Local-Habitat, Watershed, and Biotic Features Associated with Bull Trout Occurrence in Montana Streams

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Abstract.—We evaluated the association of local-habitat features, large-scale watershed factors, the presence of nonnative brook trout *Salvelinus fontinalis*, and connectivity to neighboring populations with patterns of occurrence of threatened bull trout *S. confluentus* in 112 first-order to fourth-order streams in the Bitterroot River drainage in western Montana. Species presence or absence was estimated via single-pass electrofishing, local-habitat features were measured in 500-m sampling reaches, watershed variables were obtained from topographic maps, and potential demographic support from nearby bull trout populations occupying larger main-stem streams was estimated from electrofishing data records. We defined a set of nine candidate models that represented various combinations of these four main factors and used an information-theoretic approach to evaluate the relative plausibility of competing models. Models combining local habitat (width, gradient, and woody debris) with brook trout presence and the main-stem abundance of bull trout and a global model (all variables) were the best approximating models. In contrast, watershed models based on elevation, basin area, and tributary slope and models with local-habitat or biotic variables alone were poor predictors of bull trout occurrence. Bull trout occurrence was positively associated with channel width, large woody debris, and the presence of a ''strong'' neighboring main-stem population and negatively associated with channel gradient and the presence of brook trout. Our findings suggest that bull trout have increased resistance to invasion by brook trout in streams with high habitat complexity and connectivity. Consideration of abiotic and biotic factors at multiple scales, along with a means for ranking their relative importance, is needed to perform more comprehensive assessments of landscape and local influences on species distribution patterns.

A growing body of literature suggests that the patterns of distribution for many fishes are the result of both local-habitat conditions and larger-scale biotic and abiotic processes (e.g., Rabeni and Sowa 1996; Dunham et al. 1997; Schrank et al. 2001). The physical characteristics of streams at the small scale of individual habitat units or stream reaches have often been associated with variation in fish density (e.g., Rabeni and Sowa 1996; Watson and Hillman 1997). However, large-scale watershed or landscape features such as stream size, basin area, spatial geometry, and stream temperature or surrogates for climate (Bozek and Hubert

1992; Fausch et al. 1994; Rieman and McIntyre 1995; Dunham et al. 1997, 1999; Harig and Fausch 2002) as well as biotic factors such as the presence of nonnative species and degree of isolation from other populations (Osborne and Wiley 1992; Dunham and Rieman 1999; Schrank et al. 2001) have also been implicated. Large-scale processes are likely to be important because landscape features influence (1) local-scale habitat features (Rabeni and Sowa 1996), (2) species interactions or individual physiological responses (Fausch et al. 1994), and (3) dispersal, colonization, and gene flow within and among local populations (Luttrell et al. 1999; Rieman and Dunham 2000).

Patterns of the occurrence of bull trout *Salvelinus confluentus* provide a good illustration of the influence of both local and large-scale factors on species distribution. Several studies have linked bull trout density in stream reaches to local-habitat features such as pool frequency, amount of large wood and fine sediments, water temperature, and the presence of groundwater (Saffel and Scarnecchia 1996; Watson and Hillman 1997; Jakober et

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al. 1998; Baxter and Hauer 2000). Bull trout abundance has also been linked to local biotic features, in particular the presence of nonnative brook trout *S. fontinalis* (Leary et al. 1993; Watson and Hillman 1997). Other work has shown that large-scale factors such as elevation, climate, and geomorphology may strongly influence the broad distribution of suitable habitat networks (Rieman et al. 1997; Dunham and Rieman 1999; Baxter and Hauer 2000) and that the size and relative isolation of those networks may influence the occurrence and persistence of local populations (Dunham and Rieman 1999). It is unclear, however, how local and large-scale factors interact to influence bull trout distribution.

Bull trout were recently listed as threatened in the Pacific Northwest of the United States (USFWS 1998) and are considered a ''species of special concern'' in Canada (Haas 1998). Like many other native salmonids, bull trout have declined due to a variety of abiotic and biotic factors that include habitat degradation, migration barriers, overexploitation, and displacement by nonnative species (Rieman and McIntyre 1993; Rieman et al. 1997). In addition to experiencing declines in abundance and distribution, many populations that once supported migratory life histories now persist only in isolated headwater streams with restricted potential for gene flow or demographic support from other areas (Rieman and McIntyre 1993; Nelson et al. 2002). A better understanding of the factors that affect bull trout occurrence in fragmented habitats could be key to effective conservation management.

