

TRANSACTIONS

OF THE AMERICAN FISHERIES SOCIETY

Volume 124

May 1995

Number 3

Transactions of the American Fisheries Society 124:285–296, 1995
American Fisheries Society

Occurrence of Bull Trout in Naturally Fragmented Habitat Patches of Varied Size

BRUCE E. RIEMAN AND JOHN D. MCINTYRE

*U.S. Forest Service, Intermountain Research Station, Boise Forest Sciences Laboratory
316 East Myrtle, Boise, Idaho 83702, USA*

Abstract.—Bull trout *Salvelinus confluentus* and other salmonids in the Pacific Northwest are believed at risk of local and regional extinctions because of ongoing habitat loss and fragmentation. Biologists have focused on defining and protecting critical stream channel characteristics, but there is little information regarding the scale or spatial geometry of habitat that may be necessary for the species' long-term persistence. We investigated the influence of habitat patch size on the occurrence of bull trout by determining the presence or absence of fish in naturally fragmented watersheds of the Boise River basin in Idaho. We defined patches of potential habitat for bull trout as watersheds above 1,600 m elevation, a criterion based on the presumed restriction of local populations by stream temperature. We used logistic regression to investigate the possible influence of patch size as well as stream width and gradient on the occurrence of bull trout at reach, stream, and patch scales of analysis. Both stream width and patch size were significant in the models, but individual effects could not be clearly resolved because of collinearity. The predicted probability of occurrence based on patch size alone was less than 0.10 for patches smaller than about 1,000 ha and more than 0.50 for patches larger than about 2,500 ha. Our results support the hypothesis that area of available habitat influences the distribution of disjunct populations of bull trout. An area effect is consistent with the predictions of island biogeography and metapopulation theory, and our work suggests that larger-scale spatial processes may be important to the persistence of species like bull trout.

Bull trout *Salvelinus confluentus* is a recent addition to the growing list of salmonid fishes considered under the Endangered Species Act (Office of the Federal Register 59[June 10, 1994]:30254). Populations have declined throughout much of the range; some local populations are believed extinct, whereas others are viewed as remnants isolated in shrinking patches of suitable habitat (see papers in Howell and Buchanan 1992; Rieman and McIntyre 1993). As with other salmonids, declines can be attributed to habitat degradation (Fraley and Shepard 1989; Howell and Buchanan 1992), displacement by exotic species (e.g., Leary et al. 1993), increased mortality caused by fishing, or

dams and diversions that influence migratory corridors. Fishery managers are attempting to minimize mortalities and to preserve habitat. Biologists are attempting to characterize critical habitat primarily through the more-or-less traditional measures of stream channel structure studied at the scale of habitat units or stream reaches (e.g., Hawkins et al. 1993). Effective conservation of sensitive populations, however, may require more than just reducing mortality and maintaining as much of the remaining critical habitat as possible. The larger-scale spatial geometry of habitat is now viewed as important to the persistence of many species. Effective conservation may imply main-

taining or restoring a critical amount or mosaic of habitat as well (Simberloff 1988).

Spatially influenced processes have received considerable attention in study of the dynamics and distribution of a variety of species. Island biogeography (MacArthur and Wilson 1967) and the emerging theory of metapopulation dynamics (Hanski 1991; Hanski and Gilpin 1991) hold that the distribution of populations among patches or "islands" of suitable habitat will be a function of local extinction and of dispersal and colonization processes (Hanski 1991, 1994). In essence, smaller, more isolated populations are less likely to persist because (1) small populations face higher risk of extinction through demographic and environmental stochasticity and Allee effects (Leigh 1981; Gilpin and Soulé 1986; Simberloff 1988; Saunders et al. 1990; Boyce 1992); and (2) isolated populations have a lower probability of demographic support or recolonization through dispersal from surrounding populations (Brown and Kodric-Brown 1977; Pulliam 1988).

Metapopulation concepts have been strongly embraced in conservation biology. The spatial geometry of habitat reserves is a central issue in the conservation of species and populations (Simberloff 1988). But are these ideas relevant to the management of salmonids? Recent discussions on conservation of seriously depressed and fragmented western salmonid stocks have invoked spatial concepts and metapopulation theory (Nehlsen et al. 1992; Reeves and Sedell 1992; Frissell et al. 1993; Rieman and McIntyre 1993). There is a notable lack, however, of empirical evidence or spatially explicit models necessary to guide such management. Watershed or basin geometry may influence the diversity in fish communities (Sheldon 1988; Schlosser 1991; Osborne and Wiley 1992), but little information is available regarding the dynamics of individual species. Area effects appear important across a wide range of taxa (Gilpin and Diamond 1981; Hanski 1991, 1992; Kindvall and Ahlen 1992), but the nature of the response may also vary widely among species (Gilpin and Diamond 1981; Hanski 1991; Taylor 1991). Some salmonid populations have persisted for extended periods in small habitat patches isolated by natural barriers (Northcote 1992). Are salmonids generally resistant to chance extinctions? Or, like other animals, are some species predictably sensitive to local extinction while others are not (Cutler 1990)? These questions are relevant for many salmonids that face increasing habitat loss. Although fish population declines can be tied to reduced habitat qual-

ity, introduction of exotics, and overfishing, it is not clear how population and species losses are aggravated by habitat fragmentation and isolation.

Hanski (1991, 1992, 1994) and others (Gilpin and Diamond 1981) have shown that the distribution of animals structured as metapopulations in fragmented systems may reflect the underlying dynamics of local extinction and recolonization through dispersal. Incidence functions that relate the presence or absence of animals in local populations to the amount or other characteristics of available habitat have been widely used to draw inferences about factors likely to influence the persistence of populations (Adler and Wilson 1985; Taylor 1991; Hanski 1994). Incidence functions have been viewed as particularly important where long-time series of detailed information on population demographics and dynamics are unavailable or unlikely in the future (Taylor 1991; Hanski 1994). Such analyses are a logical first step for addressing questions about the spatial dynamics of salmonids in fragmented habitats.

