

## METAPOPULATION STRUCTURE OF BULL TROUT: INFLUENCES OF PHYSICAL, BIOTIC, AND GEOMETRICAL LANDSCAPE CHARACTERISTICS

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**Abstract.** Metapopulation structure of species in fragmented landscapes is ultimately the result of spatial variability in demographic processes. While specific information on demographic parameters is desirable, a more practical approach to studying metapopulations in fragmented landscapes may begin with analyses of species' occurrence in relation to large-scale habitat variability. Here, we analyzed occurrence of stream-living bull trout (*Salvelinus confluentus*) in relation to physical, biotic, and geometrical characteristics of habitats. Bull trout occurrence was analyzed at several spatial ( $10^x$  m) scales. Data were from nested sampling of 720 sites (10 m), 179 reaches ( $10^2$  m), and 81 patches ( $\geq 10^3$  m) of stream habitats within the Boise River basin of central Idaho. Based on previous findings, patches were defined as stream catchments with suitable conditions for spawning and rearing of bull trout ( $>1600$  m elevation). Patch-scale bull trout occurrence was significantly related to patch area and isolation (stream distance between occupied patches). Lack of spatial autocorrelation between patches indicated that isolation effects were more likely the result of limited interaction among habitats (such as dispersal), rather than of correlated environmental conditions. A third factor, human disturbance in the form of roads, was associated with reduced bull trout occurrence at the patch-scale. Analyses of occurrence among reaches within occupied patches showed bull trout may select larger ( $>2$  m width) stream habitats. Occurrence of bull trout was not associated with nonnative brook trout (*Salvelinus fontinalis*) at large (patch), intermediate (reach), or small (site) spatial scales. Definition of a metapopulation structure for bull trout in the Boise River basin was complicated by uncertainties in the frequency and magnitude of dispersal. From the distribution of patch sizes and isolation among occupied patches, we suggest that the metapopulation is a complex mosaic of several elements found in conceptual models. This complexity poses a challenge to empirical and theoretical attempts to study stream-living bull trout. Future work to define the structure of bull trout metapopulations must relate temporal and spatial patterns of patch occupancy with complex patterns of dispersal that likely interact with habitat spatial structure, life history variability, and the historical context of regional climate changes. Results of this work suggest that conservation of bull trout should involve protection of larger, less isolated, and less disturbed (as indexed by road densities) habitats that may serve as important refugia or sources of recolonization. Bull trout populations in smaller, isolated, and more disturbed habitats may be at risk of extinction. Finally, metapopulation structure implies the existence of suitable, but presently unoccupied habitat, which should be managed carefully to facilitate potential natural recolonization or reintroductions of bull trout.

**Key words:** bull trout; extinction risk; habitat fragmentation; incidence functions; landscape ecology; metapopulations; *Salvelinus*; stream ecology.

### INTRODUCTION

Natural landscapes are mosaics of habitats affected by a variety of physical and biotic processes that operate on different spatial and temporal scales (Hansson et al. 1995, Wu and Loucks 1995, Collins and Glenn 1997). Accordingly, the distribution of organisms is rarely homogeneous across landscapes, and populations may be subdivided or patchy (Karieva 1990). Due to extinction of local populations and/or movements of

animals across landscapes, not all suitable habitat patches will be occupied at any single point in time. Populations with these characteristics are typically described as metapopulations (Hanski and Gilpin 1996). Patterns of habitat (patch) occupancy in metapopulations are ultimately the result of spatial variation in demographic processes, namely rates of natality, mortality, immigration, and emigration (Pulliam 1988). Estimates of these population parameters are difficult to obtain (Ims 1995, Ims and Yoccoz 1996), and typically available for only one or a limited number of subpopulations, which may not represent status of the metapopulation (Middleton and Nisbet 1997). An alterna-

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tive approach to studying metapopulations is to analyze patterns of presence or absence of organisms (occurrence) in relation to landscape characteristics (Hanski 1994, Sjögren-Gulve 1994, Bolger et al. 1997). Inferences from patterns of occurrence may be subject to a variety of limitations (see Taylor 1991, Hanski et al. 1996, Sjögren-Gulve and Ray 1996), but can nonetheless provide practical insights into the structure and dynamics of metapopulations.

In this study, we investigated patterns of occurrence in stream-living bull trout (*Salvelinus confluentus*) in relation to physical, biotic, and geometrical landscape characteristics. Bull trout occupy a naturally fragmented and complex mosaic of stream habitats that may be increasingly fragmented by human-related disturbances, including introductions of nonnative fishes, habitat degradation, dams, and altered disturbance regimes (Rieman and McIntyre 1993, 1995, Rieman et al. 1997a). The large-scale geometry of fragmented landscapes is characterized by the size, shape, spatial distribution, and isolation of habitats (Fahrig and Merriam 1994). The interaction of these geometrical characteristics with life histories, local and regional environmental variability, and human disturbance is one of the central problems of landscape ecology and metapopulation dynamics (Wiens 1996). Increasingly, studies of stream-living salmonids (such as bull trout) are revealing important patterns and processes at large ( $\geq 10^3$  m) spatial scales that may not be apparent at smaller spatial scales (e.g., Fausch et al. 1994, Rieman and McIntyre 1995, 1996, Keleher and Rahel 1996, Dunham and Vinyard 1997, Wiley et al. 1997).

Previously, Rieman and McIntyre (1995) analyzed bull trout occurrence in relation to large-scale habitat variability in the Boise River basin of Idaho. They found occurrence to be positively related to two measures of habitat size: stream width and patch (stream catchment) area. This suggested that habitat size may play an important role in the persistence of bull trout populations. A second geometrical feature of fragmented habitats, patch isolation, also may be important to population persistence (MacArthur and Wilson 1967, Kindvall and Ahlén 1992, Hanski et al. 1996, Sjögren-Gulve and Ray 1996). Furthermore, the effects of reduced habitat area and increased isolation may act together to increase the risk of extinction of species in fragmented landscapes (Fahrig and Merriam 1994). Here, we combined data from the original 46 habitat patches considered by Rieman and McIntyre (1995) with data from an additional 35 patches surveyed in the Boise River basin in 1993–1994 to look for evidence of such effects. Isolation was defined as stream distance separating a particular patch from the nearest occupied patch in a drainage network. Because drainage networks are linear systems, dispersal can only occur in an up- or downstream direction, a constraint that may increase vulnerability of stream-living organisms to habitat fragmentation (Zwick 1992, Rieman and

McIntyre 1995, Nakano et al. 1996, Rahel et al. 1996, Dunham et al. 1997).