To consider these issues, we examined the patterns of occurrence of bull trout in a large river basin in relation to local stream habitat features and watershed or landscape characteristics. In addition to local and watershed-level physical habitat features, we included the potential biotic influences represented by the occurrence of brook trout and the proximity of strong bull trout populations. We hypothesized that bull trout would be less likely to occur in otherwise suitable streams that also supported brook trout or that were not in close proximity to strong bull trout populations that served as sources for colonization or demographic support. Because we were interested in models with both local and watershed-scale effects, we used an information-theoretic approach (Burnham and Anderson 1998) that allowed us to explicitly contrast the relative plausibility of competing models.
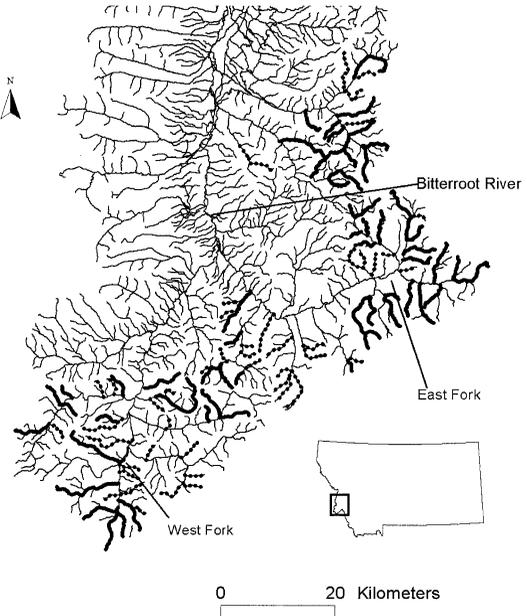

FIGURE 1.—Presence (bold lines) and absence (dotted lines) of bull trout in 112 tributaries sampled in the upper Bitterroot River drainage.

Study Area

The upper Bitterroot River in western Montana is composed of two major forks that join to form the main river at Conner, Montana (Figure 1). The geology of the western and southern parts of the basin is predominantly granitic Idaho batholith, and the eastern side is predominantly sedimentary rock. Elevation ranges from about 1,000 to 2,200 m.

Bull trout are now patchily distributed in headwater tributaries throughout the drainage. The resident life history form dominates most local populations, but migratory fish are still present in limited numbers (Jakober et al. 1998; Nelson et al. 2002). In addition to bull trout, native fishes in the basin include westslope cutthroat trout *Oncorhynchus clarki lewisi*, slimy sculpin *Cottus cognatus*, mountain whitefish *Prosopium williamsoni*, and longnose sucker *Catostomus catostomus*. Nonnative species include brown trout *Salmo trutta*, brook trout, and rainbow trout *O. mykiss*. Brown and rainbow trout are common in the main stem of the Bitterroot River and the lower sections of most major tributaries (Nelson et al. 2002). Brook trout are common in small, low-elevation streams throughout the drainage (Clancy 1993).

Methods

Presence–Absence Sampling

We recorded the occurrence of bull trout in samples from 112 small, first-order to fourth-order

streams during the summer low-flow period (June–August) over a 3-year period (1993–1995). Within each of four major watersheds, we sampled nearly all tributary streams with sufficient flow to support fish year-round. No sampling occurred above apparent fish migration barriers (waterfalls >2 m and gradients >20%), so that all of the streams that we sampled were ultimately interconnected and bull trout and other species could have accessed any stream within the study area. Sampling was confined to streams that were small enough to effectively sample with a backpack electrofisher. Bull trout occurrence in larger streams was based on data from previous sampling with boat-mounted electrofishers that were obtained within 5 years of our own (Clancy 1993).

Because our objective was to assess bull trout distribution patterns over a large area, we used a presence–absence sampling design. Presence–absence sampling strives to achieve a balance between maximizing the probability of detecting a species when it is present and minimizing the probability of declaring it absent when it is present (i.e., ''false absences''; Bayley and Peterson 2001). The latter issue is particularly important when dealing with rare species like bull trout (Rieman and McIntyre 1995; Peterson et al. 2002). We adopted the presence–absence sampling protocol designed for bull trout by Rieman and McIntyre (1995). Each tributary stream was first divided into three 500-m study reaches equally spaced over the estimated length of suitable habitat. Stream length varied from 0.9 to 31.5 km (mean, 5.2 km). To optimize the detection probability and number of streams sampled, we focused our sampling effort on habitats known to support bull trout (e.g., those with pools, woody debris, and boulder cover; Watson and Hillman 1997; Jakober et al. 1998) within each study reach. 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 Hz, a pulse duration of 500 ms, and a voltage of 500–1,000 V depending on water conductivity (range, 20–220 μS/cm).

Bull trout were declared present in a tributary if they were detected in any of the three study reaches and absent if none were collected in all three reaches. Once bull trout were collected in a reach, they were considered present in the tributary and sampling of additional study reaches ceased. In some streams the second or third reaches were not sampled if the probability of bull trout presence was considered very low due to very steep gradients, low discharge, and the absence of cutthroat trout (which occurred over a greater range of conditions than bull trout). Thus, we attempted to maximize probability of detection and to minimize false absences by sampling the sites most likely to hold bull trout and by sampling additional reaches when fish were not detected. Rieman and McIntyre (1995) estimated that the probability of detecting bull trout at low densities (15/km) was greater than 0.8 with a similar sampling design, assuming a random distribution of fish and a minimal capture efficiency of 0.25.