Bull trout have patchy distributions within watersheds throughout their range (Rieman and McIntyre 1993). Although distributions are probably influenced by habitat loss, dams, diversions, and exotic species, bull trout also appear to be naturally restricted to colder stream temperatures (Fraley and Shepard 1989; Rieman and McIntyre 1993). Because of the association with temperature, elevation should define habitat patches or "islands" in the headwaters of many larger watersheds that are at least partially isolated by distance across warmer waters. Such isolation could be particularly important near the southern limits of the species' range, where fragmentation of habitat by temperature may be more evident (Flebbe 1993). In this paper we define suitable habitat patches for bull trout from the observed relationship of fish distribution with elevation (and presumably temperature). We examine the association of patch size and other habitat features (stream width and gradient) with the distribution of bull trout throughout a large river basin. We hypothesize that area of available habitat is important to the persistence of local populations. If that is true, patch size should have a significant influence on occurrence of bull trout throughout the basin.

Study Area

The upper Boise River basin in southwestern Idaho is composed of three major subbasins (North Fork, Middle Fork, and South Fork) all isolated from the lower river since 1915 by Arrowrock

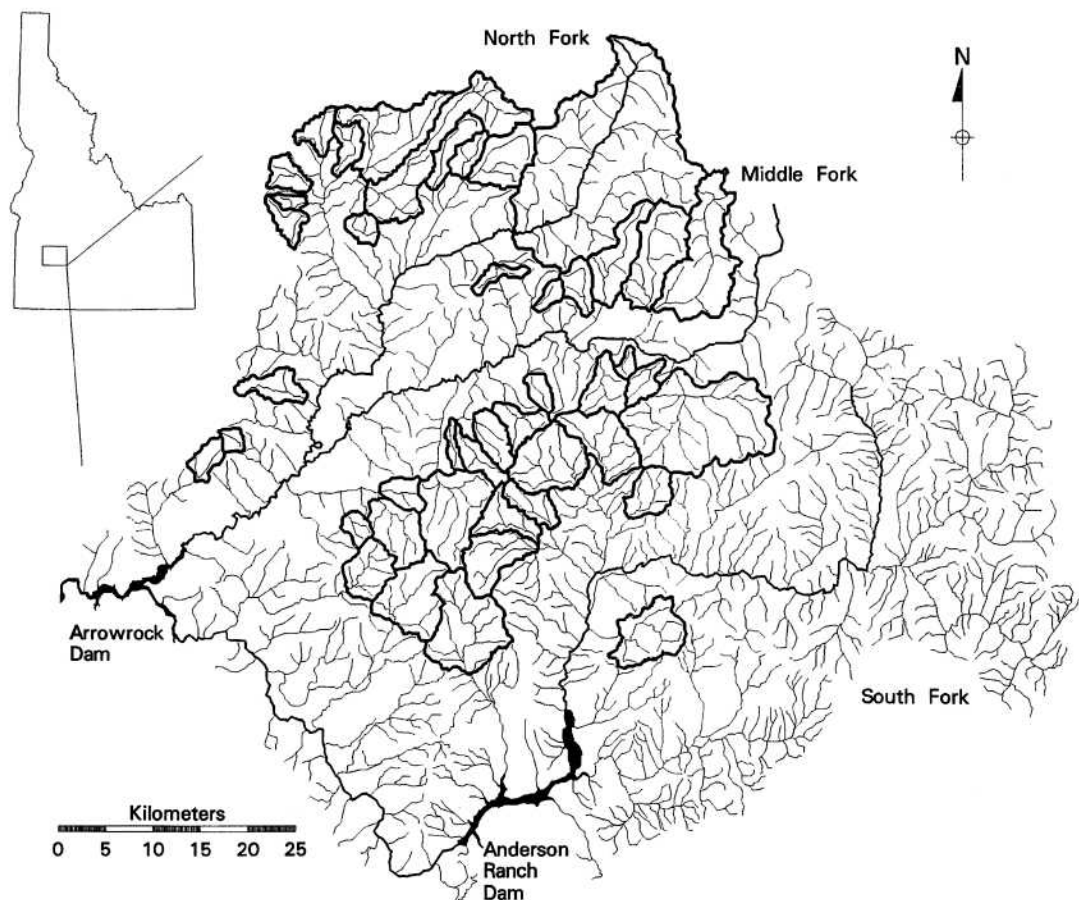


FIGURE 1.—The upper Boise River basin in Idaho. Patches of potential habitat for local populations of bull trout were defined as watershed areas above 1,600 m. Patches larger than 400 ha sampled in this study are outlined.

Dam which is impassable for fish (Figure 1). The South Fork subbasin was further isolated from the North Fork–Middle Fork subbasins by Anderson Ranch Dam, also a barrier to fish, constructed in 1950.

The upper basin covers approximately 5,700 km² and is contained almost wholly within the southern batholith section of the northern Rocky Mountain physiographic province. The geology is dominated by granitic rock of the Idaho Batholith. The elevation of available stream habitat ranges from about 1,000 m to about 2,500 m above sea level. Annual precipitation averages about 40 cm, predominantly as snow. Stream flows are dominated by snowmelt, but summer thunderstorms also occur. Mean annual air temperature at 1,600 m is about 5°C.

