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Spatial and Temporal Variability in Bull Trout Redd Counts

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Abstract.—We analyzed redd counts of bull trout *Salvelinus confluentus* in northern Idaho and northwestern Montana and found evidence of stronger correlation in the number and year-to-year change in number of redds between streams that were closer together than between streams that were far apart. The pattern was weak, however, indicating that spatial heterogeneity in habitat, in population demographics, or in life history at a local scale is important to stability of regional populations. The weak correlations also indicate that monitoring only a few index populations may not clearly represent the dynamics of larger regional populations. If synchrony is weak and not masked by sampling error, conservation management should favor the maintenance of high-quality habitats and strong local populations in proximity to each other to facilitate dispersal and demographic support. Common declining trends among all streams within a single lake basin show that even well-dispersed regional populations face important risks. Conservation management of species like bull trout must maintain populations at both local and regional scales.

Bull trout *Salvelinus confluentus* are a focus of growing concern among fisheries managers in the Pacific Northwest (Howell and Buchanan 1992; Rieman and McIntyre 1993). Bull trout are presently listed as a category 1 species under the Endangered Species Act (Office of the Federal Register [June 10, 1994]:30254); formal listing is deemed warranted but precluded because of other priorities. Local extinctions appear to be widespread (Howell and Buchanan 1992), and distributions are typically patchy, fragmented by habitat disruption, by the natural influence of temperature and elevation (Rieman and McIntyre 1995), and by the use of tributary streams rather than mainstem rivers or lakes as spawning and rearing sites. Although migratory bull trout share common lake or river environments throughout much of life, homing to natal streams is probably an important isolating mechanism. Such isolation creates the potential for local adaptation and some distinction among local populations (see Ricker 1972 and Quinn 1993 for evidence with other salmonids) associated with habitat patches or tributary watersheds. Preliminary analyses based on observations of temporal variability and patterns of occurrence in fragmented habitats suggest that local populations of bull trout may face important risks of extinction through both demographic and random processes (Rieman and McIntyre 1993, 1995). Persistence at both local and regional scales may be influenced by the distribution, connection, and interaction among local populations, as well as the conditions in the local environments (Rieman and McIntyre 1993).

Understanding the dynamics of populations at larger scales may be important to the conservation management of species like bull trout. Rieman and McIntyre (1995), for example, found evidence that the occurrence of bull trout was associated with the amount or size of watersheds available for spawning and initial rearing. Those data suggest that there may be a minimum amount of suitable habitat necessary to support persistent populations. Because available habitat may be fragmented naturally (Rieman and McIntyre 1995) or by habitat loss, it may not be possible to conserve large amounts of habitat in contiguous waters. Managers may be left with a collection of habitat "patches" spread across the landscape. Should the remaining patches be close together or far apart? Does the spatial geometry of patches contribute to the stability of regional populations, or because bull trout from different streams often share a common river or lake environment at some point in life, do fish associated with patchy spawning and rearing areas still fluctuate as a single large population?

The temporal and spatial variability among local populations of many species may strongly influence regional stability and persistence. Heterogeneity among habitats or in phenotypic characteristics can lead to asynchrony among populations responding to environmentally related disturbance (den Boer 1968). Because the multiple populations are less likely to go extinct simultaneously, maintenance of that heterogeneity can tend to stabilize the larger regional population and minimize the risks of regional extinction (den Boer 1968; Simberloff 1988).

Metapopulation theory draws heavily on the

idea of spatial heterogeneity and the existence of local populations in fragmented or patchy environments (Simberloff 1988; Hanski and Gilpin 1991; Hanski 1991; Dunning et al. 1992). In the most restricted view, metapopulations are seen as a collection of local populations in a fragile balance between extinction and refounding through dispersal (Harrison 1993). The risk of regional extinction is reduced if the risk of simultaneous extinctions among local populations is small; that is, the local populations behave independently. Regional persistence may depend strongly on spatial geometry of available habitat and the tradeoff between the correlation in local population dynamics and the effectiveness of dispersal among the populations (Hanski 1989, 1991; Harrison and Quinn 1989; Hanski and Gilpin 1991; Hansson 1991; Dunning et al. 1992). In less restrictive views, some local populations are resistent to extinction and serve as "sources" or "mainlands" that support surrounding populations (Dunning et al. 1992; Harrison 1993; Bowers 1994). In such cases spatial diversity might not be critical to regional persistence (Harrison 1993), but could still contribute to stability of the larger system.