Apparent influences of patch isolation may alternatively be due to spatially correlated environmental conditions within a drainage network. Accordingly, spatial proximity of habitats may lead to correlated population dynamics (Harrison and Quinn 1989), and relationships between patch isolation and occurrence may be due to spatial correlation in unmeasured habitat characteristics, rather than to dispersal alone. To distinguish these alternative explanations, we tested for spatial independence of bull trout occurrence (spatial autocorrelation) using straight-line, rather than stream distance between patches, regardless of patch occupancy (occupied or absent). Recent work on other fish has shown that spatial autocorrelation may strongly affect inferences about large-scale distributional patterns (Hinch et al. 1994, but see Rieman and McIntyre 1996).

While Rieman and McIntyre (1995) considered habitat size, and possibly isolation, to play a key role in the persistence of bull trout populations, an analysis of purely geometrical factors may not provide specific information on factors that directly govern rates of extinction and recolonization within habitat patches (Sjögren-Gulve and Ray 1996). Rieman and McIntyre (1995) considered only stream gradient as an alternative to patch size (stream width or patch area) to explain bull trout occurrence. Here, we examined patch-scale patterns of bull trout occurrence in relation to three additional factors, including occurrence of nonnative brook trout *Salvelinus fontinalis*, road density, and solar radiation.

Nonnative brook trout are frequently implicated in the decline of bull trout, impacting populations through introgressive hybridization, and possibly through interactive segregation (reviewed in Rieman and McIntyre 1993). The negative impacts of roads on salmonid habitats are well known, and include increased erosion and sedimentation of stream basins, alterations in stream channel morphology, changes in flow regimes, migration blockage, and increased human access (Furniss et al. 1991, Lee et al. 1997). Aspect and solar radiation may affect stream temperatures and bull trout, which appear to be associated with relatively cold water temperatures (Fraley and Shepard 1989, Rieman and McIntyre 1993, Rich 1996, Buchanan and Gregory 1997, Rieman et al. 1997b).

While the central focus of this study was on patch-scale patterns, we also considered relationships at smaller spatial scales. Distributional patterns of species in landscapes may be the product of several processes operating on different spatial and temporal scales (Wu and Loucks 1995). Recent work on other salmonids, for example, has clearly demonstrated the importance of considering multiple scales (cf. Fausch et al. 1994, Dunham and Vinyard 1997, Wiley et al. 1997). Our sampling design emulated previous hierarchical classifications of stream habitats (Frissell et al. 1986), and

TABLE 1. List of variables, units of measurement, and spatial scales at which variables were analyzed. See *Methods* for definition of site, stream, and patch terms.

Variable	Units	Scale
Brook and bull trout occurrence	category (0, 1)	site, reach, patch
Stream width	m	reach
Stream gradient	percent	reach
Solar radiation	GJ·m <sup>-2</sup> ·y <sup>-1</sup>	patch
Road density	m/ha	patch
Patch area	ha	patch
Distance to nearest occupied patch	m	patch

covered spatial scales ranging from 10 to 10<sup>5</sup> m (Table 1).

In particular, we focused on segregation between brook trout and bull trout, as previous work has emphasized the importance of scale-dependent interactions in other stream-living *Salvelinus* species (Fausch et al. 1994). We also analyzed bull trout occurrence among stream reaches within occupied patches in an attempt to resolve collinearity between stream width and patch size observed by Rieman and McIntyre (1995). We considered the influence of both stream width and gradient on bull trout occurrence among stream reaches within occupied patches.

Our primary aim in this study was to determine the status of bull trout in the Boise River basin with regard to potential factors affecting occurrence. Resulting patterns of bull trout occurrence in relation to physical, biotic, and geometrical factors were then evaluated to determine the relevance of alternative models of metapopulation structure (Harrison and Taylor 1996). In addition, the influences of potentially confounding factors (scale dependence, spatial autocorrelation, multicollinearity) were considered in the analysis. Collectively, these results were used to evaluate the efficacy

of presence-absence analyses (incidence functions) as a practical approach to studying metapopulations in complex landscapes, such as those inhabited by bull trout.

#### METHODS

Study areas were described in detail by Rieman and McIntyre (1995). Study areas were located in the upper Boise River basin in southwestern Idaho, which consists of three major subbasins (North Fork, Middle Fork, and South Fork), covering ~5700 km<sup>2</sup> (Fig. 1). These three subbasins were all isolated from the lower Boise River by dams constructed prior to the 1950s. Bull trout populations in the South Fork Boise River are presently isolated behind Anderson Ranch Dam, while those in the North and Middle Forks are potentially interconnected.

Bull trout exhibit a variety of life history patterns. Juveniles typically rear in natal or adjacent streams for 2–3 yr. Some fish may assume a “resident” life history, remaining in the natal or closely associated streams for life, while others may migrate to larger rivers or lakes, returning to the natal streams at maturity to spawn (Rieman and McIntyre 1993). Larger, migratory bull trout

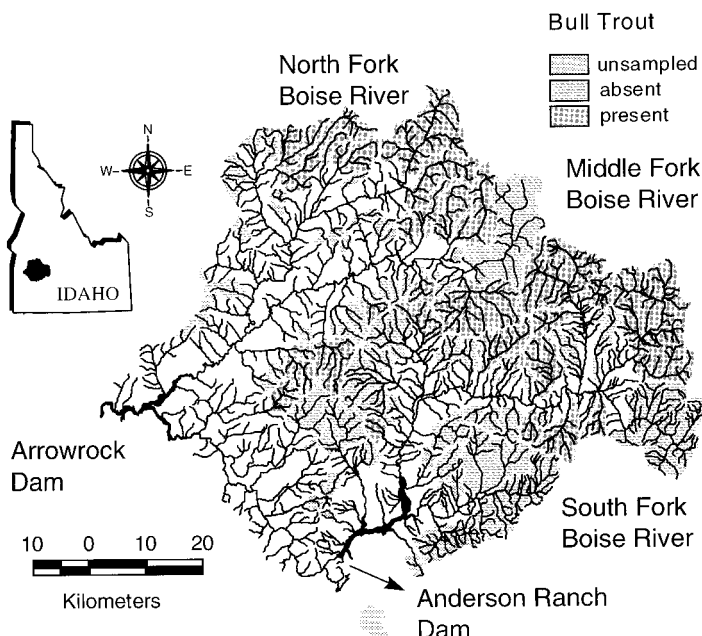


FIG. 1. Map of Boise River basin, west-central Idaho, showing outlines of 104 habitat patches (stream catchments) within the basin. Shading indicates patches occupied (present) or unoccupied (absent) by juvenile bull trout, and unsampled patches.