In addition to bull trout, native fishes reported from the upper basin include several cyprinids,

rainbow trout *Oncorhynchus mykiss*, sculpins *Cottus* sp., and mountain whitefish *Prosopium williamsoni*. Brook trout *Salvelinus fontinalis* are introduced. Cyprinids and whitefish are restricted to lower elevations of the upper basin, and brook trout have been reported from only four watersheds tributary to the larger subbasins. Rainbow trout and sculpins are widely distributed and have been reported from all streams sampled in earlier work (Idaho Department of Fish and Game, unpublished data).

Bull trout have been reported throughout the basin. Biologists have documented their presence in watersheds tributary to both the highest and lowest reaches of the three subbasins (Idaho Department of Fish and Game, unpublished data). We assume that bull trout have had the opportunity to colonize all of the streams tributary to the basin that are not blocked by impassable barriers.

Both migratory and resident life history forms of bull trout exist in the Boise River basin. In other systems migrant forms rear in tributary streams for several years before moving to a larger river or lake to mature. Resident forms typically remain in tributary streams throughout life (Rieman and McIntyre 1993). Migrant individuals can reach large sizes (>400 mm), whereas residents typically mature at less than 300 mm (Rieman and McIntyre 1993). The life histories have not been described in detail for the Boise River basin, but most local populations appear to be dominated by the resident form, in that mature fish throughout the basin are typically small.

Methods

Patch definition.—To enable inferences to be drawn about processes influencing local populations, patches should be consistent in scale with the habitat defining local populations (Haila et al. 1993). We defined patches for bull trout as the contiguous stream areas believed suitable for spawning or initial rearing. Although seasonal movements may result in mixing fish from separate patches, segregation to the natal environments is likely during spawning. Because spawning salmonids generally home to natal streams and even reaches (Quinn 1993), occupied patches separated by unsuitable habitat likely represent populations with some reproductive isolation. Thus, bull trout originating from a particular patch have a higher probability of mating with bull trout from that patch than with those from other patches.

Because stream temperature has been identified as an important factor influencing local distribution of bull trout (Pratt 1984; Fraley and Shepard 1989; Rieman and McIntyre 1993) and because stream temperature is related to elevation (Meisner 1990; Flebbe 1993), we used occurrence of bull trout to infer the elevation below which stream temperatures are probably unsuitable for sustaining local populations. This elevation formed the downstream boundary of each patch. We summarized unpublished observations of bull trout in various watersheds and supplemented that information with our own preliminary observations. Our observations were limited to streams known to support bull trout. All sampling was by snorkeling or electrofishing at multiple sites from 1,020 m to 2,256 m. Sampling was conducted during low-flow periods from August through October, well after young-of-year bull trout are expected to emerge from the gravel (Fraley and Shepard 1989). Observations used to define patch

boundaries were limited to fish less than 150 mm because larger fish have been observed to move to lower areas on a seasonal basis. We summarized data for 128 sites, each approximately 100 m long, from 13 watersheds within 100 km of the Boise River basin.

Small (<150 mm) bull trout were found at elevations as low as 1,520 m, but the frequency of occurrence increased sharply at about 1,600 m (Figure 2). Therefore, in further sampling we assumed that 1,600 m elevation approximated the lower limits of habitat suitable for spawning and initial rearing of bull trout throughout the Boise River basin. We defined potential habitat patches for bull trout as the areas of contiguous stream above 1,600 m that were not isolated from the larger subbasin by a physical barrier to fish passage (Figure 1). We assumed, then, that bull trout had the opportunity to colonize all of the potential habitat. We could not use stream lines from existing topographic maps to reliably estimate available habitat because many lower-order streams depicted as perennial were actually intermittent or non-existent. We therefore used watershed area above 1,600 m measured from 1:24,000 topographic maps as a simple measure of patch size.

Presence-absence sampling.—Patches were sampled from mid-July through September 1993. We initially hoped to sample all patches that were large enough to support any fish within the North Fork and Middle Fork subbasins. The order of sampling was random, but access to some patches was too difficult for us to complete sampling within our time frame. The sample of patches within the North Fork and Middle Fork was also more heavily weighted to small than medium or large patches. We chose to augment the sample with samples from additional larger patches from the South Fork subbasin. We did not include patches with dry channels or those with streams clearly too small to support fish. We therefore limited our sample and subsequent analyses to patches larger than 400 ha (Figure 1).

To evaluate stream channel characteristics that might influence the presence of bull trout, we also sampled tributary streams within some of the larger patches. We expected stream width, for example, to be correlated with patch size and therefore to confound the analysis. Bozek and Hubert (1992) found that stream size and gradient were important among streams in determining the presence or absence of three species of salmonids. Others have suggested that bull trout distributions may be influenced by stream size (Mullan et al. 1992; C.

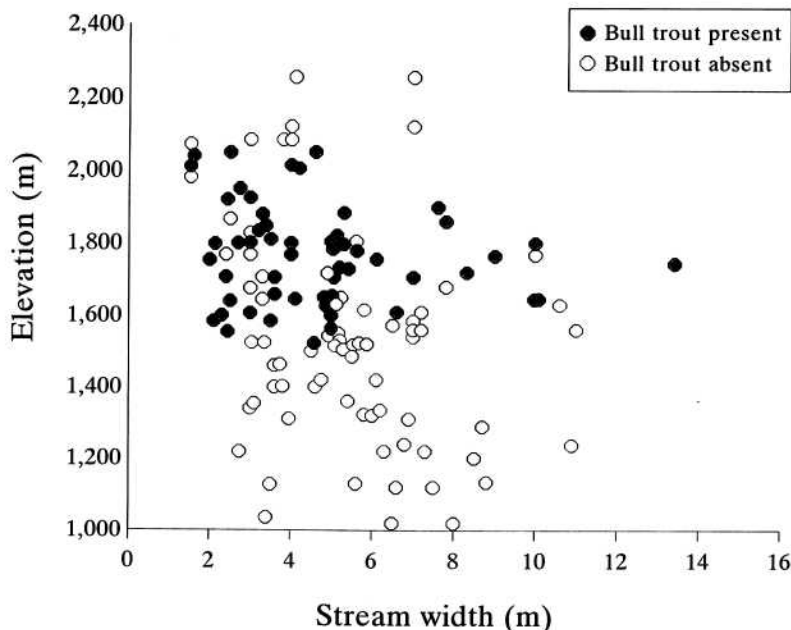


FIGURE 2.—Presence and absence of bull trout less than 150 mm long against stream width and elevation. Data were summarized from unpublished records for streams within 100 km of the Boise River basin, Idaho (S. Adams, University of Idaho, and D. Corley, Boise National Forest, personal communications) and from preliminary work in this study.