Conservation biologists have embraced metapopulation concepts (Hanski and Gilpin 1991; Doak and Mills 1994). Issues of spatial geometry are clearly viewed as important in conservation and restoration biology (Bowers 1994; and see Sedell et al. 1990; Moyle and Sato 1991; Reeves and Sedell 1992; Frissell et al. 1993; Rieman and McIntyre 1993). Despite the theoretical and applied emphasis, there are few data to judge the relative importance of spatial patterns or metapopulation dynamics for most species (Karieva 1990; Harrison 1993; Murdoch 1994).

Estimation of the number of redds has been important in monitoring abundance and trends in salmonid populations (Pratt 1985; Konkel and McIntyre 1987; Weaver 1992). Redd counts in bull trout spawning streams in Montana and Idaho provide an index of the number of reproducing adults over a wide geographic region incorporating several regional and many local populations. We used those data to determine whether correlation in adult number among local populations is influenced by the distance between populations and by common lake or river environments shared at some point in the life history.

Bull Trout Life History and Redd Counts: Background

Populations of migratory bull trout are associated with large river and lake systems throughout the western United States and Canada. The "lacustrine" or "adfluvial" form is associated with lakes and the "riverine" or "fluvial" form with large river systems. There are no known examples of both migratory forms occurring in sympatry. Bull trout typically spawn from August through October in second- to fourth-order tributary streams. The adfluvial juveniles rear for 1–3 years before migrating to the lake to mature at 5–7 years of age (Bjornn 1957; Fraley and Shepard 1989; Pratt 1992). Once mature, adults may migrate and spawn in multiple years (Block 1955; Fraley and Shepard 1989; Pratt 1992), but postspawning mortality, longevity, and repeat-spawning frequency are not well known.

Bull trout populations that support noted fisheries for large adfluvial fish exist in the Flathead, Swan, and Pend Oreille lakes in the Upper Columbia River basin in Idaho and Montana (Figure 1). Historically, fish could have moved among all of the lakes and may have been part of a large, regional metapopulation. Genetic differentiation is apparent among fish within the Flathead Lake basin, (R. Leary and F. Allendorf, University of Montana, personal communications), indicating some restriction in gene flow among populations in individual streams. At present, downstream movement is possible but upstream movement among lakes is blocked by impassable dams. Spawning migrations still occur throughout the basins associated with each lake. The adults in these populations are typically 400–600 mm in total length (Pratt 1992) and construct large, easily visible redds.

For up to 16 years, biologists in Montana and Idaho have monitored annual spawning escapements by counting redds of migratory bull trout in streams within two subbasins of the Flathead River basin, within the Swan River basin, and within Pend Oreille Lake basin (Figure 1). The data thus represent trends in populations structured at three scales; among 3 lakes, among 4 basins or subbasins, and among 18 streams.

Redd surveys were typically conducted by two people walking a stream in September and October. Multiple surveys have been used to identify the duration of the spawning period and to select survey times that produce estimates of the complete spawning population (Pratt 1985; Weaver 1991). Identical sections of streams were surveyed in most years, and many streams were surveyed from an upstream migration barrier, such as a waterfall, to the mouth of the stream (Pratt 1985; Weaver 1992). Basinwide surveys were used to

