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

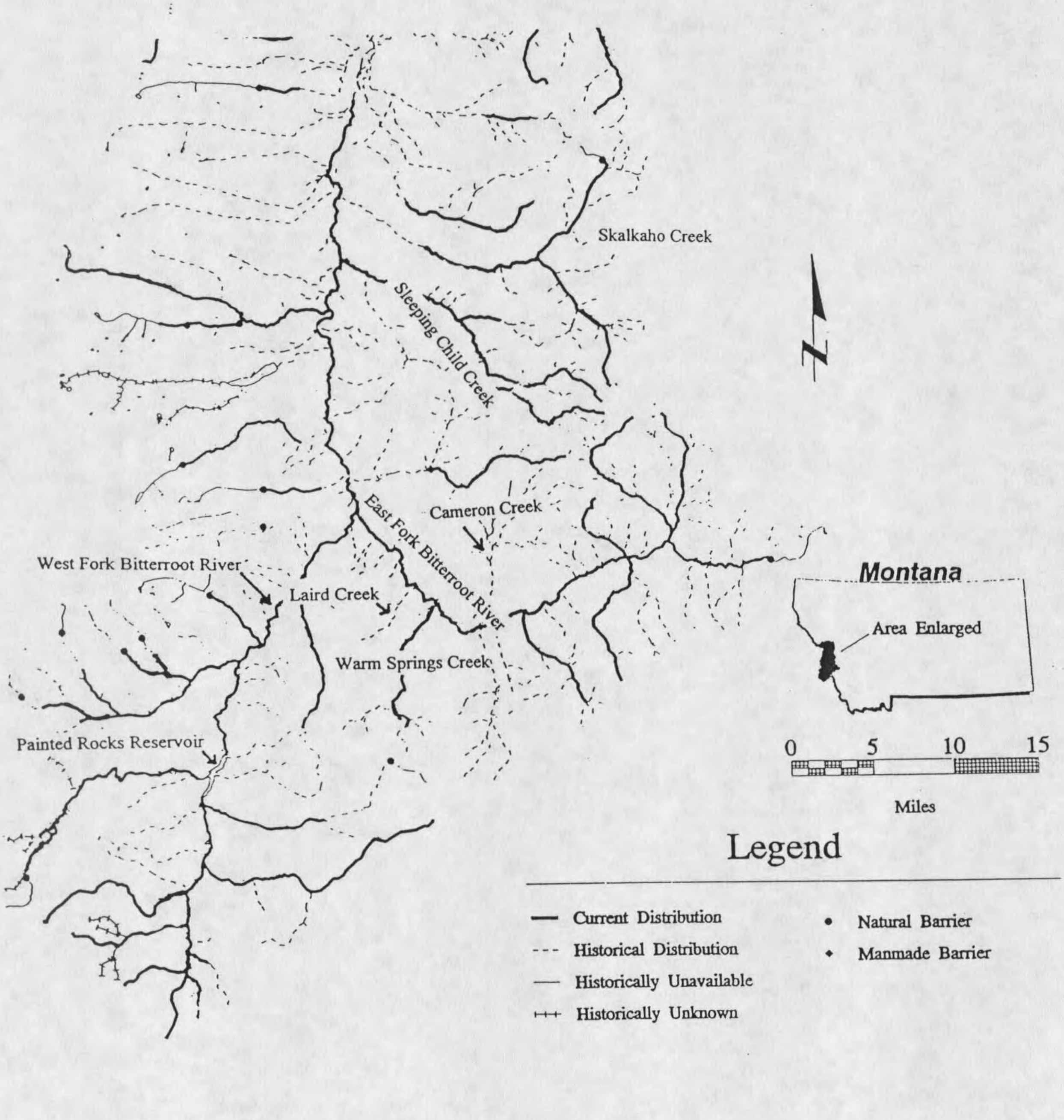

Figure 1. Bull trout distribution in the upper 2/3 of the Bitterroot River basin from survey data collected by the Montana Department of Fish, Wildlife, and Parks.

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.

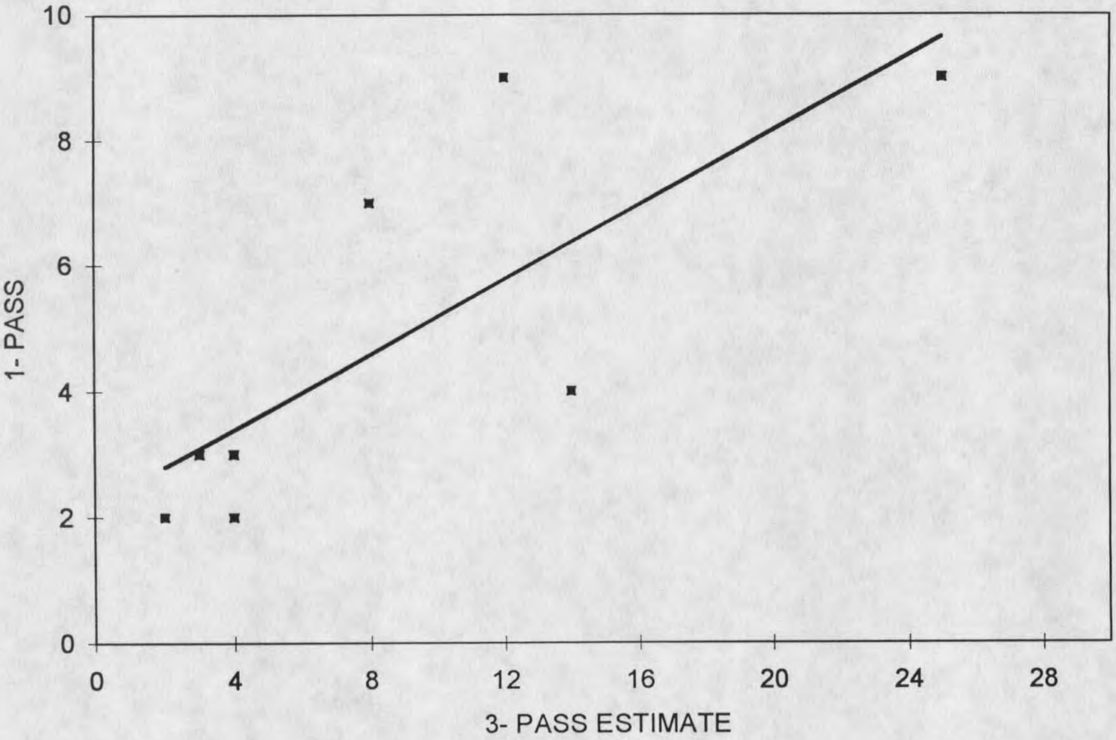

Figure 2. Relative bull trout electrofishing efficiency for 1 - pass versus a 3 - pass population estimate (y = 2.192 + 0.298(x); R^2 = 0.60; P = 0.024; n = 8).

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).