Clancy, Montana Department of Fish Wildlife and Parks, unpublished data). Thus, we sampled tributary streams that provided a range of stream sizes and channel gradients within occupied patches.

We chose to minimize sampling effort within patches and streams to maximize the number of patches and streams in the sample. Our objective was to determine the presence or absence of bull trout rather than to make precise estimates of abundance. The basic sampling unit was the main stream within each patch. If bull trout of any size were found in that stream, they were considered present in the patch. If distributions were random and not influenced by patch boundaries or size, the probability of detecting bull trout in larger patches would be higher if effort was in proportion to patch size. To avoid a positive bias in detection of bull trout related to patch size, sampling effort and protocol for detection was the same for each patch regardless of size. We sampled one to three reaches of the main stream in each patch. Each reach was about 0.5 km long and contained five sample sites that were each 30 m long. The first reach was selected near (but above) the 1,600-m patch boundary. We located the sample reaches and sites in what we judged to be the most suitable habitat. The distribution of bull trout within streams has

been associated with cover and hydraulic complexity (Pratt 1984). Whenever possible, we prioritized reaches providing high-quality pools, cover in the form of woody debris or boulder clusters, or other forms of hydraulic complexity. We spaced the five sample sites throughout the reach but favored the best habitats rather than using a strictly random or systematic sampling scheme. Streams within occupied patches were sampled by the same procedure.

In each patch or stream we always sampled five sites in the first reach. If no bull trout were found, we sampled a second reach. A third reach was sampled when no bull trout were found in the second reach. Whenever multiple reaches were sampled, the second and third reaches were located to represent the middle and upper portions of the stream. In some cases, if the stream clearly had become too small to support fish, the second or third reach was not sampled.

Each site was either electrofished or searched by snorkelers. Only one method was used in any stream. Electrofishing crews made a single pass through the site with a backpack electroshocker. Care was taken to fish slowly and extensively through all possible cover. In higher-gradient sections, a handheld drift net was often used to collect

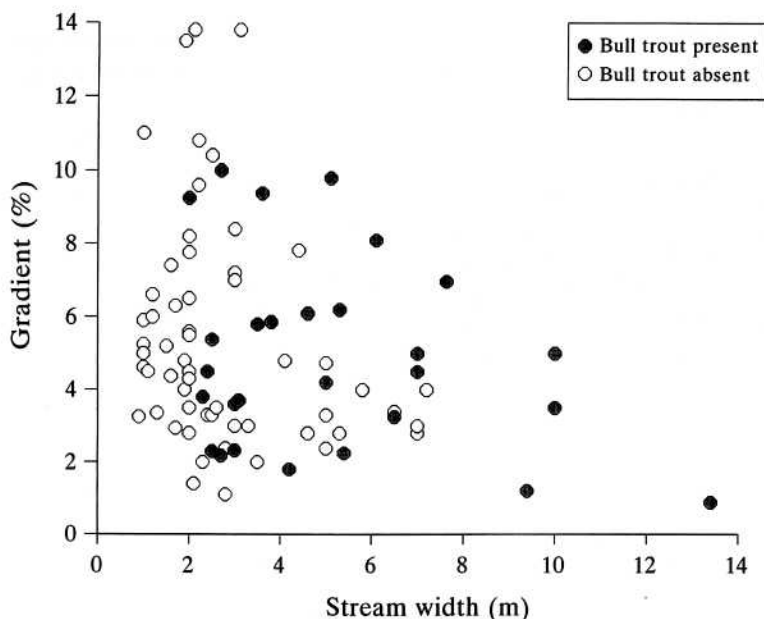


FIGURE 3.—Presence and absence of bull trout against gradient and stream width for stream reaches sampled within the Boise River basin, Idaho. Observations were limited to reaches within occupied patches.

stunned fish difficult to observe because of the turbulence. Daytime snorkeling was used in remote sites where transport of the electroshocker was too difficult. Two snorkelers moved upstream through each reach. Because bull trout seem to prefer complex cover, snorkelers carried underwater lights and carefully examined all undercut banks and cover such as root wads or rock crevasses. Snorkelers routinely moved cobbles to locate concealed fish and took care to examine off-channel pools or stream margins.

Our sampling goal was to provide a reasonable probability of detecting bull trout populations and still allow extensive sampling. If we assume a minimum detection efficiency of 0.25 for each site, a Poisson sampling distribution, and a minimum population of 150 fish in 10 km of stream, the probability of detection should exceed 0.80. Thus, if the expected minimum number of fish detected was $\mu = (150/10,000 \text{ m}) \times 450 \text{ m sampled} \times 0.25$ and the probability of detecting no fish was $P(0) = e^{-\mu}$ (Zar 1984), then $P(1 \text{ or more}) = 0.82$. From existing population work and stable age-structured models, a population of 150 fish would represent an adult population of fewer than 20 to 30 adults (Rieman and McIntyre 1993). We assumed a population of that size or smaller would be at high risk of extinction through demographic stochasticity, Allee effects, or other small population ef-

fects (Gilpin and Soulé 1986). We therefore considered the reduced probability of detection irrelevant. In reality, the probability of detection for our streams was probably higher than estimated because we prioritized likely habitats rather than sampling randomly and because available habitat was often less than 10 km long. Recent sampling work showed that daytime snorkeling may underestimate bull trout abundance in some streams (Bonneau 1994). However, estimates of sampling efficiency with either of our methods in streams comparable to ours consistently exceed our assumed level of 0.25 (R. Thurow, U.S. Forest Service, unpublished data; Bonneau 1994).