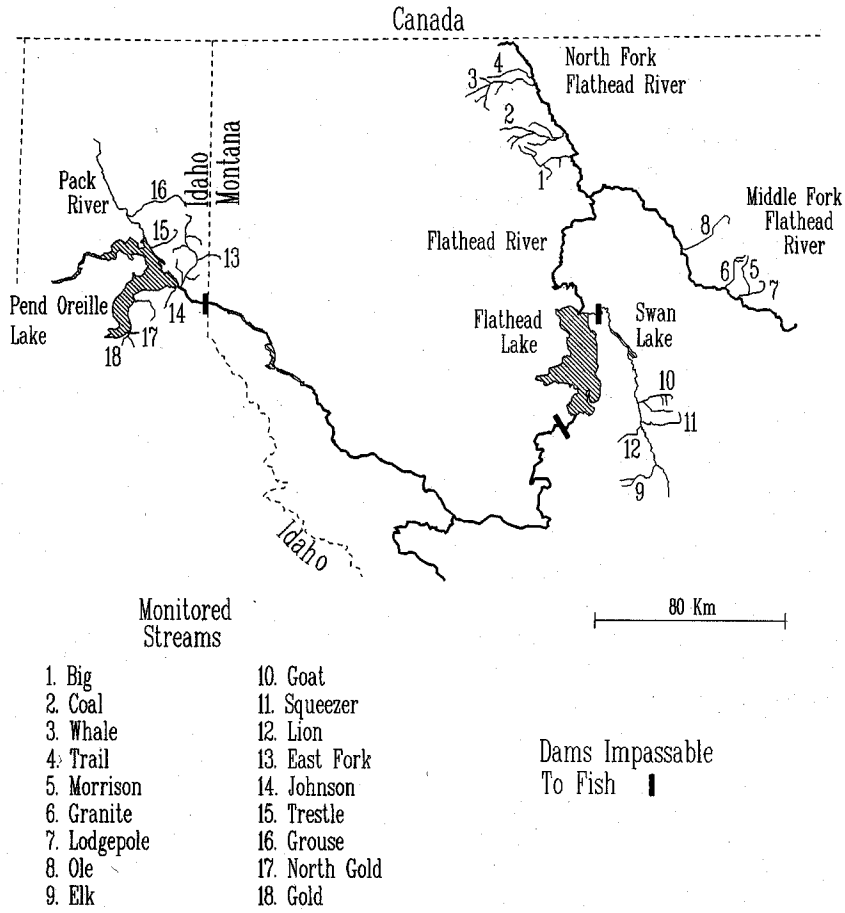

FIGURE 1.—Streams where bull trout redds were counted in northern Idaho and northwestern Montana.

select streams that represent the largest or most consistent populations for the extended monitoring. In the early years of sampling in Montana, counts in some streams were considered incomplete relative to those made in later years (T. Weaver, Montana Department of Fish Wildlife and Parks, personal communication) and were not considered in the analyses.

Methods

Correlation Patterns

We looked for spatially influenced correlations in the redd count data by relating correlation coefficients to the distance between stream pairs and by a principal components analysis (PCA) (Dunteman 1989). A positive association in redd count between two streams could result from common interannual variation or from common trends in abundance through time. Both could be important, but the inferences regarding factors influencing the populations and the implications to managers might be very different. We conducted our analysis with raw redd counts and with data that was transformed in an attempt to remove trends or serial correlation. We used the instantaneous rate of change in redd numbers between 2 years as a transformation. The annual transitions were calculated as $\log_e (N_i/N_{i-1})$, where N_i is the redd count in year i. We used the instantaneous rate of change because it is used as a measure of temporal variability in population viability analyses (e.g., Dennis et al. 1991; Foley 1994), because the variance of the instantaneous rate provides a relative measure of variation independent of population size making it useful for comparison among populations, and because it should minimize potential bias through autocorrelation that results from time trends or serial correlation. We found no serial correlation in the first- through third-order autocorrelations of the transformed data (higher-order

autocorrelations were not practical because of the limited time series available) and no significant correlations of the transformed observations against year.

