0.006
Stream order	(3-1, 29-2, 30-3, 5-4)	(15-1, 24-2, 4-3, 2-4)	X^2 = 26.33	<0.001
Site				
Canopy closure (low, mod, high)	(9 l, 37 m, 21 h)	(2 l, 26 m, 17 h)	X^2 = 2.57	0.276
Mean depth (m)	0.16 (0.05 - 0.71)	0.08 (0.03 - 0.42)	Z = 5.09	<0.001
Fine Sediment (low, mod, high)	(36 l, 28 m, 3 h)	(26 l, 12 m, 7 h)	X^2 = 5.50	0.064
Channel gradient (%)	5.6 (1.0 - 15.6)	8.0(1.9 - 20.2)	Z = 3.23	0.001
Pool frequency (no. per 100m)	10.0 (2.8 - 16.4)	7.2(2.0 - 15.0)	Z = 3.69	<0.001
Wetted width (m)	3.1 (1.0 - 6.8)	1.5(0.9 - 3.9)	Z = 5.99	<0.001
Woody debris (no. per 100m)	17.2 (3.4 - 92.9)	6.4(0.0 - 27.0)	Z = 5.97	<0.001
Biotic				
Brook trout (present/absent)	(9 pres, 58 abs)	(14 pres, 31 abs)	X^2 = 7.60	0.006
Mainstem relative abundance of bull trout (absent, weak, str)	(4 abs, 12 wk, 51 str)	(11 abs, 18 wk, 16 str)	X^2 = 19.17	<0.001

[a] Variables are described in Table 1 and 2.
[b] Median (range) for continuous variables and observed frequencies for categorical variables for sites/subbasins with bull trout present/absent.
[c] Sample sizes for streams with bull trout present/absent are 67/45.

Bull trout and brook trout distribution showed little overlap, occurring together in only a small proportion of streams (9 of 112). Habitat preferences of the two species appeared dissimilar. Brook trout occurred in significantly smaller and shallower streams of lower elevation and lower stream order than

those occupied by bull trout (Table 5). Brook trout streams also had fewer pools and about one-third the amount of woody debris as bull trout streams (Table 5).

Table 5. Mann-Whitney and chi-square analysis to test for differences between watershed and site habitat variables for streams with only bull trout present versus only brook trout present in the Bitterroot River basin, Montana.

Variables [a]	Brook trout present [b]	Bull trout present [b]	Test	P [c d]
Watershed				
Basin aspect	(8 south, 8 north)	(30 south, 37 north)	$X^2 = 0.06$	0.807
D-link	30(2 - 241)	18(2 - 471)	$Z = 0.86$	0.390
Basin area (km^2)	6.7(3.5 - 32.0)	11.2(2.0 - 129.7)	$Z = 0.80$	0.423
Tributary slope (%)	10.1(4.8 - 19.0)	8.1(2.7 - 17.7)	$Z = 1.16$	0.245
Elevation (m)	1564(1341- 1786)	1744(1353 - 1945)	$Z = 3.35$	<0.001
Link magnitude	3.5(1 - 20)	4.0(1.0 - 89.0)	$Z = 0.90$	0.368
Stream length (km)	3.8(2.0 - 12.5)	5.2(0.9 - 31.5)	$Z = 0.13$	0.896
Stream order (1 - 4)	(5-1, 7-2, 2-3, 2-4)	(3-1, 29-2, 30-3, 5-4)	$X^2 = 13.67$	<0.001
Site				
Canopy closure (low, mod, high)	(2 l, 7 m, 7 h)	(9 l, 37 m, 21 h)	$X^2 = 1.00$	0.606
Mean depth (m)	0.10(0.06 - 0.13)	0.16(0.05 - 0.70)	$Z = 3.74$	<0.001
Fine Sediment (low, mod, high)	(12 l, 2 m, 2 h)	(36 l, 28 m, 3 h)	$X^2 = 8.90$	0.064
Channel gradient (%)	6.2(1.9 - 11.3)	6.1(1.0 - 15.6)	$Z = 0.43$	0.665
Pool frequency (no. per 100m)	7.2(2.7 - 13.1)	10.3(2.8 - 16.4)	$Z = 2.50$	0.012
Wetted width (m)	1.9(1.4 - 3.9)	3.0(1.0 - 6.8)	$Z = 3.25$	<0.001
Woody debris (no. per 100m)	5.5(1.9 - 26.0)	18.0(3.4 - 92.9)	$Z = 3.59$	<0.001
Biotic				
Mainstem relative abundance of bull trout (abs, weak, strong)	(9 ab, 7 wk, 0 st)	(4 ab, 12 wk, 51 st)	$X^2 = 49.63$	<0.001

[a] Variables are described in Table 1 and 2.
[b] Median (range) for continuous variables and observed frequencies for categorical variables for sites/subbasins with bull trout present/absent.
[c] Sample sizes for streams with bull trout present/brook trout present are 58/16.
[d] P value for two-tailed test.

Logistic regression models

At the watershed scale, elevation, tributary slope, and basin area were important in determining bull trout occurrence (model $P = 0.0001$; Table 6). The addition of the "mainstem abundance" of bull trout variable to the watershed model significantly improved goodness of fit ($X^2 = 11.676$; $P = 0.0001$) but increased classification accuracy by 6.2 % (Table 7).

At the site scale, stream width, woody debris, and gradient were significantly related to occurrence of bull trout (model $P = 0.0001$; Table 6). The site model correctly classified 81.3% of the streams surveyed (Table 7). The addition of either "brook trout presence" or "mainstem abundance" to the site model significantly improved model goodness of fit ($X^2 =$ 15.223 and 15.500 respectively; $P < 0.0001$) but did not increase classification accuracy (Table 7).

Correlation among variables

Watershed scale variables were highly correlated to site level variables suggesting that watershed variables may be surrogates for site level variables. Of those watershed scale measures of stream size (stream order, link magnitude, stream length, and basin area), basin area had the strongest correlation to wetted width (Table 8). Tributary slope was strongly correlated with channel gradient and elevation was strongly correlated with woody debris (Table 8). Elevation was also strongly positively correlated with mainstem abundance of bull trout and negatively correlated with the presence of brook trout (Table 8).