At each sample site, we measured wetted channel width and channel gradient with a clinometer. We made visual estimates of the percent surface area in pools, amount of riparian canopy cover, and amount of fine sediment, and we noted habitat-forming features such as woody debris, bedrock, and boulders. We used width and gradient in our statistical analyses but not other habitat features. Because the other habitat features were assessed subjectively rather than measured, and because the limited scope of sampling for those features might not reflect conditions throughout the stream, we did not incorporate those data in the formal analyses. Rather, we used them to flag unusual conditions that might represent seriously degraded

habitat. None of the observed stream reaches were considered unsuitable for bull trout because of consistently poor or unusual habitat features.

Analyses.—We conducted analyses at three scales associated with our sampling: reaches, streams, and patches. Stream reach or channel characteristics are not easily pooled or represented at the patch scale but may still influence the presence or absence of fish in a sample. We conducted the analyses at the finer scales to look for evidence of both channel and patch characteristics that might influence distributions. We included all reaches in a first analysis at the finest scale. We also limited observations to reaches within patches that supported bull trout in a second analysis at the reach scale. Width and gradient were summarized as the mean of the five sites within each reach. We conducted the analysis at the stream scale by including both stream width (mean of the first reach) and patch size as independent variables. Our final analysis was conducted at the patch scale with patch size as the only independent variable.

Because of the binomial nature of the dependent variable, we considered both logistic regression and discriminant function analysis as possible analytic methods. We selected logistic regression for four reasons: this model requires no assumptions regarding normality or covariance structure, its form is consistent with the anticipated incidence function, it provides a probabilistic prediction that can reflect the underlying gradient in the environmental effect, and it is the method most commonly employed for analysis of incidence functions (Adler and Wilson 1985; Taylor 1991; Trexler and Travis 1993). We used the SYSTAT LOGIT module (Steinberg and Colla 1991)¹ for all analyses. We used untransformed and log-transformed [$\log_e(x)$] width, patch size, and gradient data. The transformed data produced better-fitting models and are the only results presented here. We evaluated each of the independent variables through the likelihood ratio test (Trexler and Travis 1993). We fit a hierarchy of models beginning with the full model (all variables and their interactions) proceeding to the simplest models through iterative elimination. We determined the significance ($P \leq 0.05$) of each coefficient with the likelihood-ratio chi-square

TABLE 1.—Results of logistic regression analyses to describe the potential influence of stream width and gradient on the presence of bull trout in sample reaches of streams within the Boise River basin. Analyses were conducted for all reaches and only for reaches within occupied patches.

Model ^a	N	Rho ²	P ^b			
			Model	Coefficients		
All reaches						
W + G + W·G	85	0.216	<0.001	0.237,	0.647,	0.414
W + G	85	0.210	<0.001	<0.001,	0.524	
W + W·G	85	0.214	<0.001	0.003,	0.353	
G + W·G	85	0.202	<0.001	0.060,	<0.001	
W·G	85	0.120	<0.001	0.001		
W	89	0.222	<0.001	<0.001		
G	85	0.004	0.536	0.536		
Reaches within occupied patches only						
W + G + W·G	46	0.076	0.197	0.547,	0.975,	0.406
W + G	46	0.065	0.135	0.059,	0.690	
W + W·G	46	0.070	0.115	0.206,	0.490	
G + W·G	46	0.076	0.096	0.158,	0.046	
W·G	46	0.042	0.107	0.107		
W	46	0.063	0.050	0.050		
G	46	0.001	0.830	0.830		

^a Model includes constant + listed variables; W = $\log_e$ width, G = $\log_e$ gradient.

^b Probability likelihood-ratio chi-square test for each variable is based on elimination from the model. Probabilities are in the same order as in the model statement.

following variable removal from the preceding model (Trexler and Travis 1993). We evaluated each model by the magnitude of rho² and by the likelihood-ratio test against a constant-only model (Steinberg and Colla 1991; Trexler and Travis 1993).

For analyses considering patch size, we used both weighted and unweighted data (Steinberg and Colla 1991). Weights were based on the frequency distribution of area to minimize any bias related to uneven distribution of patch sizes. Weighting made no important difference in model coefficients or tests of significance, so we present unweighted data only.

Results

We sampled 67 streams within 46 patches throughout the basin. We sampled 37 of 51 possible patches in the North Fork and Middle Fork subbasins, and 9 of 37 possible patches in the South Fork. Sampled patches ranged from 425 to 26,600 ha. We observed bull trout in 30 streams and 17 patches. Bull trout were never observed in a tributary stream without also being observed in the mainstem of the associated patch.