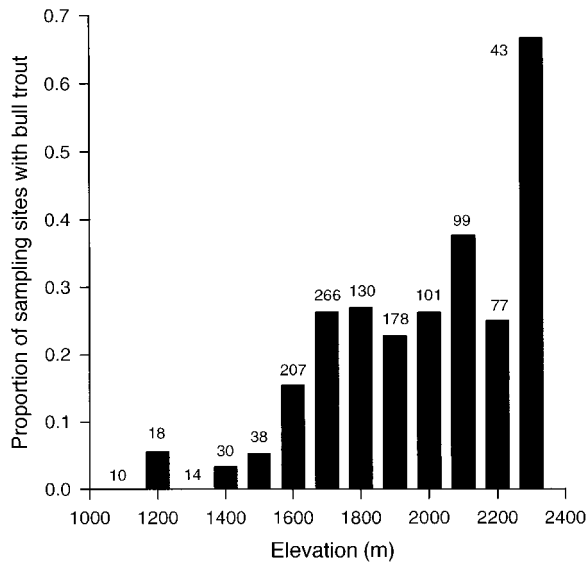


FIG. 2. Occurrence of small (<150 mm) bull trout from 1045 sample sites distributed across a gradient of stream size and elevation in 18 streams (including and surrounding the Boise basin) that were known to support extant bull trout populations. Numbers over bars indicate number of samples in each bin. Data include those reported in Rieman and McIntyre (1995: their Fig. 2) and additional observations from studies conducted by the U.S. Forest Service Rocky Mountain Research Station, Boise, Idaho, and are independent of the work reported in this paper.

may occur throughout the Boise River basin and similar systems (Rieman et al. 1997a, Swanberg 1997). Our observations of juvenile fish, however, suggest spawning and initial rearing occur almost exclusively in higher elevation headwater streams (Fig. 2; also see Rieman and McIntyre 1993, Swanberg 1997). Bull trout distributions and densities have been consistently linked with colder waters than those of other salmonids (Rieman and McIntyre 1993, Buchanan and Gregory 1997), so this pattern is presumably a result of a temperature constraint or preference (Rieman and McIntyre 1995). Other details of bull trout life history can be found in Pratt (1992), and Rieman and McIntyre (1993).

Habitat selection by salmonid fishes may be reinforced through strong breeding-site fidelity (homing, Dittman and Quinn 1996), and, consequently, local breeding populations of stream-living salmonids are best defined on the basis of the distribution of smaller, presumably "pre-migratory" or resident individuals (Allendorf and Waples 1995, Rieman and McIntyre 1995). Migratory or large resident bull trout adults may use habitats well outside of areas used for spawning and initial rearing (Pratt 1992, Rieman and McIntyre 1993, Swanberg 1997). These larger fish and the habitats they use may be important in terms of among-patch dispersal and other life history characteristics, but patch structure must be defined according to the condition that constrains the reproductive portion of the life cycle (Haila et al. 1993, Hanski 1996). For bull

trout, this is represented by headwater stream networks (Rieman and McIntyre 1995). Recent work with similar bull trout populations has confirmed genetic structuring among tributary populations at this scale (P. Spruell and F. W. Allendorf, *unpublished data*). Based on observed distributions of juvenile bull trout (<150 mm), Rieman and McIntyre (1995) defined habitat patches as the stream catchments above 1600 m elevation and with an accessible perennial stream. Watersheds <400 ha were not included in the analysis because they rarely supported perennial streams large enough to support fish. We retained that definition for this analysis and identified a total of 104 potential habitat patches throughout the basin (Fig. 1).

Sampling of stream habitats and fish occurrence followed methods in Rieman and McIntyre (1995). Fish sampling intensity was evenly distributed among all habitat patches and involved electrofishing or snorkeling (Rieman and McIntyre 1995). To determine occurrence within patches, sampling was conducted in one to three reaches of the main stem of each patch. The term "main stem" refers to the largest perennial stream draining a patch. Each reach was ~0.5 km in length and contained five sample sites, each 30 m in length. Sampling continued until bull trout were detected, or when three reaches, located in the lower, middle, and upper portions of the main stem were sampled, unless the middle or upper portions of the streams clearly had become too small to support fish.

Assuming a minimum detection efficiency of 0.25 for each site, a Poisson sampling distribution, and minimum density of 15 fish/km in a 10-km stream, Rieman and McIntyre (1995) estimated a minimum detection efficiency of 0.82 for cases where all three reaches were sampled. Recent comparisons of day and night snorkeling to electrofishing estimates of bull trout abundance in a nearby stream suggest minimum detection efficiencies were actually much higher (Thurow and Schill 1996). Accordingly, detection efficiencies in this study may be much larger than 0.82, but it is possible that some "false absences" were recorded during surveys (e.g., Reed 1996). We assumed most false absences, if present at all, were likely due to very small population sizes. Such small populations are likely to be at high risk of extinction, and therefore destined to become bona fide absences in the near future (Lande 1993).

To consider factors that may influence bull trout distributions at finer scales, we sampled additional sites and reaches in tributary streams within occupied patches. Reaches in tributaries were at least 500 m above the mouth of the stream, but because of problems with access they were not randomly or systematically distributed across the accessible length of a stream. Sites (30 m) represented the smallest spatial scale (10<sup>1</sup> m), reaches (0.5 km) represented an intermediate spatial scale (10<sup>2</sup> m), and patches represented the largest spatial scales (≥10<sup>3</sup> m) for the subsequent analysis. This

sampling strategy emulated hierarchical classification of stream habitats (e.g., Frissell et al. 1986), and permitted an analysis of processes occurring at different spatial scales. A total of 81 of 104 potential patches (Fig. 1), 179 reaches, and 720 sites were sampled for occurrence of bull trout.

Fish occurrence, stream width, and gradient were measured following Rieman and McIntyre (1995). Briefly, brook trout and bull trout were considered present in a patch, reach, or site if any individuals were observed in the relevant samples. Wetted widths were taken at a random point for each site and averaged for a reach. Because sampling occurred during late summer, widths approximated base flow conditions. Stream gradients were measured at each site with a clinometer and averaged for a reach. Patches were identified as the catchments above 1600 m and delineated from U.S. Geological Survey 30 m Digital Elevation Models (DEM) using ARC/INFO GRID 1 extension. An estimate of annual solar radiation was assigned to each 30-m grid cell in each patch based on the slope and aspect of the cell and approximated annual solar radiation for 63 slope-aspect classes from Buffo et al. (1972). The estimates for each cell were averaged for the patch. Road densities were calculated as the total length of all forest system roads within a patch divided by patch area. Digitized road coverages were provided by the Boise National Forest, Boise, Idaho.