Table 6. Variables listed in order of the absolute magnitude of the standardized coefficient for site and watershed scale logistic regression models explaining the presence of bull trout in tributaries of the Bitterroot River, Montana.

Variable set	Coefficient [a]	Standardized coefficient [b]	Significance [c]	Model			
				-2 log likelihood	X^2	df	*P* value
Site							
Wetted width (m)	1.0150	3.2605	0.0011				
Site gradient (%)	-0.2118	-2.8777	0.0040				
Woody Debris (no. per 100m)	0.1012	2.8669	0.0042	91.586	59.330	3	0.0001
Site and biotic							
Site gradient (%)	-0.3278	-3.5515	0.0004				
Wetted width (m)	1.2896	3.4574	0.0005				
Brook trout (pres/abs)	-2.8856	-1.5289	0.0007				
Woody Debris (no. per 100m)	0.0924	2.3042	0.0212	76.363	74.553	4	0.0001
Site gradient (%)	-0.3112	-3.5164	0.0004				
Mainstem (abs/weak/str)	1.6531	3.4986	0.0005				
Wetted width (m)	1.0707	3.0444	0.0023				
Woody Debris (no. per 100m)	0.0865	2.2010	0.0276	76.086	74.830	4	0.0001
Watershed							
Elevation (m)	0.0045	3.4696	0.0005				
Tributary slope (%)	-0.2614	3.3173	0.0009				
Basin area (km^2)	-0.0528	1.8243	0.0682	105.554	45.361	3	0.0001
Watershed and mainstem abundance							
Mainstem (abs/weak/str)	1.7793	4.2843	0.0001				
Tributary slope (%)	-0.2490	3.0255	0.0025				
Basin area (km^2)	0.0861	2.6739	0.0322	93.879	57.037	3	0.0001

[a] The sign of a coefficient indicates the predicted direction of the variables effect on the occurrence of bull trout (given the effects of the other variables in the model).

[b] The relative importance of each variable in the model is indicated by absolute magnitude of the standardized coefficients.

[c] Significance level was determined by the Wald chi-square test.

Table 7. Summary of classification table results for bull trout models.

Variable set[a]	Percent Correct	Kendall's Tau-a [b]	Classification table (prior = 0.5)[c]		
				Predicted	
			Observed	Absence	Presence
Site	81.3%	0.380	Absence	35 (77.8%)	10 (15.2%)
			Presence	11 (23.9%)	56 (83.6%)
Site and brook trout	82.1%	0.410	Absence	35 (85.1%)	10 (14.9%)
			Presence	10 (22.2%)	57 (85.1%)
Site and mainstem	80.4%	0.410	Absence	33 (73.3%)	11 (14.9%)
			Presence	10 (23.3%)	57 (85.1%)
Watershed	76.8%	0.337	Absence	30 (66.7%)	15(21.1%)
			Presence	11 (26.8%)	56(83.6%)
Watershed and mainstem	83.0%	0.370	Absence	32 (82.2%)	13 (17.6%)
			Presence	6 (15.8%)	61 (91.0%)

[a] Variables are described in Table 1 and 2.
[b] Index of rank correlation for assessing the predictive ability of the model.
[c] Prior = 0.5 means the response is predicted to be an event if the predicted probability is 0.5 or greater.

? NOT ASSUMED/EXPECTED PROB'Y W/IN POPULATION ?

Table 8. Spearman rho test for association between pairs of variables. No asterisk indicates independence between variables X and Y, one asterisk indicates significant association at $0.05 < P \leq 0.10$ and two asterisks indicate significance at $P \leq 0.05$. A minus sign indicates a negative association between variables (Gibbons 1993).

	Basin aspect (south/north)	D-link	Basin area	Tributary slope	Elevation	Link magnitude	Stream length	Stream order	Brook trout (+/-)
Basin aspect		0.04	-0.05	0.02	0.05	-0.02	-0.01	0.02	-0.08
D-link	0.04		0.23**	-0.07	-0.36 **	0.46 **	0.38 **	0.19 **	0.21 **
Basin area	-0.05	0.22 **		-0.60 **	-0.04	0.55 **	0.86 **	0.59 **	0.22 **
Tributary slope	0.02	-0.31 **	-0.37 **		-0.04	-0.40 **	-0.37 **	-0.24**	-0.29**
Elevation	0.05	-0.36 **	-0.04	-0.04		0.21 **	-0.21**	0.28 **	-0.41 **
Link magnitude	-0.02	0.46 **	0.55 **	-0.32 **	0.21 **		0.53 **	0.68 **	0.12
Stream length	-0.01	0.38 **	0.86 **	-0.46 **	-0.21 **	0.53 **		0.43 **	0.25**
Stream order	0.02	0.19 **	0.59 **	-0.46 **	0.28 **	0.68 **	0.43 **		-0.05
Brook trout (+/-)	-0.08	0.21 **	0.22 **	-0.15	-0.41 **	0.12	0.25**	-0.05	
Canopy closure	-0.22**	-0.05	-0.11	0.21 **	-0.21 **	-0.13	-0.09	-0.29**	0.01
Mean depth	0.06	0.02	0.60 **	-0.34 **	0.26 **	0.40 **	0.47 **	0.53 **	-0.11
Fine sediment	0.08	-0.07	-0.16 *	0.15	0.00	-0.19 **	-0.14	-0.08	-0.14
Tributary slope	0.02	-0.31**	-0.37 **	1.00	-0.04	-0.32 **	-0.46 **	-0.46**	-0.15
Pool frequency	-0.11	-0.19 **	0.10	-0.07	0.36 **	0.11	0.01	0.16 *	-0.16 *
Wetted width	-0.01	0.02	0.78 **	-0.50 **	0.22 **	0.51 **	0.61 **	0.58 **	0.03
Woody debris	-0.16 *	-0.25 **	0.26 **	-0.16 *	0.29 **	0.16 **	0.08	0.29 **	-0.19 **
Mainstem abundance	0.05	-0.17 *	-0.08	-0.01	0.49 **	-0.07	-0.19 **	0.22 **	-0.70 **
Bull trout (+/-)	-0.17 *	-0.03	0.42 **	-0.44 **	0.32 **	0.36 **	0.26 **	0.45 **	-0.26 **

Table 8. Continued.