We found bull trout in 29 of 48 reaches sampled within the occupied patches. Mean widths of

¹ The use of trade or firm names in this paper is for reader information only and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

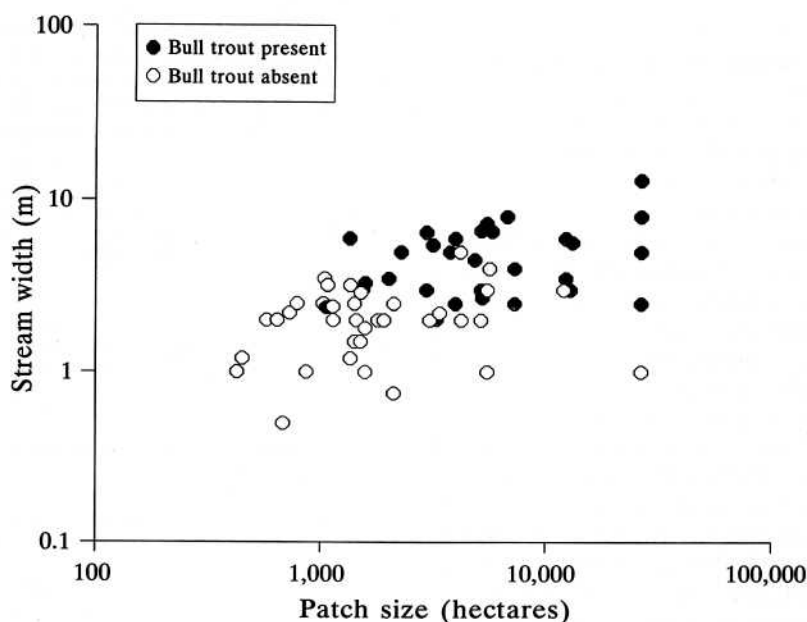


FIGURE 4.—Presence and absence of bull trout against stream width and patch size for streams sampled within the Boise River basin, Idaho, in 1993.

reaches ranged from 1.0 m to about 14 m, and mean gradients ranged from less than 1% to nearly 14% (Figure 3). We found bull trout in the widest reaches we sampled but none in reaches less than 2 m wide. Bull trout previously had been observed in a 1.5-m-wide reach, according to unpublished data we summarized for distribution in relation to elevation (Figure 2). We found bull trout throughout the range of gradients. Gradient was not significant in any of the analyses at the reach scale (Table 1). Width was significant in the simplest

models. The estimated ρ^2 , however, indicated width explained little of the distribution when observations were limited to reaches within occupied patches (Table 1).

At the stream scale, both patch size and stream width appeared to be important (Figure 4). Stream width and patch size were also correlated as we had anticipated. The lack of bull trout in any stream reach less than 2 m wide suggests that very small streams may be unsuitable. Because the incidence function analysis assumes that all patches represent suitable habitat, we analyzed the data set by including only observations for streams 2 m wide and larger. The best models were the simplest ones that incorporated both variables (i.e., $W + A$ or $W \cdot A$) (Table 2). Based on the likelihood-ratio test and ρ^2 , stream width was slightly better at explaining the distribution of bull trout than patch

TABLE 2.—Results of logistic regression analysis to describe potential influence of stream width and patch size (area) on presence of bull trout in streams within the Boise River basin. Analysis was limited to streams larger than 2 m wide.

Model ^a	N	Rho ²	p ^b	
			Model	Coefficients
A + W + A·W	54	0.41	<0.001	0.212, 0.318, 0.465
A + W	54	0.41	<0.001	0.023, 0.001
A + A·W	54	0.40	<0.001	0.284, 0.001
W + A·W	54	0.39	<0.001	0.449, 0.025
A·W	54	0.38	<0.001	<0.001
A	54	0.25	<0.001	<0.001
W	54	0.33	<0.001	<0.001

^a Model includes constant + listed variables; A = $\log_e$ area, W = $\log_e$ width.

^b Probability for likelihood-ratio chi-square test for each variable is based on elimination from the model. Probabilities are in the same order as in the model statement.

TABLE 3.—Results of logistic regression analysis to describe potential influence of patch size (area) on presence of bull trout within the Boise River basin. Analysis was limited to patches with streams larger than 2 m wide.

Model ^a	N	Rho ²	p ^b	
			Model	Coefficient
Area	39	0.237	<0.001	<0.001

^a Model includes constant + area.

^b Probability for likelihood-ratio chi-square test is based on comparison with the constant-only model.

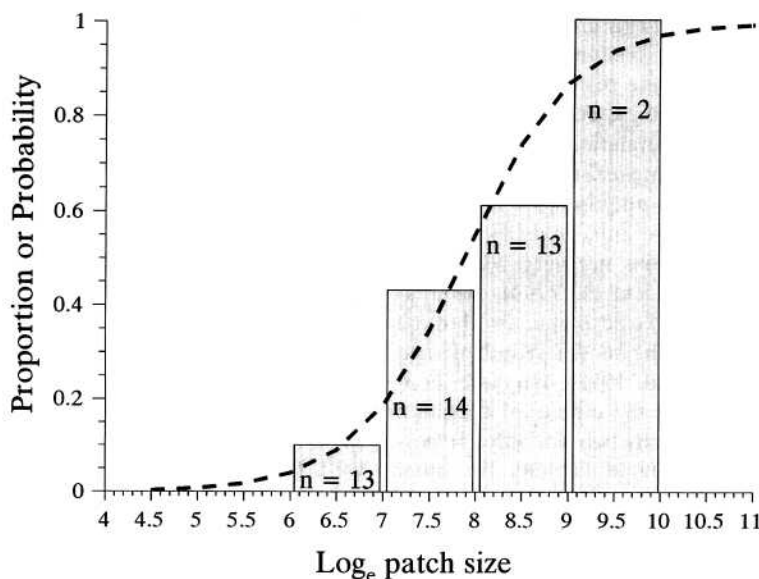


FIGURE 5.—Observed frequency (proportion) of occurrence (histogram) and probability of occurrence predicted from the logistic regression model (dashed lines) for bull trout against patch size in the Boise River basin, Idaho. The centers of the histogram bars are on the midpoints of the bins used in the frequency distribution. Analyses are from observations limited to streams 2 m wide and larger.

size, but the best models included both variables. Collinearity between patch size and stream width makes it impossible to distinguish the individual effects (Trexler and Travis 1993).