Potential Predictors

Local habitat.—We used the lowermost study reach as an index of local-habitat conditions for each tributary. Local habitat was characterized by recording channel width, mean depth, gradient, the percentages of fine sediment and canopy cover, pool frequency, and the amount of woody debris. Gradient was measured with a clinometer at several points along each reach. At 15 evenly spaced transects, we measured channel width and mean depth and visually estimated the percentage of fine sediment (<6.35 mm in diameter: high, >40%; moderate, 20–40%; and low, <20%) and the percentage of canopy cover (high, >75%; moderate, 25–75%; and low, <25%). The number of pools (>15 cm deep) and number of pieces of woody debris (>3 m in length and >10 cm in diameter) were counted for the entire reach.

Watershed characteristics.—Watershed variables were measured from 1:24,000 topographic maps. Variables included aspect (north or south), stream length, basin area, elevation at mouth, stream order, tributary slope (slope from the mouth to the end of the highest first-order tributary), link magnitude (number of first-order tributaries; Osborne and Wiley 1992), and D-link number (spatial position of the tributary in the watershed, expressed as the cumulative link magnitude at the nearest downstream confluence; Osborne and Wiley 1992).

Biotic factors.—To consider the potential influence of demographic support from bull trout in adjacent main-stem streams, we used information from other sampling to represent main-stem abundance. Main-stem abundance was coded as absent (0 = no bull trout sampled), weak (1 = <5 fish/100 m of stream length), or strong (3 = >5 fish/100 m; Montana Fish, Wildlife, and Parks, Hamilton, Montana, data files). To consider the pos-

TABLE 1.—Model selection results for a candidate set of logistic regression models containing various combinations of local-habitat (stream width, channel gradient, amount of large woody debris [LWD]), watershed (basin area, tributary slope, elevation), and biotic variables (relative abundance of adjacent main-stem bull trout population, presence of brook trout) in relation to bull trout occurrence in 112 streams in the Bitterroot River drainage, Montana. Models were ranked in terms of the difference (ΔAICc) between their AICc score and the lowest score (86.93). The global model included all the variables shown.

Model	Number of parameters	ΔAICc	Akaike weight
Width, gradient, LWD, brook trout	5	0	0.49
Width, gradient, LWD, main-stem abundance, brook trout	6	0.98	0.30
Width, gradient, LWD, main-stem abundance	5	2.75	0.12
Global	9	3.40	0.09
Width, gradient, LWD	4	13.03	<0.01
Area, slope, elevation, brook trout	5	15.84	<0.01
Area, slope, elevation, main-stem abundance, brook trout	6	16.44	<0.01
Area, slope, elevation, main-stem abundance	5	17.82	<0.01
Area, slope, elevation	4	27.00	<0.01

sibility of a negative influence of brook trout on bull trout, brook trout occurrence in each tributary stream we sampled was also incorporated into our analysis as a categorical variable representing presence or absence in our samples.

Model Development and Analysis

Development of candidate models.—To assess the relative importance of the local-habitat, watershed, and biotic characteristics associated with bull trout occurrence, we defined a set of nine candidate logistic regression models (Table 1) that represented various combinations of these three main factors, including an all-variable global model. Inclusion of variables in the local-habitat or watershed models was determined by first comparing the values for each variable with bull trout presence and absence by means of a Mann–Whitney test (for continuous variables) or a chi-square test (for categorical variables). Nonsignificant ($P > 0.05$) variables (basin aspect, D-link number, canopy cover, and fine sediment) were eliminated from further analysis. Because many of the variables we measured often covary, we performed a rank correlation analysis to assess interactions between the remaining variables. The local-habitat variables width and mean depth were significantly correlated, as were pool frequency and woody debris ($P < 0.05$). Watershed variables associated with stream size (basin area, link magnitude, and stream length) also showed high intercorrelation. Among correlated variables, we selected those that had the most likely functional significance (e.g., woody debris is the main driver of pool frequency rather than vice versa); that were intercorrelated with several other variables (e.g., basin area); or that had the strongest univariate relationship with

bull trout occurrence (e.g., width versus mean depth). Based on this analysis, the final local-habitat variables selected were width, gradient, and woody debris and the final watershed variables were basin area, tributary slope, and elevation. To assess the effects of biotic variables on bull trout occurrence, we included main-stem abundance and brook trout occurrence, alone and together, in the local-habitat and watershed models.

Model analysis.—We adopted the information-theoretic approach first developed by Akaike (1973) and further expanded by Burnham and Anderson (1998) to compare the relative plausibility of competing models. The first step was to build a global logistic regression model relating bull trout presence or absence to all local, watershed, and biotic variables combined (Table 1). We then conducted a Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989) to assess how well this model met the assumptions underlying logistic regression. If the global model adequately met these assumptions ($P > 0.10$ for the goodness-of-fit test), we considered the relative plausibility of each model as determined by model ranking and selection results.