	Canopy closure	Mean depth	Fine sediment	Channel gradient	Pool frequency	Wetted width	Woody debris	Mainstem abundance
Basin aspect	0.22**	0.06	0.08	0.02	-0.11	-0.01	-0.16 *	0.05
D-link	-0.05	0.02	-0.07	-0.31 **	-0.20 *	0.02	-0.25 **	-0.17 **
Basin area	-0.11	0.60 **	-0.16 *	-0.37 **	0.10	0.78 **	0.26 **	-0.08
Tributary slope	0.21**	-0.34**	0.15	0.53 **	-0.07	-0.50 **	-0.16 *	-0.01
Elevation	-0.21 **	0.26**	0.00	-0.04	0.36 **	0.22 **	0.29 **	0.49 **
Link magnitude	-0.13	0.40**	-0.19 **	-0.40 **	0.10	0.51 **	0.16 *	-0.07
Stream length	-0.09	0.47 **	-0.09	-0.37 **	0.01	0.61 **	0.08	-0.19 **
Stream order	0.29 **	0.53 **	-0.08	-0.24 **	0.17 *	0.58 **	0.29 **	0.22 **
Brook trout (+/-)	0.01	-0.11	-0.14	-0.29**	-0.16 *	0.03	-0.20 **	-0.69 **
Canopy closure		0.30 **	-0.26 **	0.27 **	-0.01	-0.15	-0.01	-0.20 **
Mean depth	-0.30**		-0.08	-0.15	0.23 **	0.78 **	0.42 **	0.33 **
Fine sediment	-0.28	-0.08		-0.10	-0.02	-0.17 *	0.00	0.09
Channel gradient	0.27 **	0.02	-0.37 **		-0.01	-0.28 **	-0.16 *	0.21*
Pool frequency	-0.01	0.23 **	-0.02	-0.01		0.16 *	0.36 **	0.29 **
Wetted width	-0.15	0.78 **	-0.17 *	-0.28 **	0.16 *		0.54 **	0.18 *
Woody debris	-0.16 *	0.42 **	0.00	-0.03	0.36 **	0.54 **		0.34 **
Mainstem abundance	-0.20	0.33 **	0.09	0.21 **	0.29 **	0.18 *	0.34 **	
Bull trout (+/-)	-0.11	0.48 **	-0.01	-0.31 **	0.35 **	0.57 **	0.50 **	0.41 **

Site level variables were also correlated to each other. Wetted width was strongly correlated to average depth, woody debris, pool frequency, and channel gradient (Table 8). Woody debris and pool frequency were highly correlated to each other and both were positively correlated with average depth (Table 8).

Bivariate analysis

Both woody debris and mainstem abundance influenced the relationship between stream size and bull trout occurrence. Bull trout were seldom found in streams less than 2 to 3 m wide unless the frequency of woody debris was high and/or there was a strong adjacent mainstem population of bull trout (Figures 4 and 5). Small streams (< 2 m wide) with high frequency of woody debris were about 3 times more likely to contain bull trout (0.6 for streams 2 m in width) than streams with low frequency of woody debris (Figure 4). Similarly, small streams (< 2 m wide) with "strong" nearby mainstem had about two times greater predicted probability of containing bull trout than streams with either "absent" or "weak" mainstem populations (Figure 5). A relatively high proportion (> 0.80) of streams greater than 3 m wide contained bull trout regardless of woody debris frequency or mainstem bull trout relative abundance (Figures 4 and 5). A high frequency of woody debris or a strong mainstem population also increased the likelihood that bull trout would occur in higher gradient streams (Figure 6 and 7). These factors increased the predicted probability of bull trout occurrence in streams with 10% gradient from less than 0.10 to about 0.70.

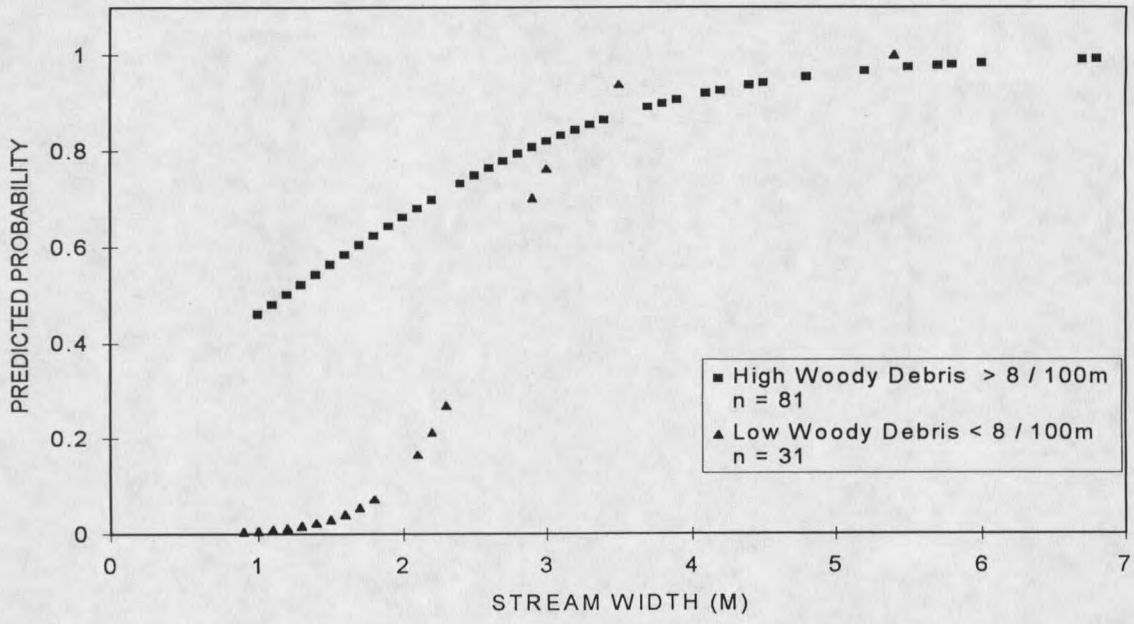

Figure 4. Predicted probability of bull trout occurrence by stream width for streams with low and high woody debris density.