At the patch scale of analysis, we considered only patch size as an independent variable and limited the analysis to patches with streams 2 m wide and larger. Patch size was highly significant (Table 3). The logistic regression model and the empirical frequency distribution suggest that the probability of observing bull trout exceeded 0.80 at the largest patch sizes, was about 0.50 for patches between 2,000 and 3,000 ha, and was less than 0.10 for patches less than 1,000 ha (Figure 5).

Discussion

Our findings support the hypothesis that patch size influences the occurrence of bull trout. Hanski (1991, 1992, 1994) and others (Gilpin and Diamond 1981; Adler and Wilson 1985; Taylor 1991; Thomas et al. 1992) interpreted similar results for a variety of terrestrial species as evidence of populations sensitive to local extinction through random processes. Two mechanisms are relevant. First, smaller patches are likely to support smaller local populations. Population size has been linked to the risks of extinction of animals through environmental and demographic variation (Leigh 1981; Gilpin and Soulé 1986; Simberloff 1988;

Boyce 1992). Second, smaller patches are likely to support fewer or less diverse habitats. A lack of spatial diversity or complexity in habitat could result in lower phenotypic diversity among individuals and a lack of refuges in the environment, leading to greater temporal variation in populations (den Boer 1968; Poff and Ward 1990). In both cases, smaller patch size leads to higher risk of extinction. Under this scenario, the probability of finding populations across the landscape reflects the rate of local extinctions balanced against recolonization among populations.

Local bull trout populations as we have defined them in the Boise River basin probably are not completely isolated. Recent work in Montana found little genetic differentiation among bull trout populations within subbasins similar in size to those in the Boise, but significant differentiation among subbasins (R. Leary, University of Montana, unpublished data). Those data suggest that dispersal among populations may be important at this scale. We thus anticipate that proximity to an occupied patch would also influence the probability of occurrence. Such measures of isolation have been useful predictive variables in similar analyses with other species (Sjögren 1991; Thomas et al. 1992; Hanski 1994). Such analyses would be useful here but will be possible only with a complete survey of the basin to measure interpatch distances.

Although our observations are consistent with theory, they are not proof that metapopulation processes are important in the distribution and persistence of bull trout. The pattern associated with area might only reflect correlation with other more important habitat characteristics (Simberloff 1988). A fundamental assumption in this analysis is that habitat patches are either equally suitable or that habitat quality does not vary with patch size (Hanski 1992; Haila et al. 1993). Alternatively, habitat area could be accounted for through additional variables in the model (Kindvall and Ahlen 1992; Thomas et al. 1992). We either controlled for or discounted the effects of elevation (temperature) and gradient, two variables important in determining suitable habitats for other salmonids (Bozek and Hubert 1992). It is still possible, however, that bull trout could be sensitive to differences among streams that were not accounted for by the limited scope of our study. Our data show that stream width covaries with patch size. Small patches exist only as small streams, and large streams are found only in large patches (though small streams exist throughout large patches). The association with area might reflect a simple preference for larger streams or other channel characteristics that are correlated with stream width (e.g., Lanka et al. 1987).

We cannot resolve the stream size (habitat preference or quality?) versus patch size (stochastic?) effects. The relative importance of each variable cannot be determined because of their collinearity (Trexler and Travis 1993). Both appear to be important (the best models incorporate both variables), but we suspect patch size is the dominant influence. Although we never found bull trout in channels less than 2 m wide, stream size explained little of the distribution of bull trout among reaches within occupied patches (Table 1). Other work with bull trout (Platts 1979) and other salmonids including brook trout (Lanka et al. 1987; Kozel and Hubert 1989; Bozek and Hubert 1992) showed that fish abundance or apparent habitat quality declined rather than increased with stream size. Bull trout do use small streams (down to 2 m) but apparently at a lower frequency than larger streams. We suggest that the presence of bull trout in such streams may be influenced by habitat preference, but their persistence depends on the demographic support or displacement of individuals from adjacent larger and more stable systems.

Even if we are wrong, patch size will inevitably be an important component of bull trout habitat if suitable channel characteristics are inherent in wa-

tershed area. In this case both the availability of larger streams and the probability of encountering the right collection of critical channel characteristics increases with watershed area. The mechanisms influencing distribution and the implications for population viability, however, are very different from those associated with the patch size-extinction hypothesis.

Further work on spatially influenced processes and habitat preferences relevant to bull trout and other salmonids is needed. If the persistence of local populations is sensitive to stochastic events, conservation of threatened stocks implies more than just conservation of remaining habitat. The scale and geometry of that habitat are critical as well. For example, our work suggests that habitat conservation would be most beneficial in larger watersheds, and that conservation of smaller systems would be irrelevant unless they are linked to a larger system through active dispersal (Harrison 1991). If we fail to recognize important area effects, we may also risk an accelerated loss of populations. Further isolation of populations in shrinking patches of suitable habitat caused by human disturbance could well lead to increasing rates of extinction not proportional to the simple loss of habitat area. With a growing emphasis on species conservation and ecosystem management, recognition of the appropriate habitat mosaics and connections (Frissell et al. 1993) may well be crucial.

Our results suggest incidence functions can provide useful information. Further work could incorporate additional spatial considerations such as isolation (e.g., Sjögren 1991; Thomas et al. 1992; Hanski 1994) or more specific habitat characteristics (Taylor 1991). Recognition of potential spatial effects in sampling design might also improve the understanding or recognition of local habitat suitability.

There is an extensive body of work on habitat use and requirements for salmonids (e.g., Salo and Cundy 1987; Fausch et al. 1988; Marcus et al. 1990; Meehan 1991). Most of the work has focused on relationships with channel structure and spatial scales characteristic of stream reaches and habitat or microhabitat units. Often these models lack the generality for application beyond the stream or watershed in which they were developed (Fausch et al. 1988; Hawkins et al. 1993). The larger-scale spatial geometry of available habitat may be important for species like bull trout.