We used the small-sample-size adjustment to Akaike's information criterion (AIC; Akaike 1973), referred to as AICc (Hurvich and Tsai 1989), to rank candidate models. AICc is defined as

$$\text{AICc} = \text{AIC} + \frac{2k(k+1)}{n-k-1},$$

where $\text{AIC} = -2 \cdot \log_e[L(\hat{\theta}|\text{data})] + 2k$, $\log_e[L(\hat{\theta}|\text{data})]$ is the maximized log-likelihood over the unknown model parameters (θ) given the data, k is

the number of estimable parameters in the model, and *n* is the number of observations (Buckland et al. 1997; Burnham and Anderson 1998). We checked the Pearson χ^2 statistic divided by its degrees of freedom for the global model to assess whether a quasi-likelihood correction ($\hat{c}$) was needed for AICc (called QAICc). This would be the case if the data were overdispersed (i.e., $\hat{c} > 1$) such that the sampling (observed) variance exceeded the theoretical variance of the underlying model, which is common in count data (Burnham and Anderson 1998). Our data did not show evidence of overdispersion ($\hat{c} = 0.84$), so we used AICc as our model selection criterion.

Because AICc is a relative ranking statistic, we ranked the candidate models by subtracting the lowest value from all the other values (yielding the ΔAICc values) and then reordering these ΔAICc values and their associated models from low to high (Burnham and Anderson 1998). We interpreted the relative plausibility of each model for our data set in accordance with its Akaike weight,

$$w_i = \frac{e^{(-\Delta\text{AICc}_i/2)}}{\sum_{j=1}^{R} e^{(-\Delta\text{AICc}_j/2)}},$$

where ΔAICc_i is the ΔAICc value for the *i*th model in a set of $j = 1$ to R candidate models (Buckland et al. 1997). Thus, the w_i sum to 1. Following from likelihood-based inference (Edwards 1992; Royall 1997), Akaike weights correspond to the strength of the evidence for one model versus that for another, that is, $L(M_i|\text{data})/L(M_B|\text{data})$, where M_i refers to the *i*th model and M_B to the ''best'' model (Burnham and Anderson 1998).

Because there may be more than one candidate model that is reasonably plausible for a particular set of data, we also used Akaike weights to generate weighted average estimates of parameters across relevant models, as described by Buckland et al. (1997) and Burnham and Anderson (1998). These weights also allowed us to incorporate model selection uncertainty—in addition to individual parameter uncertainty—into the estimated standard errors for each logistic regression coefficient. We did not select a single model from a candidate set and treat it as the single ''best'' model unless its Akaike weight was at least eight times the value of the next highest weight (Thompson and Lee 2000). That is, we viewed the predictor variables contained in models whose Akaike weights were more than one-eighth of the largest Akaike weight

as forming a composite model whose parameter estimates were computed based on the ΔAICc-weighted average of estimates from relevant models. Our strength-of-evidence metric (1/8) was recommended by Royall (1997) as a general cutoff point.

We evaluated the relative importance of each individual model variable using odds ratios. Odds ratios were computed by raising *e* to the value of the *i*th logistic regression coefficient (i.e., $e^{\hat{\beta}_i}$). As given, these odds ratios are based on a single-unit change, whereas larger (or smaller) units of change may be more biologically relevant. Therefore, we multiplied relevant coefficients by a constant (*C*) whose magnitude reflected a more meaningful interpretation than a single-unit change, yielding odds ratios of $e^{C\cdot\hat{\beta}_i}$ (Hosmer and Lemeshow 1989). We obtained an estimate of this constant from the difference in the median value of each variable for streams with and without bull trout and rounded to the nearest unit of 5 (except for elevation, which was rounded to the nearest 100). For example, the model coefficient for elevation was multiplied by 100 m because a 100-m change in elevation from one stream to another had more meaning than a 1-m change with respect to the environment potentially affecting the fish therein.

We did not simply rely on statistical significance to interpret model results because an odds ratio could be small enough to be considered biologically unimportant but still be statistically significant (Yoccoz 1991). Note that statistical significance can be inferred if the confidence interval for an odds ratio does not include 1; this is equivalent to testing, for example, $\beta_1 = 0$, which can be respecified in terms of an odds ratio, $e^{\beta_1} = e^0 = 1$. After computing 95% confidence intervals for the scaled odds ratios (e.g., $e^{C\cdot\hat{\beta}_i \pm 1.96 \cdot C\cdot\text{SE}(\hat{\beta}_i)}$, where $z_{0.975} = 1.96$; Hosmer and Lemeshow 1989) for each variable in the composite model, we evaluated the biological importance of each statistically significant predictor by interpreting the magnitude of the value at either the lower bound (positive coefficient) or upper bound (negative coefficient) of its confidence interval. The SAS statistical package (SAS Institute 1999) was used in our analyses.

Results

We sampled 204 reaches within 112 streams throughout the upper Bitterroot River basin. Bull trout were detected in 60% ($n = 67$) of all streams and in 41% ($n = 83$) of all reaches sampled (Figure 1). When present in a stream, bull trout were nearly always first detected in the lowermost reach sam-

TABLE 2.—Model-averaged estimates and associated measures of local-habitat, watershed, and biotic variables in the composite logistic regression model for bull trout occurrence. See text for details; CI = confidence interval.