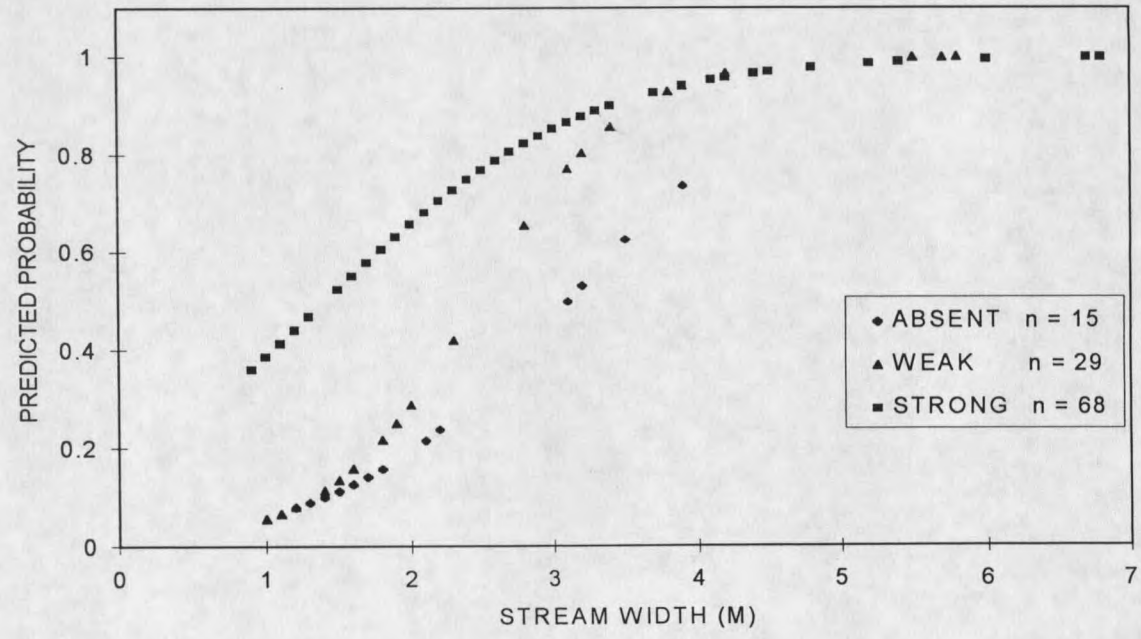

Figure 5. Predicted probability of bull trout occurrence for streams with "absent", "weak", and "strong" mainstem bull trout abundance.

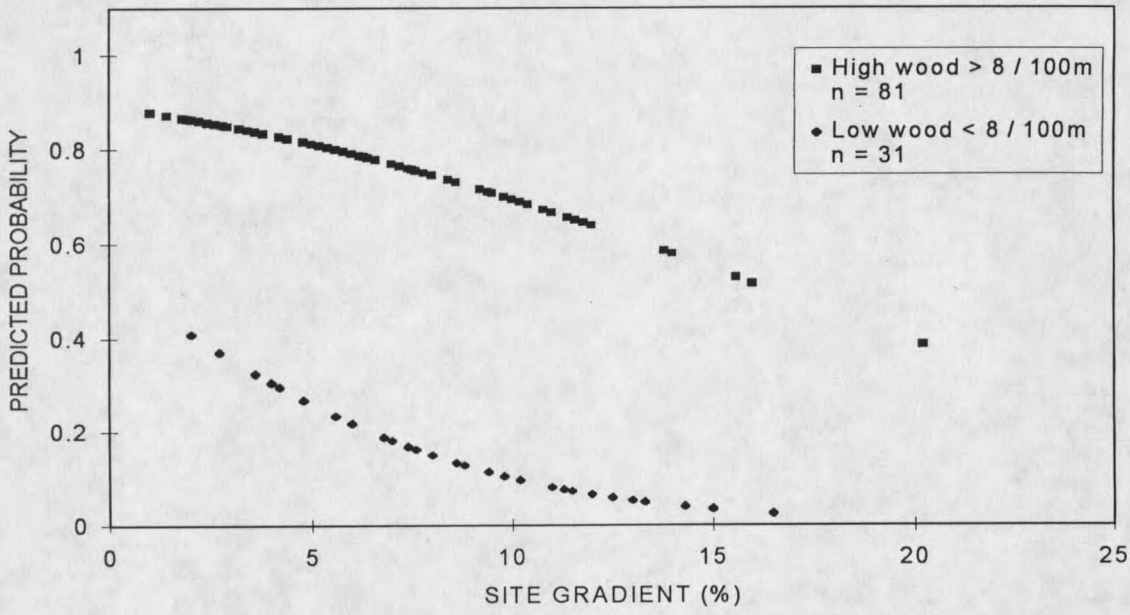

Figure 6. Predicted probability of bull trout occurrence by channel gradient for streams with low and high woody debris.