Interpatch distances were calculated as the minimum distance between patches along the network of streams connecting those patches, using the ARC/INFO NETWORK extension and the U.S. Geological Survey 1:24 000 digitized hydrography. Interpatch distances were calculated only where the connecting stream corridors were not blocked by dams or natural barriers to fish dispersal. We considered distance to nearest occupied patch as a measure of patch isolation (Table 1). Factors other than linear stream distance (e.g., isolation due to other biotic or physical barriers) were not considered in the analysis. Isolation may be indirectly related to environmental factors that could affect migratory behavior, such as proximity to downstream feeding habitats (e.g., large rivers, lakes, reservoirs). Habitats in areas with a greater probability of supporting migratory individuals may be more likely to support bull trout for at least two reasons. First, migratory individuals generally are larger, and therefore may have greater reproductive potential. Second, migratory individuals use areas outside of spawning and rearing habitat, therefore reducing the chance that disturbance to such habitats will extirpate all individuals in a breeding population ("risk-spreading" in space, den Boer 1968). Because little is known in general about life history variability in bull trout and relations to dispersal behavior, we considered only the simplest measure of patch isolation (Table 1). Another issue with our measure of isolation concerns the potential effects of dams in the Boise basin. A major dam prevents bull trout

movement between formerly connected habitats in the South Fork Boise River from other habitats in the Boise basin. We did not consider such long-distance dispersal in this study, and the dam had no influence when distance to nearest occupied patch was considered (see Fig. 1).

Data analyses began with patterns of patch-scale bull trout occurrence (Table 1). All data analyses used logistic regression (Hosmer and Lemeshow 1989, SAS Institute 1995). Best subsets logistic regression (SAS Institute 1995) was initially used to screen the five patch-scale predictors (Table 1). Logistic regression analysis, in contrast to other methods (e.g., discriminant function analysis, ordinary least-squares regression), is considerably more flexible in terms of model assumptions, such as the assumption of a linear relationship between response and predictor variables, normality, and equal variance among groups. If, however, these conditions are satisfied, the power of logistic regression to detect relationships may be increased (Tabachnick and Fidell 1996).  $\log_{10}$  transformations of patch area, interpatch-patch distances, and solar radiation, and an inverse transformation of road density, resulted in the best fitting model (using the score statistic, Hosmer and Lemeshow 1989, SAS Institute 1995). Unless otherwise specified, all further references to these variables refer to transformed values. Jackknifed classification rates from logistic regression models were calculated using SAS (SAS Institute 1995).

Multicollinearity among predictor variables was first addressed by evaluating pairwise correlations. A second, common multicollinearity diagnostic, the variance inflation factor (VIF), was estimated by regressing each predictor variable in relation to others in the model. Variance inflation factors estimate how much the variances of regression coefficients are inflated relative to the case when predictor variables are not linearly related (orthogonality). The VIF for each variable was calculated as  $1/(1 - R^2)$ , where  $R^2$  is the coefficient of determination from ordinary least-squares regression of a predictor variable in relation to all other predictors in the model (Phillipi 1994). Variance inflation factors of 10 or greater were considered to indicate problems with multicollinearity (see Phillipi 1994). Finally, we evaluated the possible influence of collinearity by checking the sensitivity of parameter estimates from logistic regressions to removal of each predictor variable (Hosmer and Lemeshow 1989).

Spatial autocorrelation in patch-scale occurrence of bull trout was examined with Mantel tests (Fortin and Gurevitch 1994). The Mantel test is used to test for associations between pairwise distance matrices (Manly 1997). We used Mantel tests to look for associations between pairwise distances between patches and bull trout occurrence. Pairwise distances between patches were estimated from Universal Transverse Mercator (UTM) map projections. Euclidean distances between

TABLE 2. Results of variable selection with best subsets logistic regression of patch-scale bull trout occurrence.

Number of variables	Score value	Variables included in model
1	14.83	patch area
1	14.17	stream distance to nearest occupied patch
2	28.07	patch area, stream distance to nearest occupied patch
2	23.75	patch area, road density
3	30.95	patch area, stream distance to nearest occupied patch, road density
3	28.70	patch area, stream distance to nearest occupied patch, solar radiation
4	32.24	patch area, stream distance to nearest occupied patch, road density, solar radiation
4	30.95	patch area, stream distance to nearest occupied patch, road density, brook trout
5	32.31	all patch-scale predictors (see Table 1)

all pairs of patches were calculated with X–Y coordinates determined as eastings and northings, respectively, measured in meters. Both linear and inverse Euclidean distances were used in Mantel tests of spatial autocorrelation. Values in the pairwise matrix of bull trout occurrences were coded as zeros when both patches shared the same state (e.g., both habitats were either occupied or not occupied), and as ones when they were in different states (e.g., occupied vs. not occupied). This coding was similar to design matrices used by Fortin and Gurevitch (1994).

Mantel tests were conducted with the “R” package for spatial analysis (Legendre and Vaudor 1991). The Mantel  $Z$  statistic was normalized ( $r$ ) so that  $r$  values varied between  $-1$  and  $1$ , similar to the familiar values of Pearson’s linear correlation coefficient (Fortin and Gurevitch 1994). The significance of  $r$  values was evaluated with a reference distribution of  $r$  values created by Mantel tests on 9999 randomizations of matrix elements, which also contained the original  $r$  value for a total of 10 000 observations (see Jackson and Somers 1989, Manly 1997).

Finally, covariation between bull trout occurrence and selected variables was analyzed at smaller spatial scales with logistic regression. Stream width and gra-

dient were analyzed in relation to variability in bull trout occurrence among stream reaches within occupied patches only. Restricting the analysis of stream width and gradient to reaches within patches was necessary to distinguish width (and potentially gradient) effects due to habitat selection by bull trout, as hypothesized by Rieman and McIntyre (1995). Previous analyses could not distinguish patch-scale stream width and patch-area effects due to collinearity (Rieman and McIntyre 1995).