Variable	Parameter estimate	Standard error	Scaling factor	Scaled odds ratio	95% CI for scaled odds ratio
Intercept	−1.44	1.50			
Width	1.19	0.40	1	3.29	(1.50, 7.23)
Gradient	−0.32	0.10	5	0.20	(0.08, 0.52)
LWD	0.09	0.04	10	2.47	(1.12, 5.47)
Area	0.02	0.05	5	1.10	(0.67, 1.83)
Slope	−0.19	0.10	5	0.38	(0.14, 1.07)
Elevation	0.001	0.002	100	1.11	(0.70, 1.79)
Main-stem abundance	0.79	0.66	1	2.21	(0.61, 8.00)
Brook trout	−2.56	1.03	1	0.08	(0.01, 0.58)

pled (66 of 67 streams). Brook trout were encountered much less frequently than bull trout, being detected in only 22% ($n = 25$) of the streams sampled, whereas cutthroat trout were detected in all but three streams (97%). Bull trout were detected in streams ranging from 0.9 to 31.5 km in length (median, 5.6 km), from 1.0 to 6.8 m in wetted width (median, 3.1 m), from 1.0% to 15.6% in channel gradient (median, 5.6%), and from 2.0 to 129.7 km^2 in basin area (median, 11.7 km^2). Other fish species were rarely encountered: slimy sculpin occurred in 7 of the 112 streams, rainbow trout in 3, and brown trout in 2.

The global model adequately fitted the data (Hosmer and Lemeshow goodness-of-fit statistic = 4.02, df = 8, $P = 0.85$) and had no obvious outliers (all Pearson χ^2 residuals <2). Therefore, we assumed that the logistic regression model was appropriate for these data.

The model containing the local-habitat features channel width, channel gradient, and woody debris in combination with the biotic variable brook trout presence was the best approximating model. However, three other models, two comprising local-

FIGURE 2.—Bull trout presence ($n = 67$) and absence ($n = 45$) in relation to stream width and woody debris.

habitat and biotic variables and one comprising all of the variables (the global model), had sufficiently large Akaike weights that they could not be discounted (Table 1). Models containing watershed variables and biotic variables alone or in combination were highly implausible relative to those containing local-habitat and biotic variables. Further, models with local-habitat and biotic variables in combination were considerably more plausible than the model with local-habitat variables only (Table 1).

All four predictors in the composite model (width, gradient, presence of brook trout, and large woody debris) had statistically significant odds ratios (Table 2). Bull trout occurrence was positively associated with channel width and large woody debris and negatively associated with channel gradient and the presence of brook trout. Bull trout occurred in nearly all streams wider than 3 m and with abundant large woody debris (>15 pieces per 100 m; Figure 2). Smaller streams (<2 m wide) were less likely to contain bull trout unless woody debris was abundant. A 1-m increase in channel width was also associated with at least a 50% (1.50/1) increase in the predicted odds of bull trout presence. A 5-percentage-point increase in channel gradient was associated with at least a 92% (1/ 0.52) decrease in the predicted odds of bull trout presence (Figure 3; Table 2).