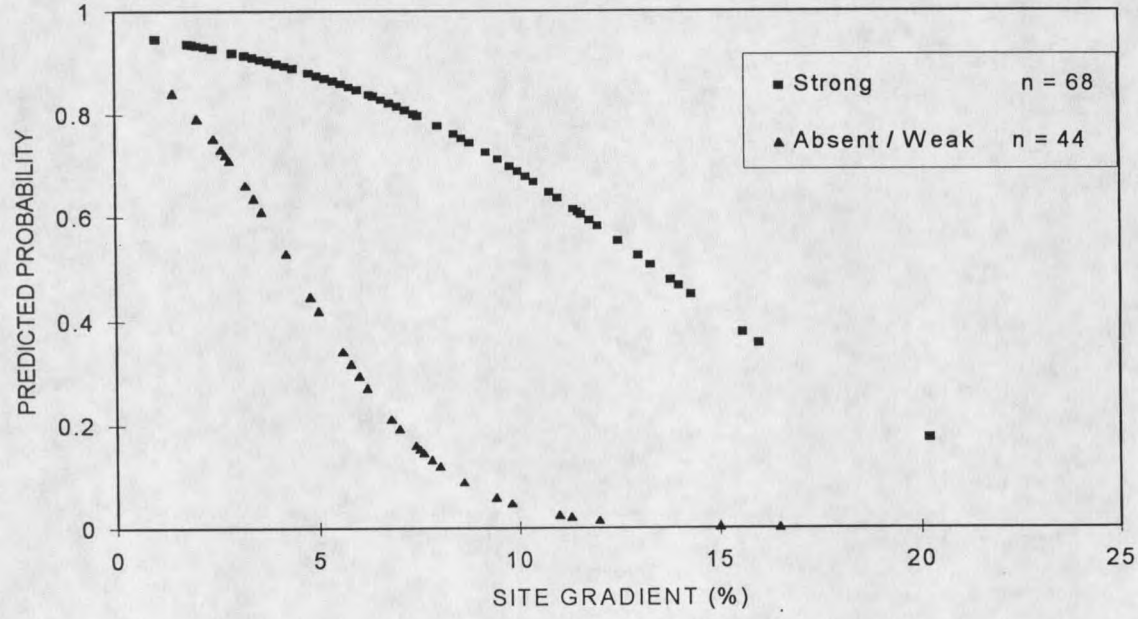

Figure 7. Predicted probability of bull trout occurrence by channel gradient for streams with a absent/weak or strong mainstem abundance of bull trout.

DISCUSSION

Patterns of habitat occupancy

I found that the distribution of bull trout in the Bitterroot basin (60% of 112 streams surveyed) was much more restricted than that of westslope cutthroat trout (97% of surveyed streams). Of 204 reaches sampled, 83 (41%) contained bull trout while 195 (96%) contained cutthroat trout. Moderate-sized streams (order or width) have been identified as important rearing habitats for juvenile bull trout (Fraley and Graham 1981; Shepard et al. 1984b; Pratt 1984; Goetz 1991; Mullan et al. 1992). Previous studies found bull trout were restricted to a subset of available streams and stream reaches (Shepard et al. 1984b; Mullan et al. 1992), suggesting bull trout have more specific habitat requirements than other sympatric salmonids.

At the stream scale, I found that variables related to stream size (wetted width, stream order, basin area, and average water depth) and habitat quality (frequency of woody debris and pool habitats), differentiated sites where bull trout were present and absent (Table 4 and 6). In their sampling of 67 streams and 46 subbasins in Idaho, Rieman and McIntyre (1995) found that stream width and basin area were important in explaining bull trout occurrence. They were not able to separate the effects of stream size from basin area due to collinearity between variables. Since both variables are measures of stream size, Rieman and McIntyre (1995) speculated that the strong association between habitat

patch size (basin area) and bull trout occurrence they found may simply be an indicator of other characteristics of stream habitat that vary with stream size (e.g., woody debris, number of pools). I also found that stream width and basin area were highly correlated with each other and with bull trout occurrence (Table 8). Because these variables also were highly correlated with other habitat variables important in describing bull trout habitat such as woody debris, pool frequency, depth, and mainstem abundance, it appears that stream size variables act as "surrogates" for other habitat variables which functionally influence the presence of bull trout.

In an extensive study of bull trout distribution in Oregon, Dambacher et al. (in press) examined the occurrence of bull trout in 103 reaches from 38 Oregon streams using ordination techniques and found six stream attributes to be important descriptors of bull trout habitat (volume and number of large woody debris, shade, riffle gravel and fines, and bank erosion). Of these factors, I examined woody debris, canopy closure, and fine sediments, and found woody debris significantly distinguished between streams with and without bull trout in univariate comparisons and in logistic regression models (Tables 4 and 6). Woody debris was the most common pool-forming element in small mountain streams in the study area, while pools in larger streams are most often formed by boulders (this study; Jakober 1995). In small streams, woody debris provides both pool habitats and cover (Lisle 1986). These two habitat components, are usually lacking in small streams which lack woody debris. Woody debris was

one of the best indicators of bull trout occurrence in small streams (< 2-3 m wide). Small streams with high frequencies of woody debris (> 8 / 100 m) had a higher probability of containing bull trout than small streams with low woody debris densities (Figure 4). Bull trout were also more likely to be in high gradient streams if woody debris was abundant, suggesting that woody debris mitigates the negative effect of high gradient (Figure 6). This relationship may be confounded, however, by the negative correlation between gradient and stream size as high gradient streams also tend to be small (Table 8).

Elevation and basin aspect also influenced bull trout occurrence in the Bitterroot River basin. Rieman and McIntyre (1995) found that the occurrence of spawning and rearing bull trout increased sharply above 1,600 m elevation and attributed this to the relationship between elevation and temperature. This elevation is similar to the lower quartile of 1,550 m elevation for streams containing bull trout in this study. The lower elevation threshold in my study may be due to higher latitude than Rieman and McIntyre's (1995) study in Idaho. Bull trout were more likely to be found in streams with northerly aspects. Although I have found no studies relating basin aspect with stream temperature, it is likely that streams in south facing basins have warmer water temperatures and thus be less suitable for bull trout, a species well known for its preference for cold temperatures (Goetz 1991; Adams 1994).

I was not able to define factors associated with the occurrence of westslope cutthroat trout or tailed frogs as they occurred in most streams

sampled. Tailed frogs were likely more widespread than I documented because my sampling protocol did not always sample in higher gradient reaches where bull trout were absent but tailed frog larvae are typically common (Daugherty and Sheldon 1982).

Support from adjacent populations

In addition to physical habitat, strong mainstem populations appeared to be a major factor influencing bull trout occurrence in the Bitterroot River basin. Rieman and McIntyre (1995) suggested that the persistence of bull trout in small streams depends on demographic support from adjacent larger systems. The distribution of bull trout in the upper Bitterroot basin support this hypothesis since I found that small streams adjacent to strong mainstem populations were more likely to contain bull trout than streams adjacent to a mainstem where bull trout were absent or weak (Figure 5). This pattern suggests that populations in small streams (< 4 or 5 m wide) may not be able to maintain themselves without dispersal from a strong neighboring population. The strong association between strong mainstem populations and bull trout occurrence in smaller streams further suggests that a minimum stream size is necessary for bull trout populations to persist. While smaller streams may be occupied, their occupancy relies on support from a population which occupies larger mainstem habitats. I also found a similar relationship with mainstem bull trout abundance and gradient, with small, high gradient streams more likely to be occupied by bull trout when

adjacent to a strong mainstem population (Figure 6). The fact that I usually found bull trout occupying the lowermost reach (nearest to the mouth) of any tributary where they were present further supports the strong link between populations in small streams and adjacent strong mainstem populations. These patterns of occurrence suggest that where bull trout populations are highly fragmented in basins without strong mainstem populations, they are probably at high risk of extinction, especially in streams < 4 m wide.