Because results of the patch-scale analysis strongly suggested that bull trout may not have free access to stream habitats in unoccupied patches, due in part to patch isolation, we restricted the analysis of stream width and gradient effects to variability among stream reaches within occupied patches. Similarly, co-occurrence of bull trout and brook trout was analyzed among stream reaches and sites within patches occupied by bull trout (brook trout effects were not significant at the patch scale, where all potential patches were analyzed). Segregation between potentially interacting species may be more apparent at smaller spatial scales, especially for stream-living salmonids, which typically defend holding positions within streams, while larger scale patterns may result from large-scale variability in abiotic factors (Fausch et al. 1994).

## RESULTS

### Patch-scale analyses

In all, 81 patches were used in patch-scale analyses of bull trout occurrence. Bull trout were present in 29 patches and absent in 52. Based on the score criterion (Hosmer and Lemeshow 1989), a logistic regression model of bull trout occurrence with four predictors (patch area, distance to nearest occupied patch, road density, and solar radiation) was selected as the best subset (Table 2). Logistic regression analyses of the four-variable model revealed a highly significant and positive relationship between bull trout occurrence and patch area, and inverse relationships with distance to nearest occupied patch and road density (Table 3, Fig. 3). Solar radiation was not significant ( $P = 0.16$ ) and was dropped from the model. Pairwise interactions were tested among all significant predictors and none were detected. The resulting model (Table 3) correctly

TABLE 3. Results of logistic regressions of patch-scale bull trout occurrence (transformed predictors, see *Methods*). Values in parentheses are lower and upper 95% confidence limits for parameter estimates.

Variable	df	Parameter estimate	SE	Wald chi-square	$P$
Intercept	1	-3.2	3.49	0.84	NS
Patch area	1	1.26 (0.61, 2.05)	0.36	12.05	0.0005
Distance to nearest occupied patch	1	-0.84 (-1.48, -0.30)	0.30	8.10	0.004
Road density <sup>†</sup>	1	1.59 (0.07, 3.19)	0.79	4.10	0.04

<sup>†</sup> Note that the sign of the slope parameter estimate for road density is for an inverse transformation, and thus the sign is reversed from that expected with untransformed data.

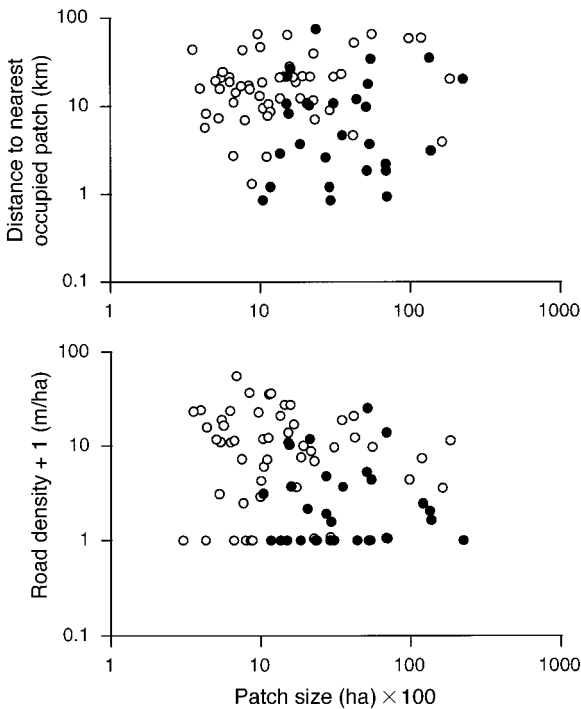


FIG. 3. Relationships between bull trout occurrence (solid circles = present, open circles = absent) and patch size, distance to nearest occupied patch (top), and road density (bottom). An  $X + 1$  transformation was necessary to display road density values of zero.

predicted >80% of bull trout occurrences at the 0.50 probability cutoff.

**Multicollinearity.**—A highly significant correlation between distance to nearest occupied patch and road density was apparent ( $r = -0.41$ ,  $P = 0.0002$ ). The potential influence of this collinearity on variance inflation and regression coefficients was therefore evaluated in more detail. Regressions of the predictor variables in Table 2 (results not shown) indicated that none of corresponding VIF values was  $>1.25$ , while the average VIF of all variables was 1.16. This value indicates that multicollinearity is of little concern (Phillipi

TABLE 4. Results of logistic regressions of bull trout occurrence to evaluate the potential influence of multicollinearity. See *Results* for details.

Variable	df	Parameter estimate	SE	Wald chi-square	P
a) Model without distance to nearest occupied patch					
Intercept	1	-10.58	2.57	17.00	0.0001
Patch area	1	1.18	0.318	13.67	0.0002
Road density	1	2.27	0.71	10.08	0.0015
b) Model without road density					
Intercept	1	-0.75	3.18	0.06	0.81
Patch area	1	1.27	0.35	13.05	0.0003
Distance to nearest occupied patch	1	-1.04	0.29	12.86	0.0003

TABLE 5. Mantel matrix correlations of bull trout occurrence in relation to two measures of interpatch distance. Probabilities are for a one-tailed test (to test alternative hypothesis that geographically proximate sites are more similar).

Distance	$r$	$P$
Euclidean	0.30	0.12
Inverse Euclidean	-0.29	0.15

1994). Separate logistic regressions of bull trout occurrence with and without road density and distance to nearest occupied patch were conducted to test if the inclusion (or exclusion) of either in the model affected parameter estimates (see Hosmer and Lemeshow 1989). From the results in Table 4, it can be seen that point estimates of regression slopes do change to a small degree. Confidence limits for regression slopes (Table 3) indicate that these changes are of little significance, however.

**Spatial autocorrelation.**—Mantel tests with Euclidean and inverse Euclidean measures of pairwise geographic distances indicated that bull trout occurrence was not spatially autocorrelated among patches (Table 5). A plot of bull trout occurrence in relation to geographic distances similarly showed no obvious spatial patterns (Fig. 4).

#### Analyses at finer spatial scales

Logistic regression indicated bull trout occurrence among stream reaches within occupied patches ( $n = 72$ ) was positively related to stream width (Wald  $X^2 = 6.09$ ,  $P = 0.01$ ). Occurrence of bull trout in stream reaches was not related to stream gradient. Logistic regression of bull trout occurrence in relation to occurrence of brook trout revealed no significant associations at patch, stream, or site scales.