Bull trout and brook trout occurred together in only 9 of 112 streams sampled (8%) despite brook trout's being present in all four watersheds. The predicted odds of bull trout absence were at least 72% (1/0.58) higher when brook trout were present (Table 2). This pattern is shown graphically in plots displaying the presence and absence of bull trout for a range of channel gradients and widths for streams in which brook trout were present and absent (Figure 3). Bull trout were present in a wide range of streams in the absence of brook trout,
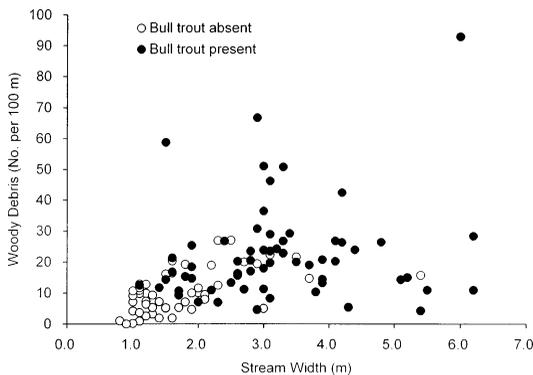
Brook trout absent
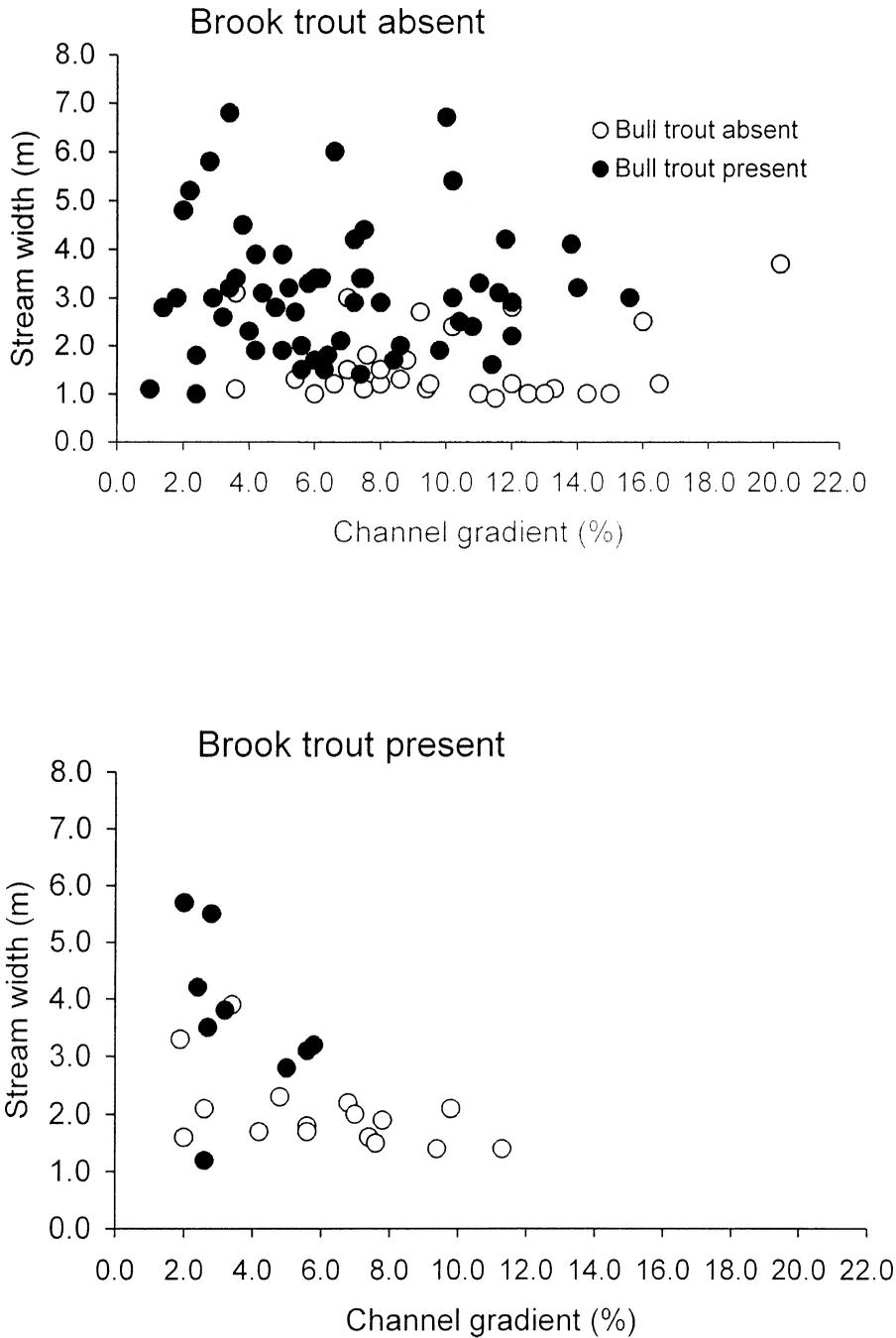

Brook trout present

FIGURE 3.—Bull trout presence and absence in relation to channel gradient and stream width in streams with and without brook trout.

although they were present in only 43% (18 of 42) of small, high-gradient streams (<3 m wide and with a gradient of >6%). Bull trout were largely absent from small streams when brook trout were present. The co-occurrence of brook and bull trout was confined mostly to wider (>3 m), lower-gradient (2–6%) streams (Figure 3). Streams where brook trout were present were also at lower

elevations (median, 1,564 m versus 1,725 m) and had fewer pools (7.2 versus 10.3 per 100 m) and pieces of large woody debris (5.5 versus 18.0 per 100 m) than streams occupied by bull trout.

Main-stem abundance also appeared to influence bull trout occurrence. It was included as a predictor variable in three of the four best-fitting models, and its inclusion in a local-habitat model (width, gradient, woody debris, and main-stem abundance) improved the plausibility of that model by a factor of more than 12 relative to a competing model based on local-habitat features alone (Table 1). Although the lower bound of the odds ratio included 1 and thus this variable was not statistically significant (Table 2), the confidence interval is sufficiently skewed to the right to suggest that the association with bull trout occurrence may be biologically significant (Hosmer and Lemeshow 1989). The predicted odds of bull trout presence were at least 64% (1/0.61) higher when a ''strong'' adjacent main-stem population was present. The main-stem abundance of bull trout also appeared to influence brook trout distribution. Of the 25 streams where brook trout were present, adjacent main-stem abundance of bull trout was either ''absent'' or ''weak''; none had a ''strong'' adjacent main-stem population.