Small tributary streams may be seasonally occupied by bull trout. Recent reviews of the importance of movement for salmonids suggest that fitness of resident populations may be increased through movements to complete life-history requirements or to search for optimum habitat when current locations become unsuitable (Northcote 1992; Gowan et al. 1994). This study documented summer habitat use and distribution patterns and the distribution and habitats used by bull trout during other seasons may be different. Winter stream temperatures (sometimes below 0 °C) may limit overwinter habitat in headwater streams due to formation of anchor ice (Chisholm et al. 1987; Adams 1994). Some resident bull trout have been shown to make fall downstream migrations into deeper larger streams (Jakober 1995). Small streams may serve as seasonal spawning and rearing areas or as habitats where predation from larger bull trout or avian predators is less intense. Moreover, bull trout are highly piscivorous as adults (Shepard et al. 1984a) and an abundant prey base found in larger streams and lakes may be a critical requirement for strong

populations. The low densities of juvenile bull trout relative to cutthroat trout in this study support the idea that bull trout are not effective invertebrate predators and they may be dependent on piscivory to maintain a strong, persistent population. Small tributaries may thus constitute sink habitats supported by dispersal from nearby stronger source populations in larger, more productive mainstem habitats (Pulliam 1988). Strong mainstem populations and weak populations in small often high gradient streams are analogous to the large, central populations and ecologically marginal populations discussed by Scudder (1989). Scudder (1989) suggested that marginal habitats supported by dispersal from nearby central populations represent an important genetic resource for the population as a whole and recommended conservation of marginal habitats as one of the best ways to conserve genetic diversity important to the long-term persistence of populations.

Influence of brook trout

I found little evidence that brook trout were replacing bull trout through competitive exclusion across the upper Bitterroot basin. Instead, different habitat requirements between the two species appeared to be the most important factor influencing their distributions. I found that brook trout occupied streams having habitat conditions where bull trout were normally absent. Using discriminant analysis, Clancy (1993) compared habitat between streams containing bull trout versus those containing brook trout and found bull trout in

wider streams at higher elevations with lower canopy closure. It has been hypothesized that brook trout are more likely to replace bull trout in drainages where habitat has been disrupted (Rieman and McIntyre 1993). On the Bitterroot National Forest, brook trout predominantly occupy drainages where a high level of disturbance has occurred (Clancy 1993). Habitat conditions where brook trout were found were characteristic of habitats that have been degraded by land use activities (i.e., low woody debris and few pools; Table 5). Although these data suggest that bull and brook trout preferred different habitats, a more complete analysis of streams over the range of elevations used by both species is needed. In the Bitterroot River drainage, bull trout normally occupy streams averaging 1,640 m elevation (Clancy 1993; this study), but brook trout are generally found at lower elevations (average of 1,400 m; Clancy 1993). Because bull trout are generally found at lower temperatures than brook trout (Adams 1994) and average stream temperature increases with decreasing elevation, brook trout may be more likely to replace bull trout in lower elevation streams than those sampled in this study. Fausch (1989) found that gradient and elevation appeared to influence competitive interactions of brook trout and other trout species. Gradient was not significantly different between bull trout and brook trout streams in this study, however, bull trout were found at higher elevations than brook trout (Table 5). It is not clear whether colder temperatures are a barrier to brook trout at higher elevations.

Use of bivariate plots

Logistic regression analysis of patterns of species presence or absence over large areas has proven to be a useful approach for elucidating factors that influence species distribution and persistence at large spatial scales (e.g., Taylor 1991; Beauchamp et al 1992; Nadeau et al. 1995; Rieman and McIntyre 1995). While logistic regression models can indicate which combination of variables most strongly influence species occurrence, they do not readily show how levels of a particular independent variable affect presence or absence. Previous studies examining relationships between species occurrence and habitat variables have utilized incidence functions (Gilpin and Diamond 1981; Hanski 1991; Taylor 1991; Rieman and McIntyre 1993). These studies have examined relationships between frequency of species occurrence and habitat patch size, degree of isolation, and the number of species present, in order to test predictions of metapopulation theory and to draw inferences about factors affecting population persistence. While past studies focused on the influence of a single variable on occurrence, I examined the joint influence of two variables on species occurrence using bivariate plots. For example, while logistic regression analysis indicated that bull trout occurrence increased with stream width and woody debris, bivariate plots illustrated that high frequencies of woody debris influenced occurrence more strongly in small streams than larger streams (Figure 4).

Conclusions and management implications

Stream width, channel gradient, woody debris, brook trout presence, and a strong mainstem population of bull trout were the most important factors defining potential bull trout habitat. I recommend using these factors to better direct future sampling efforts to those areas where bull trout are likely to occur. The fact that streams adjacent to strong mainstem populations were more likely to contain bull trout supports the conservation strategy of protecting and securing remaining strong bull trout populations (i.e., Moyle and Sato 1991; Frissell 1993; Rieman and McIntyre 1993). This research supports recommendations by the Montana Bull Trout Scientific Group (Thomas 1995) that protection of remaining strong bull trout populations in "core" habitats may be an important first step in preventing regional extinction.

Because the watershed scale model was nearly equally effective at correctly classifying bull trout presence or absence as the site-scale model, and watershed and site scale variables were highly correlated, I suggest that future work should involve the verification of watershed-scale models using data collected in other parts of the Bitterroot basin. A verified and refined model could then be compared to distributions in other basins including those with an intact migratory population to assess the general applicability of these models. Following model verification, the watershed scale model may be useful in predicting bull trout distribution over large areas. Since resources available to

fishery and land managers is limited, the ability to identify potential bull trout habitat at a landscape scale using map-derived data has many uses. Managers need information on which areas are within the range of conditions used by bull trout so they can better assess risk to the species as a result of management actions proposed for these areas. Predictive models developed with watershed scale variables and refined over a regional scale could be used to construct maps of potential habitat over large parts of the species range and identify gaps in species and habitat protection. Repeated surveys of these streams over time could document extinction and colonization rates which may provide additional insights concerning habitat suitability and population viability. Repeated sampling can also define the trends in distribution necessary to evaluate the success of management efforts.