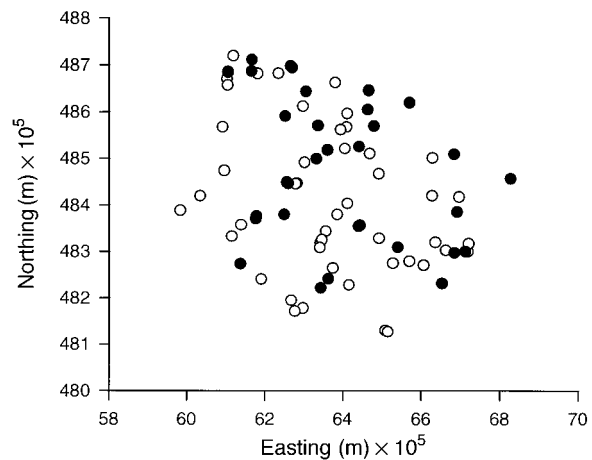


FIG. 4. Scatterplot of geographic coordinates (eastings and northings, in meters), and bull trout occurrence (solid circles = present, open circles = absent) in the Boise River basin.

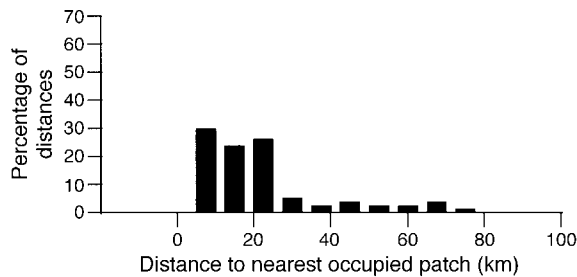


FIG. 5. Distribution of distances to nearest occupied patch for 81 patches of potentially occupied bull trout habitat in the Boise River basin.

#### DISCUSSION

Results of this study confirm earlier findings (Rieman and McIntyre 1995) that habitat size may play an important role in the patch-scale persistence of stream-living bull trout populations. It also appears that patch-scale persistence may depend on habitat connectivity and human disturbance in the form of road density. Within occupied patches, bull trout were found to select wider stream habitats, but gradient and occurrence of nonnative brook trout did not explain bull trout occurrence.

##### *Factors affecting patch-scale persistence of bull trout*

Habitat size may be positively related to local population persistence for at least two reasons. First, larger habitats may support larger populations. Larger populations should be less vulnerable to extinction due to stochastic demographic factors, and may be less vulnerable to the effects of environmental variability and catastrophes (Lande 1993). The effects of environmental variability and catastrophes on population persistence may interact with habitat complexity, which may be greater in larger stream habitats (Frissell et al. 1986, Schlosser 1987). In large habitats, localized disturbances are less likely to affect all segments of a population, thus reducing the chance that all individuals will be killed or displaced by a single event (Harrison and Quinn 1989). Effects of physical disturbance in stream basins may be very localized (Resh et al. 1988, Reeves et al. 1995, Schlosser 1995, Rieman et al. 1997a), and thus populations in larger and more complex stream basins may be more resistant to local extinction. It is possible that habitat size may increase population vulnerability, by facilitating occurrence of predators (Sjögren-Gulve 1994), for example, or by intensifying intraspecific competition when resources are concentrated around habitat edges (Pearman 1993). Such does not appear to be the case for bull trout in this study, however.

The significant relationship between distance to nearest occupied patch and bull trout occurrence suggests dispersal also may be important to local population persistence (Fig. 5). The potential for spatial

autocorrelation due to unmeasured environmental characteristics was examined but rejected as a likely alternative explanation to dispersal. Some bull trout have been shown to move over relatively long (>50 km) distances in streams (Bjornn and Mallet 1964, Swanberg 1997). Larger (>150 mm) individuals may undergo extensive seasonal feeding and spawning migrations within stream basins (Swanberg 1997), but juveniles and resident individuals may be restricted in their movements (Rieman and McIntyre 1993). Some bull trout may easily move the distances separating local populations in the Boise River basin. We know little, however, about the actual rates of dispersal (or "straying" of reproducing adults from natal habitats) necessary to link those populations demographically. It is reasonable to assume that such dispersal is more likely among populations that are closer together, and that it is more likely in populations with migratory life history patterns than in those that are strictly resident. The relationship between dispersal and migration of small bull trout in relation to life history variability is a critical area of uncertainty (see *Implications for metapopulation structure*).

We found that bull trout occurrence was negatively related to density of roads within stream basins. Roads increase human access to streams, which may facilitate increased angling mortality and introductions of nonnative salmonids (Furniss et al. 1991, Lee et al. 1997). Erosion and sedimentation caused by roads may lead to stream channel instability and habitat degradation that may increase vulnerability of bull trout as well (Rieman and McIntyre 1993). Details of road location, construction methods, and variability in local geology and hydrologic regimes may all affect the impact of roads on salmonid habitats (Furniss et al. 1991), which may lead to greater variability in the response of bull trout populations. Roads also are related to other human land uses, such as mining, timber harvest, and livestock grazing, which may affect the quality of salmonid habitat (see papers in Meehan 1991). In spite of these potential sources of variability, the significant association of roads with distribution of bull trout in the Boise River basin and across the region (Rieman et al. 1997b, Baxter et al. *in press*) suggests that the negative effects of road-related impacts may be pervasive.

##### *Implications for metapopulation structure*

Relationships between variability in patch quality (e.g., size, carrying capacity, and productivity), patch spacing, and dispersal are the key elements determining the structure and dynamics of metapopulations (Hanski and Simberloff 1996, Harrison and Taylor 1996, Fig. 6). Patch size (area) was the single most important factor determining bull trout occurrence in this study, and variability in patch area is large (Fig. 7). Patterns of occurrence for Boise River bull trout are not consistent with the simple metapopulation structure envisioned by Levins-type models (Harrison and Taylor



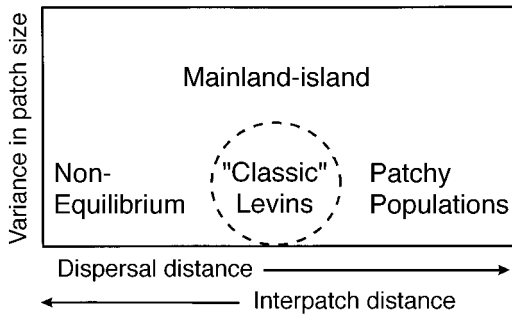


FIG. 6. Metapopulation structure in relation to variance in patch size, dispersal distance, and interpatch distance (modified from Harrison and Taylor [1996]). See *Methods* for definition of terms.

1996). Resolution of where bull trout metapopulations in the Boise River basin may lie along other parts of the continuum of potential configurations (Fig. 6) is restricted by lack of direct information on rates of dispersal and local extinction.