Discussion

Many remaining populations of native salmonids and other now-rare stream fishes occur as fragmented populations isolated in headwater tributaries. Understanding the factors that determine why they persist in some areas and not in others is a major challenge for conservation research (Rieman and Dunham 2000). We assessed the relative importance of local and large-scale habitat features, nonnative species, and the presence of a neighboring population on bull trout occurrence across a large drainage basin. Our results support our initial hypothesis that local-habitat features, in combination with the presence of nonnative brook trout and an abundant nearby bull trout population, were important in defining suitable habitat for bull trout in individual tributaries.

Physical Habitat

Local-scale habitat features.—Our results indicated that bull trout occurrence was strongly associated with larger stream size (wetted width), lower channel gradient, and greater habitat complexity (frequency of large woody debris). All three of these habitat features have been identified as important predictor variables for the occurrence of bull trout (Rieman and McIntyre 1995; Watson and Hillman 1997; Dunham and Rieman 1999) and other salmonids (Bozek and Hubert 1992; Kruse et al. 1997; Harig and Fausch 2002). The mechanisms underlying these patterns are uncertain, although differences in habitat composition, disturbance regime, and patch size may be involved (Bozek and Hubert 1992; Rieman and McIntyre 1995; Harig and Fausch 2002). Bull trout rarely occupied Idaho streams less than 2 m wide and with a gradient greater than 10% (Rieman and McIntyre 1995; Dunham and Rieman 1999). We found a similar association with stream size, although higher amounts of large woody debris increased the probability of bull trout presence in streams less than 2 m wide (Figure 2). Greater habitat complexity in small streams may provide more preferred habitat for bull trout (Watson and Hillman 1997) and refugia from high flows and other disturbances (McMahon and Hartman 1989; Pearsons et al. 1992).

Watershed-scale habitat features.—Watershed-scale features such as basin area, indices of disturbance, elevation, stream size, and channel slope have been used to predict the distribution of salmonids (Bozek and Hubert 1992; Rieman and McIntyre 1995; Kruse et al. 1997; Dunham and Rieman 1999; Paul and Post 2001; Pess et al. 2002). We selected watershed variables that described some of the main influences on stream ecology that were readily measured from topographic maps. We found, however, that these were relatively poor predictors of bull trout occurrence.

Several factors could account for the poor performance of these watershed-scale predictors. A lack of strong gradient in landscape conditions is one possibility (Schrank et al. 2001). For example, the lack of an elevation effect could be a result of sampling over a narrow range of elevations. We sampled within an elevation band of 1,341–1,945 m. A stronger elevation effect might have emerged had we included lower elevation sites where bull trout are more likely to be temperature limited (Rieman and McIntyre 1995; Dunham and Rieman 1999; Paul and Post 2001).

Another possibility is that there are differences among studies in defining a ''habitat patch'' for sampling. Patches are defined as areas of contiguous habitat supporting a local population (Rieman and McIntyre 1995). In our study individual tributaries constituted patches, whereas previous studies with bull trout used whole watersheds above 1,600 m to define a patch and thereby incorporated several tributary streams (Rieman and

McIntyre 1995; Dunham and Rieman 1999) that we considered separately. Because our sampling units were not defined at a scale consistent with the habitat defining local populations, we could not distinguish between habitat quality effects and those related to patch size (Haila et al. 1993).

Finally, most studies that have explored watershed-scale effects have not simultaneously included local-habitat features in the models or explicitly considered competing models of local- and watershed-scale variables (Poff 1997; Hawkins et al. 2000). Recent analyses that have considered scale-related effects on species occurrence have suggested that the amount of variation related to landscape features alone may be less than that explained by local-habitat features (Hawkins et al. 2000; Harig and Fausch 2002). For example, Harig and Fausch (2002) found that local-scale habitat models incorporating temperature and the number and size of pools better explained the persistence of translocated cutthroat trout populations than did watershed-scale models. In part, the predictive power of watershed models in other studies may be due to high multicollinearity between watershed variables and local-habitat features (Lanka et al. 1987; Rieman and McIntyre 1995; Harig and Fausch 2002). These findings do not exclude the utility of predictive watershed-scale models; for example, Harig and Fausch (2002) found that watershed area was useful as a coarse filter for predicting the translocation success of cutthroat trout. Other studies have shown a similar association between watershed area and bull trout occurrence (Rieman and McIntyre 1995; Dunham and Rieman 1999). Whether this area effect reflects the amount of habitat or some inherent characteristic of local habitat (such as increased habitat diversity) that is correlated with area, however, remains to be determined (Dunham and Rieman 1999).

Brook Trout

Brook trout are now widespread throughout much of the native range of bull trout and are considered an important threat to the persistence of bull trout (Rieman et al. 1997). The two species rarely occur together (e.g., Clancy 1993; Watson and Hillman 1997; Paul and Post 2001; this study). Competition and hybridization have been invoked as mechanisms of replacement of bull trout by brook trout (Leary et al. 1993; Nakano et al. 1998). Our results suggest that bull trout may be more susceptible to brook trout invasion in small, low-gradient streams where brook trout may have a competitive advantage (Nagel 1991; Paul and Post 2001).