Brook trout appear to use different habitats than bull trout. Given the difficulties and uncertainty involved in removal and suppression of introduced fish (Clancy et al. 1995), protection of strong populations of bull trout in high quality habitats and restoration of these types of habitats in other areas may be the best approach for curtailing further replacement of bull trout by nonnative species.

REFERENCES CITED

Adams, S. 1994. Bull trout distribution and habitat use in the Weiser River drainage, Idaho. Master's Thesis. University of Idaho, Moscow.

Beauchamp, J.J., S.W. Christensen, and E.P. Smith. 1992. Selection of factors affecting the presence of brook trout (*Salvelinus fontinalis*) in Adirondack lakes: a case study. Canadian Journal of Fisheries and Aquatic Science 49:597-608.

Bonneau, J. 1994. Seasonal habitat use and changes in distribution of juvenile bull trout and cutthroat trout in small, high gradient streams. Master's Thesis. University of Idaho, Moscow.

Bozek, M.A. and W.A. Hubert. 1992. Segregation of resident trout as predicted by three habitat dimensions. Canadian Journal of Zoology 70:886-890.

Buckman, R.C., W.E. Hosford, and P.A. Dupee. 1992. Malheur River investigations. Pages 47-57. *in*: Howell, P.J. and D.B. Buchanan, editors. 1992. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society. Corvallis.

Bryant, B. 1983. The role and management of woody debris in West Coast salmonid nursery streams. North American Journal of Fisheries Management 3:322-330.

Cavender, T.M. 1978. Taxonomy and distribution of the bull trout *(Salvelinus confluentus)* from the American Northwest. California Fish and Game 64:139-174.

Chisholm, I.M., W.A. Hubert, and T.A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society. 116:176-184.

Clancy, C.G. 1993. Montana statewide fisheries investigations: Bitterroot Forest Inventory. Project: F-46-R-4. Montana Department of Fish, Wildlife, and Parks, Helena.

Clancy, C., C. Frissell, and T. Weaver. 1995. The role of removal and suppression of introduced fish in bull trout recovery. Report of Montana Bull Trout Scientific Group for The Montana Bull Trout Restoration Team. Montana Department of Fish, Wildlife, and Parks, Helena.

Dambacher, J.M., P. Dupee, and K. Jones. in press. Physiography of juvenile bull trout (*Salvelinus confluentus*) populations and stream habitat in Oregon. Friends of the Bull Trout Conference, May, 1994. Calgary, Alberta.

Daugherty, C.H. and A.L. Sheldon. 1982. Age determination, growth, and life history of a Montana population of the tailed frog (*Ascaphus truei*). Herpetologica 38(4):461-468.

Elliot, S.T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. Transactions of the American Fisheries Society. 115:392-400.

Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus confluentus*) and other resident salmonids in streams? Physiology and Ecology Japan, Spec. Vol. 1:303-322.

Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950 -1985. U.S. Forest Service, Gen. Tech. Rept. PNW-GTR-213. Portland, OR.

Fausch, K.D., S. Nakano, and K. Ishigaka. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: Considering multiple factors across scales. Oecologia 100:1-12.

Fraley, J.J., and P.J. Graham. 1981. Physical habitat, geologic bedrock types and trout densities in tributaries of the Flathead River drainage, Montana. Pages 178-185 *in*: Acquisition and utilization of aquatic habitat inventory information: Proceedings of the symposium; 1981 October 28-30; Portland, OR: American Fisheries Society, Western Division.

Fraley, J.J., and B.B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout *(Salvelinus confluentus)* in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Fraser, D.F., J.F. Gilliam, and T.Hoi Yip. 1995. Predation as an agent of population fragmentation in a tropical watershed. Ecology 76(5):1461-1472.

Frissell, C.A. 1993. A new strategy for watershed restoration and recovery of Pacific salmon in the Pacific Northwest. The Pacific Rivers Council, Eugene, OR.

Gibbons, J.D. 1985. Nonparametric methods for quantitative analysis, 2nd Edition. American Science Press Inc., Columbus, Ohio.

Gibbons, J.D. 1993. Nonparametric measures of association, Series: Quantitative Applications in the Social Sciences. Sage University Press, Sage Publications, Inc., Newbury Park, California.

Gilpin, M.E., and J.M. Diamond. 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. Proceedings of the National Academy of Science 78(1):392-396.

Goetz, F. 1989. Biology of the bull trout *Salvelinus confluentus*: a literature review. Willamette National Forest, Eugene, Oregon.

Goetz, F. 1991. Bull trout life history and habitat study. Master's Thesis. Oregon State University, Corvallis.

Good, W., C. Kronberg, and D. O'dell. 1984. Bitterroot tributary study, phases 1, 2, 3. Trout Unlimited, Hamilton, MT.

Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Science 51:2626-2637.

Hanski, I. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:17-38.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3-16.

Harrison, S., D.D. Murphy, and P.R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas bayensis*: evidence for a metapopulation model. The American Naturalist 132:360-382.

Horowitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs. 48:307-321.

Hosmer, D.W. Jr., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, NY.

Howell, P.J. and D.B. Buchanan, editors. 1992. Proceedings of the Gearhart Mountain bull trout workshop; 1992 August; Gearhart Mountain, OR. Oregon Chapter of the American Fisheries Society, Corvallis.

Jakober, M.J. 1995. Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana. Master's Thesis, Montana State University, Bozeman.

Lanka, R.P., W.A. Hubert, and T.A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116:21-28.

Leary, R.F., F.W. Allendorf, and K.L. Knudsen. 1983. Consistently high meristic counts in natural hybrids between brook trout and bull trout. Systematic Zoology 32:369-376.

Leary, R.F., F.W. Allendorf, and S.H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. Conservation Biology 7:856-865.

Leathe, S.A., and M.D. Enk. 1985. Cumulative effects of microhydro development on the fisheries of the Swan River drainage, Montana. Volume I: Summary Report. Montana Department of Fish, Wildlife, and Parks, Kalispell.