Acknowledgments

Several people, including D. Lee, R. Thurow, K. Pratt, T. McMahon, C. Frissell, T. Hillman, J.

Fraley, K. Halupka, and an anonymous reviewer, provided helpful comments on earlier drafts of the manuscript. D. Myers, J. Bogesvang, C. Rabe, B. Hart, and D. Shepard assisted with collection and summary of the data.

References

- Adler, G. H., and M. L. Wilson. 1985. Small mammals on Massachusetts islands: the use of probability functions in clarifying biogeographic relationships. *Oecologia* 66:178–186.
- Bonneau, J. L. 1994. Seasonal habitat use and changes in distribution of juvenile bull trout and cutthroat trout in small, high gradient streams. Master's thesis. University of Idaho, Moscow.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–506.
- Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70: 886–890.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Cutler, A. 1990. Nested faunas and extinction in fragmented habitats. *Conservation Biology* 5:496–505.
- den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165–194.
- Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. U.S. Forest Service General Technical Report PNW-213.
- Flebbe, P. A. 1993. Comment on Meisner (1990): effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 50:883–884.
- Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake river system, Montana. *Northwest Science* 63:133–143.
- Frissell, C. A., W. J. Liss, and D. Bales. 1993. An integrated, biophysical strategy for ecological restoration of large watersheds. Pages 449–456 in D. Potts, editor. *Proceedings of the symposium on changing roles in water resources management and policy*. American Water Resources Association, Herndon, Virginia.
- Gilpin, M. E., and J. M. Diamond. 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. *Proceedings of the National Academy of Sciences of the USA* 78:392–396.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 13–34 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, Massachusetts.
- Haila, Y., I. K. Hanski, and S. Raivio. 1993. Turnover of breeding birds in small forest fragments: the "sampling" colonization hypothesis corroborated. *Ecology* 74:714–725.
- Hanski, I. 1991. Single species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society* 42:17–38.
- Hanski, I. 1992. Inferences from ecological incidence functions. *American Naturalist* 139:657–662.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* 9:131–135.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42:73–88.
- Hawkins, C., and eleven coauthors. 1993. A hierarchical approach to classify stream habitat features. *Fisheries (Bethesda)* 18(6):3–12.
- Howell, P. J., and D. V. Buchanan, editors. 1992. *Proceedings of the Gearhart Mountain bull trout workshop*. American Fisheries Society, Oregon Chapter, Corvallis.
- Kindvall, O., and I. Ahlen. 1992. Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor*, Philippi (*Orthoptera: Tettigoniidae*). *Conservation Biology* 6:520–529.
- Kozel, S. J., and W. A. Hubert. 1989. Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. *Journal of Freshwater Ecology* 5:113–122.
- Lanka, R. P., W. A. Hubert, and T. A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. *Transactions of the American Fisheries Society* 116:21–28.
- Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. *Conservation Biology* 7:856–865.
- Leigh, E. D. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90:213–239.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Marcus, M. D., M. K. Young, L. E. Noel, and B. A. Mullan. 1990. Salmonid-habitat relationships in the western United States. U.S. Forest Service General Technical Report RM-188.
- Meehan, W. R., editor. 1991. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication 19.
- Meisner, J. D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1065–1070.
- Mullan, J. W., K. Williams, G. Rhodus, T. Hillman, and J. McIntyre. 1992. Production and habitat of salmo-

- nids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service Monograph 1.
- Nehlsen, W., J. A. Lichatowich, and J. E. Williams. 1992. Pacific salmon and the search for sustainability. *Renewable Resources Journal* 10:20-26.
- Northcote, R. G. 1992. Migration and residency in stream salmonids—some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research* 67:5-17.
- Osborne, L. L., and M. J. Wiley. 1992. Influences of tributary spatial position on the structure of warm-water fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 49:671-681.
- Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. *Fisheries* (Bethesda) 4(2):5-9.
- Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.
- Pratt, K. L. 1984. Habitat use and species interactions of juvenile cutthroat (*Salmo clarki lewisi*) and bull-trout (*Salvelinus confluentus*) in the upper Flathead River basin. Master's thesis. University of Idaho, Moscow.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. *American Naturalist* 132:652-661.
- Quinn, T. P. 1993. A review of homing and straying of wild and hatchery produced salmon. *Fisheries Research* 18:29-44.
- Reeves, G. H., and J. R. Sedell. 1992. An ecosystem approach to the conservation and management of freshwater habitat for anadromous salmonids in the Pacific Northwest. *Transactions of the North American Wildlife and Natural Resources Conference* 57: 408-415.
- Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.
- Salo, E. O., and T. W. Cundy, editors. 1987. Streamside management: forestry and fishery interactions. University of Washington Institute of Forest Resources, Contribution 57, Seattle.
- Saunders, H. R., R. J. Hobbs, and C. R. Margules. 1990. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- Schlosser, J. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- Sheldon, A. L. 1988. Conservation of stream fishes: patterns of diversity, rarity and risk. *Conservation Biology* 2:149-156.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19: 473-511.
- Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42:135-147.
- Steinberg, D., and P. Colla. 1991. LOGIT: a supplementary module for SYSTAT. SYSTAT, Evanston, Illinois.
- Taylor, B. 1991. Investigating species incidence over habitat fragments of different areas—a look at error estimation. *Biological Journal of the Linnean Society* 42:177-191.
- Thomas, C. D., J. A. Thomas, and M. S. Warren. 1992. Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* 92:563-567.
- Trexler, J. C., and J. Travis. 1993. Nontraditional regression analysis. *Ecology* 74:1629-1637.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

Received May 13, 1994
Accepted December 20, 1994