Because we sampled downstream of obvious fish migration barriers, we believe that the differing distribution patterns we observed between brook and bull trout were not due to dispersal barriers (Adams et al. 2002). Segregation by elevation between bull and brook trout in the absence of dispersal barriers was noted in previous studies (Dunham and Rieman 1999; Paul and Post 2001). Streams with brook trout also had fewer pools and less large woody debris, conditions commonly associated with higher land use disturbance (Reeves et al. 1993), and lacked a strong, nearby mainstem population of bull trout. Other investigators have noted that where the two species co-occur bull trout are more common in less disturbed watersheds (Rieman et al. 1997; Dunham and Rieman 1999), whereas the opposite appears to be true for brook trout (Clancy 1993). Brook trout in our study had a relatively restricted distribution (22% of 112 streams) despite their ability to colonize small, high-gradient, high-elevation streams (Adams et al. 2000, 2002). This suggests that bull trout have increased biotic resistance to the invasion of brook trout in higher-elevation (cooler) streams with high habitat complexity and connectivity (Paul and Post 2001; Dunham and Rieman 1999; see also Dunham et al. 1999). Alternatively, the current brook trout distribution may in part reflect past stocking history (Paul and Post 2001). In the Bitterroot drainage, brook trout occur more frequently in tributaries within 1.7 km of 1920s roads, but specific stocking locations are unknown (Clancy 1993). However, in Alberta streams, where stocking history was well documented, brook trout spatial distribution was not strongly influenced by past stocking location (Paul and Post 2001).

Another possible confounding factor in our analysis is the possibility that brook trout occurrence was underestimated with our sampling design. We focused our sampling on bull trout, and in streams in which they were detected in the first sampling reach but brook trout were not, additional upstream sampling ceased and brook trout were deemed absent. Thus, we cannot exclude the possibility that brook trout were present in upstream reaches. However, we believe that the incidence of false absences was low because when brook trout were found in a stream they typically were most abundant near the mouth and their abundance declined markedly upstream. Adams et al. (2000, 2002) observed a similar pattern when sampling low-order streams similar to ours.

Connectivity

The improved plausibility of models that included main-stem abundance supported our hypothesis that bull trout are more likely to occur in areas with suitable physical habitat features that also had a nearby abundant bull trout population. A similar pattern was observed in Idaho streams, where bull trout never occurred in tributary streams without also occurring in the associated main stem (Rieman and McIntyre 1995). Either patch size (i.e., fish in the tributaries are part of a larger population) or demographic support (i.e., the tributary is repeatedly colonized from the main stem) may be important. Decreased occupancy of apparently suitable physical habitat has been linked to limited connectivity in other species. Lahontan cutthroat trout *O. clarki henshawi* occurred in 89% of stream basins in Nevada that were connected to other occupied basins, whereas they were present in only 32% of isolated stream basins (Dunham et al. 1997). Luttrell et al. (1999) found high local extirpation of populations of speckled chubs *Macrhybopsis aestivalis* that lacked connectivity to other populations.

One limitation of our modeling approach was that we did not explicitly test the role of spatial dependency as a random component in our logistic regression models. Because multiple streams were sampled within larger watersheds, there may be some ''watershed effect'' that we could not account for in the models (Carroll and Pearson 2000). Failure to account for such an effect will cause standard errors to be underestimated and, for small data sets, model coefficients to be biased to some degree (Snijders and Bosker 1999). We attempted to address this issue by including the main-stem abundance of bull trout as a model variable, but some dependency may still exist. Recent developments in hierarchical modeling may be useful in future analyses of data of a similar sort (Link et al. 2002).

Conclusions

A host of recent multiscale studies demonstrate that factors operating at both local and landscape scales interact to influence the suitability of habitat for and persistence of stream biota (e.g., Poff 1997; Hawkins et al. 2000; Schrank et al. 2001; Harig and Fausch 2002). A unique aspect of our study was its evaluation of the influence of two biotic factors considered important for salmonid occurrence—degree of connectivity and the presence of nonnative competitors—for which there has been limited empirical work (Rieman and Dunham 2000). The AIC-based model selection approach we adopted to evaluate competing models allowed us to contrast hypotheses about the factors most important to bull trout occurrence (Anderson et al. 2000; see also Thompson and Lee 2000; Harig and Fausch 2002). Coupling investigations of species occurrence in relation to abiotic and biotic factors at multiple scales with methods for ranking their relative importance holds promise for gaining a more comprehensive assessment of landscape and local influences on species distribution patterns (Wiley et al. 1997). The associations that we found in our data imply that local-habitat characteristics, the occurrence of brook trout, and the occurrence of bull trout in the main stem are important to the occurrence of bull trout in small tributary streams. Further work utilizing recent advancements in sampling (Peterson et al. 2002) and spatially explicit statistical analyses should help resolve these effects.

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