Lisle, T.E. 1986. Effects of woody debris on anadromous salmonid habitat, Prince of Wales Island, Southeast Alaska. North American Journal Of Fisheries Management 6:538-550.

Markle, D.F. 1992. Evidence of bull trout x brook trout hybrids in Oregon. Pages 58-67 *in*: Howell, P.J. and D.V. Buchanan., editors. Proceedings of the Gearhart Mountain bull trout workshop; 1992 August; Gearhart Mountain, OR. Oregon Chapter of the American Fisheries Society, Corvallis.

MacArthur, R. H. and E.O. Wilson. 1967. The theory of island biogeography. Monograph in population biology. Princeton University Press, Princeton, NJ.

Meehan, W.R., and T.C. Bjornn. 1991. Salmonid distributions and life histories. Pages 47-82 *in*: Meehan, W.R., editor. Influence of forest and rangeland management on salmonid fishes and their habitats. Special Publication 19. American Fisheries Society, Bethesda.

Moyle, P.B. 1976. Fish introductions in California: history and impacts on native fishes. Biological Conservation 9:101-118.

Moyle P.B., and G.M. Sato. 1991. On the design of preserves to protect native fishes. Pages 155-169 *in*: Minkley, W.L. and J.E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

Mullan, J.W., K. Williams, G. Rhodus, T. Hillman, and J. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. Monogr. 1. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service.

Murphy, M.L., J. Heifetz, S.W. Johnson, KV. Koski, and J.F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43:1521-1533.

Nadeau, S., R. Decarie, D. Lambert, and M. St-Georges. 1995. Nonlinear modeling of muskrat use of habitat. Journal of Wildlife Management 59(1):110-117.

Neter, J., W. Wasserman, and G.A. Whitmore. 1993. Applied statistics, 4th edition. Simon and Schuster, Inc., Needham Heights, Massachusettes.

Northcote, R.G. 1992. Migration and residency in stream salmonids - some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67:5-17.

Osborne L.L., and M.J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries and Aquatic Science 49:671-681.

Pratt, K. 1984. Habitat use and species interactions of juvenile cutthroat *(Salmo clarki lewisi)* and bull trout *(Salvelinus confluentus)* in the upper Flathead River basin. Master's Thesis. University of Idaho, Moscow.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Ratliff, D.E., and P.J. Howell. 1992. The status of bull trout populations in Oregon. Pages 10-17. *in*: Howell, P.J. and D.V. Buchanan., editors. Proceedings of the Gearhart Mountain bull trout workshop; 1992 August; Gearhart Mountain, OR. Oregon Chapter of the American Fisheries Society, Corvallis.

Rieman, B. E., and J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. Gen. Tech. Rep. INT-302. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Rieman, B.E., and J.D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-26.

Ross, S.T., J.G. Knight, and S.D. Wilkins. 1990. Longitudinal occurrence of the bayou darter (Percidae: *Etheostoma rubrum*) in Bayou Pierre - a response to stream order or habitat availability? Polskie Archiwum Hydrobiologii. 37:221-233.

Salo, E.O., and T.W. Cundy, editors. 1987. Streamside management: forestry and fisheries interactions. University of Washington, Institute of Forest Resources, Contribution 57, Seattle.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC: SAS Institute Inc.

Scheidegger, A.E. 1965. The algebra of stream-order numbers. U.S. Geol. Surv. Prof. Pap. 525B. Washington, DC.

Scudder, G.G.E. 1989. The adaptive significance of marginal populations: a general perspective. *in*: Levings, C.D., L.B. Holtby, and M.A. Henderson, editors. Proceeding of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Canadian Special Publication in Fisheries and Aquatic Science 105:180-185.

Sharber, N.G., S.W. Carothers, J.P. Sharber, J.C. de Vos, and P.A. House. 1994. Reducing electrofishing induced injury to rainbow trout. North American Journal of Fisheries Management 14:340-346.

Shepard, B., K. Pratt, and J. Graham. 1984a. Life histories of westslope cutthroat trout and bull trout in the upper Flathead River system, Montana. Montana Department of Fish, Wildlife, and Parks, Kalispell.

Shepard, B.B., S.A. Leathe, T.M. Weaver, and M.D. Enk. 1984b. Monitoring levels of fine sediment within tributaries to Flathead Lake, and impacts of fine sediment on bull trout recruitment. Pages 146-156. *in* F. Richardson and F.H. Hamre, editors. Wild Trout III, Trout Unlimited, Vienna, Virginia.

Smogor, R.A., P.L. Angermeier, and C.K. Gaylord. 1995. Distribution and abundance of American eels in Virginia streams: test of null models across spatial scales. Transactions of the American Fisheries Society 124: 789-803.

Spoon, R.L. 1987. Evaluation of management of water releases for Painted Rocks Reservoir, Bitterroot River, Montana. Montana Department Fish, Wildlife, and Parks. For Bonneville Power Administration Contract No. DE-A179-83BP13076.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Transactions American Geophysical Union. 38:913-920.

Taylor, B. 1991. Investigating species incidence over habitat fragments of different areas - a look at error estimation. Biological Journal of the Linnean Society 42:177-191.

Thomas, G. 1992. Status report: bull trout in Montana. Helena, Montana: Montana Department of Fish, Wildlife, and Parks. Helena.

Thomas, G. 1995. Bitterroot River drainage bull trout status review. Report of Montana Bull Trout Scientific Group for The Montana Bull Trout Restoration Team. Montana Department of Fish, Wildlife, and Parks, Helena.

Thomas, C.D., J.A. Thomas, and M.S. Warren. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia 92:563-567.

Trexler, J.C., and J. Travis. 1993. Nontraditional regression analysis. Ecology 74:1629-1637.

U.S. Geological Survey. 1995. Water resources data--Montana. Water year 1994. Report MT-94-1. Helena.

Weaver, T., and J. Fraley. 1991. Fisheries habitat and fish populations. Flathead basin forest practices, water quality and fisheries cooperative program. Flathead Basin Commission, Kalispell, MT.

White, G.C., K.P. Burnham, D.L. Otis, and D.R. Anderson. 1978. User's manual for program CAPTURE, Utah State University Press, Logan.