If we assume that long-distance dispersal is frequent, and that local extinctions are more likely to occur in smaller habitat patches, then we may reasonably conclude that Boise River bull trout lie somewhere along the continuum between mainland-island and patchy metapopulation configurations (Fig. 6). Alternatively, if dispersal is restricted, Boise River bull trout must lie somewhere between nonequilibrium and mainland-island metapopulation configurations. If Boise River bull trout are in an mainland-island configuration, then some local populations may be relatively persistent (e.g., those in large patches), while others may be more ephemeral, perhaps functioning as population sinks (Pulliam 1988). On the ends of this continuum, bull trout may exist in a nonequilibrium state, where all local populations are destined for extinction due to restricted dispersal (and presumably recolonization), or as a patchy metapopulation, where high rates of recolonization lead to high rates of patch occupancy (Harrison and Taylor 1996, Fig. 6). Several lines of evidence suggest bull trout in the Boise River basin may consist of a complex metapopulation structure that is a composite of these possibilities.

Overall, we found bull trout in 36% of potentially occupied habitat patches in the Boise River basin. If dispersal was widespread and local extinctions were relatively uncommon throughout the basin, we should have observed much higher occupancy rates. At finer spatial scales, Rieman et al. (1997a) observed rapid (<3 yr) recolonization of defaunated bull trout habitats following severe fires in tributaries of the Boise River. Rapid recolonization was likely facilitated both through complex life-histories with overlapping generations, and through movements within local stream systems. These observations suggest that the complexity of habitats played a key role in the persistence of bull trout populations influenced by the fires (Rieman

et al. 1997a). Because the complexity and diversity of stream habitats are expected to vary directly with patch (catchment) size (Frissell et al. 1986, Schlosser 1987, Rieman and McIntyre 1995), the risk of local extinction should as well. The few large (>10<sup>5</sup> ha) occupied patches may possibly serve as important sources of bull trout for recolonization of unoccupied habitat within the Boise River basin, and parts of the basin may function as mainland-island or patchy metapopulations (Fig. 6).

Bull trout populations in the Pacific Northwest are generally believed to be in a state of decline (Rieman and Myers 1997, Rieman et al. 1997b). Although there is no clear evidence of such a trend in the Boise River basin, fishing and habitat disruption have occurred at potentially important levels across the system. The association of bull trout occurrence with road density is an indication of such effects. If populations are in a general state of decline across the basin, the significant patch-area effect could emerge simply as an artifact of smaller populations disappearing more quickly. We suggest it is unlikely that these bull trout populations are strictly in a nonequilibrium decline, because distance to nearest occupied patch was also a significant predictor. This suggests that some recolonization does occur at broader scales. A number of patches are also found within Forest Service Wilderness or roadless areas with very limited access, and the area effect is still apparent (e.g., patches with low densities of roads in Fig. 3). Populations in these areas have likely been influenced little by habitat disruption or fishing.

Dispersal behaviors are complex, and may be a function of several biotic and abiotic processes operating on different spatial and temporal scales (Ims 1995, Ims and Yoccoz 1996). Habitat fragmentation itself may directly affect dispersal behaviors of animals (Ims 1995, Yahner and Mahan 1997). Fragmentation of stream habitats may have effects that parallel restricted dispersal observed for salmonid populations that are isolated above waterfalls (Jonsson 1983, Northcote and Hartman 1988, Northcote 1992). In such cases, the potential benefits of movement (Northcote 1992, Jonsson and Jonsson 1993) are clearly outweighed by costs. Bull trout, like many salmonids, may consist of several life history "forms" with different dispersal or migra-

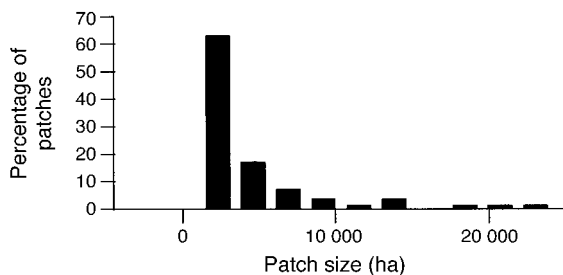


FIG. 7. Distribution of sizes (areas) for 81 patches of potentially occupied bull trout habitat in the Boise River basin.

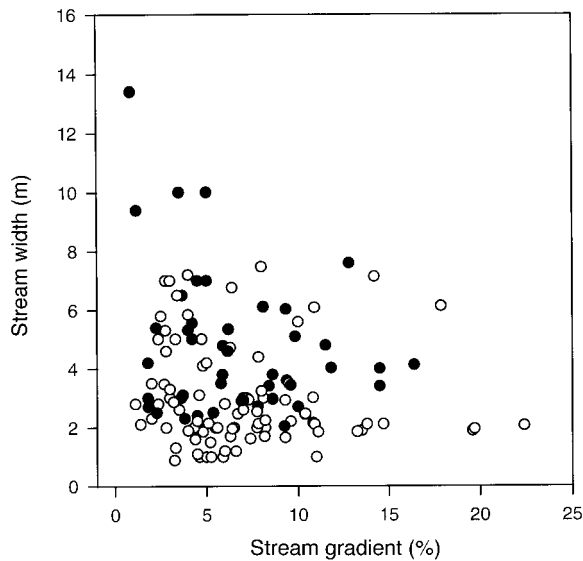


FIG. 8. Relationships between bull trout occurrence in stream reaches within occupied patches and stream width and gradient (solid circles = present, open circles = absent).

tory behaviors (Rieman and McIntyre 1993, Willson 1997). Relationships between bull trout life histories, habitat structure, and the potential for habitat fragmentation to restrict dispersal of bull trout clearly require further research.

#### *Patterns at smaller spatial scales*

Rieman and McIntyre (1995) found patch-scale occurrence of bull trout in the Boise River basin to be positively related to both patch area and stream width, but not to stream gradient. Because patch area and stream width were correlated, they could not distinguish the effects, and hypothesized that width effects may be due to habitat selection by bull trout. The positive relationship between bull trout occurrence and stream width within occupied patches found in this study supports their explanation. A pattern similar to patch-scale relationships (Rieman and McIntyre 1995) emerged within patches (Fig. 8). Bull trout were found only in streams  $>2$  m in width, even with free access to many smaller habitats within occupied patches (see also Figs. 2 and 3 in Rieman and McIntyre 1995). There are several instances in which bull trout were not found in streams  $>2$  m in width, and this may be due to low densities of fish, perhaps resulting from past disturbances (Platts and Nelson 1988), or avoidance of some other feature of the habitat.

Analyses of co-occurrence of bull trout and brook trout at stream and site scales revealed no associations, suggesting bull trout and brook trout do not segregate among habitats at spatial scales considered in this study. We strongly caution that the possibility of competition between bull trout and brook trout cannot be ruled out by this result, because co-occurrence data may be misleading (Hastings 1987). Segregation may

occur at smaller spatial scales (e.g., among microhabitats within sites), especially if feeding territories are defended (Grant and Kramer 1990, Fausch et al. 1994, Nakano and Kaeriyama 1995), but we have no data to evaluate this possibility. Larger scale patterns may emerge through time if bull trout are systematically displaced or replaced by brook trout, or if the reverse were to occur. Interspecific hybridization of bull trout and brook trout could play an important role in replacement of the former by the latter, for example (Leary et al. 1993). Finally, it is possible that the influence of brook trout on bull trout may extend outside occupied patches considered here if the presence of brook trout in downstream areas hinders dispersal through, or occupancy of, downstream habitats (see Fraser et al. 1995).

#### *Conclusions and conservation implications*

It has long been recognized that aquatic habitats are organized by processes that can be ultimately traced to landscape-scale influences on stream catchments or watersheds (e.g., Hynes 1975, Frissell et al. 1986). Technological advances in methods to acquire and analyze information on large-scale patterns and processes have dramatically increased the ability of aquatic ecologists to study such phenomena, while at the same time management policies are being revamped to incorporate large-scale perspectives of aquatic ecosystems (Johnson and Gage 1997).

Past analyses, while providing exciting insights on a number of large-scale factors, have often neglected the spatial extent and distribution of landscape elements within stream catchments (Johnson and Gage 1997). For example, assessments of fish-habitat relationships (Hinch et al. 1991) were dramatically modified after spatial autocorrelation of sites was considered (Hinch et al. 1994). In the case of bull trout, metapopulation structure implies suitable habitats are often not occupied, and attempts to relate occurrence of bull trout to habitat characteristics without accounting for patch occupancy are potentially misleading (e.g., Watson and Hillman 1997). As we have shown here for bull trout, the large-scale geometry of stream catchments can strongly influence the distribution of aquatic species, independent of other more commonly considered habitat characteristics. Our analyses revealed that additional factors operating on smaller spatial scales may be important as well. Small-scale factors should be considered together with large-scale patterns, because their effects may otherwise go undetected.

While our study of bull trout was extensive in terms of spatial dimensions, we have limited information to evaluate rigorously the influence of temporal variability. Aquatic landscapes are highly dynamic systems, and long-term data are needed to define more clearly interactions between temporal and spatial processes occurring on different scales (Schlosser 1995, Wiley et al. 1997). Furthermore, we stress the need for better

information on parameters related to dispersal success, which can dramatically affect interpretations of spatially explicit population models (including metapopulation models), as recently emphasized by Ruckelshaus et al. (1997).

Our analysis suggests that the actual structure of bull trout metapopulations is highly complex. Real metapopulations of aquatic organisms may be complex mosaics that contain several elements of the structures found in simple conceptual models (Schlosser and Angermeier 1995, Harrison and Taylor 1996). In the case of bull trout and other stream-living fish, habitat spatial structure and life history variability likely function interactively to affect patterns of migration, dispersal, and patch occupancy (Rieman and McIntyre 1993, Gresswell et al. 1994, Schlosser 1995, Schlosser and Angermeier 1995, Willson 1997). These complexities pose important challenges to empirical and theoretical attempts to understand metapopulation dynamics of fish and other aquatic organisms, but insights provided by such studies may prove critical to developing effective long-term management strategies for aquatic ecosystems.

Results of this work have several important implications for management of bull trout. Bull trout populations in larger, less isolated, and less disturbed habitats may be more likely to persist, and these habitats may prove critical in terms of providing long-term refugia and recolonization potential. Disturbance to these populations and their habitats should be minimized. In particular, disturbances associated either directly or indirectly with roads are a critical concern. On the other end of the continuum, small, isolated, and disturbed habitats may be at risk. Management to ensure persistence of these populations may be challenging. In the middle are populations and habitats of intermediate size and/or isolation, where opportunities for conservation and restoration may be greater. Furthermore, the existence of metapopulation structure implies availability of suitable, but presently unoccupied, habitat, which should be managed carefully to facilitate potential natural recolonization or reintroductions of bull trout.

We do not recommend that management activities be prioritized on the basis of this study alone. Clearly, genetic concerns and occurrence of other species of concern merit consideration (see papers in Nielsen 1995). In particular, information on the genetic structure of bull trout populations in the Boise basin would prove useful in terms of prioritizing efforts to maintain genetic diversity. Previous work on bull trout (Leary et al. 1993) and more recent genetic evidence in other basins (P. Spruell and F. W. Allendorf, *unpublished data*) suggest strong genetic divergence among populations, but relatively little within-population variability. One hypothesis to explain this pattern is that current metapopulation structure of bull trout is the result of long-term fragmentation of habitat related to historical changes in regional climate. If so, this implies that

dispersal occurs very infrequently and over long periods, perhaps on the order of centuries, and that contemporary losses of local bull trout populations may not be balanced in the near term by recolonization. This time scale may be considerably longer than that hypothesized for dispersal and recolonization for other salmonids (Reeves et al. 1995). We emphasize that further study is needed to define more clearly the temporal scale over which metapopulation dynamics of bull trout occur.

With regard to patterns we observed at smaller spatial scales, it is clear that bull trout select larger habitats, when they are available. However, we caution that results of this study regarding effects of brook trout not be extrapolated to other areas. In other cases within the range of bull trout, negative effects of brook trout on bull trout populations are evident (e.g., Howell and Buchanan 1992, Leary et al. 1993, Rich 1996) and likely scale-dependent, as emphasized above.

A final important issue for managers regards the effects of downstream dams on bull trout in the Boise basin. From a metapopulation perspective, long-term isolation of the South Fork Boise River by dams may restrict long-distance dispersal, the significance of which is unclear at this point. Reservoirs created by downstream dams do support migratory populations of bull trout, and they may be of significance to some local populations (e.g., Rieman et al. 1997a). Perhaps most importantly, dams in the Boise basin and further downstream in the Snake River have extirpated runs of anadromous salmon (primarily *Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). The importance of these species to the productivity of aquatic and terrestrial ecosystems (Willson and Halupka 1995) may have affected viability and productivity of bull trout populations directly through loss of a prey base of juvenile salmonids and indirectly through effects on associated species.

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