We used Spearman rank correlation coefficients (Zar 1984) with pairwise deletion (Wilkinson 1990) to detect patterns of correlation associated with distance. We hypothesized that populations responding to common environmental influences should be evident in strong correlations between streams that are closer together. We limited the correlation analyses to data sets with more than 10 observations. We related the correlation coefficients to straight-line geographic distance between stream mouths for all possible pairs of streams and used simple linear regression to test for significance in the slope. We also summarized the frequency distributions of correlation coefficients for three classes of distance (<80 km, 80–160 km, >160 km) between streams. We compared each of the three with a distribution generated by repeatedly and independently randomizing the order of observations for each stream and recalculating the correlation matrix. The procedure was repeated until we generated more than 1,200 pairs of observations and a distribution of correlation coefficients with no inherent association among streams. We used the Kolmogorov–Smirnov test for differences (Zar 1984) between the observed and randomized distributions.

We used the PCA to look for associations within each of the four river–lake basins and the three lakes. Because the method is useful for identifying groups of variables varying with similar patterns, we reasoned it could be useful for clarifying any underlying structure influencing the temporal variability in these bull trout populations (Dunteman 1989). We used pairwise deletion (Wilkinson 1990) to construct the matrices and conducted the analysis on the correlation matrix (Dunteman 1989). We retained only the first two principal components (PC1 and PC2) with eigenvalues larger than one and looked for similar strong (>0.5) loadings among streams for evidence of patterns associated with each lake or river basin. We hypothesized that if events within the lakes or river basins were the important determinants of annual variability or trends in redd number, then component loadings should be similarly high and of common sign among all streams in that basin, regardless of geographic proximity. To examine possible environmental factors influencing patterns among streams, we also correlated annual discharge among four rivers, representing each of the four basins–subbasins. Discharge data were obtained for the Swan River, North Fork Flathead River, Middle Fork Flathead River, and the Pack River (to represent the Pend Oreille Lake Basin; Figure 1) through the automated data processing system of the National Water Information System and the U.S. Geological Survey in Boise, Idaho.

TABLE 1.—Summary of bull trout redd counts and transformed redd counts for 18 streams in the Flathead River, Swan River, and Pend Oreille Lake basins; coefficient of variation (CV) = SD/mean.

Stream	Years of record	Mean redd count[a]	CV	SD (transformed[b])	Rank correlation against year
North Fork Flathead River basin					
Big	16	15	0.61	0.86	−0.05
Coal	16	28	0.70	0.72	−0.51
Whale	16	79	0.75	0.72	−0.24
Trail	14	41	0.61	0.49	−0.67
Middle Fork Flathead River basin					
Morrison	14	42	0.61	0.61	−0.81
Granite	14	24	0.42	0.47	−0.44
Lodgepole	16	17	0.61	0.57	−0.58
Ole	15	24	0.58	0.55	−0.38
Swan River basin					
Elk	13	106	0.54	0.69	0.63
Goat	13	37	0.39	0.52	0.11
Squeezer	13	55	0.58	1.02	0.63
Lion	13	67	0.51	0.54	0.70
Pend Oreille Lake basin					
East Fork	11	42	0.97	1.52	−0.28
Johnson	12	16	0.71	1.03	−0.23
Trestle	12	234	0.23	0.39	−0.12
Grouse	12	26	1.08	1.49	−0.21
North Gold	12	29	0.41	0.83	0.11
Gold	12	105	0.25	0.30	−0.01

[a] Geometric mean.
[b] Standard deviation of instantaneous rate of change between two sequential years was used rather than CV because the transformation is independent of mean redd number.

Results

Redd count data were available for 18 streams with time series of more than 10 years. The relative variation in both data sets showed a three- to fourfold range among streams (Table 1). In each basin the relative importance of streams was similar each year through the period of record, often with a single stream strongly dominating the counts (Figure 2). There were common weak or strong years among some streams (particularly within the Swan River and Pend Oreille Lake basins), but there was no occasion where all streams within a basin showed a common response in redd number. Redd counts for all streams in the Flathead River basins

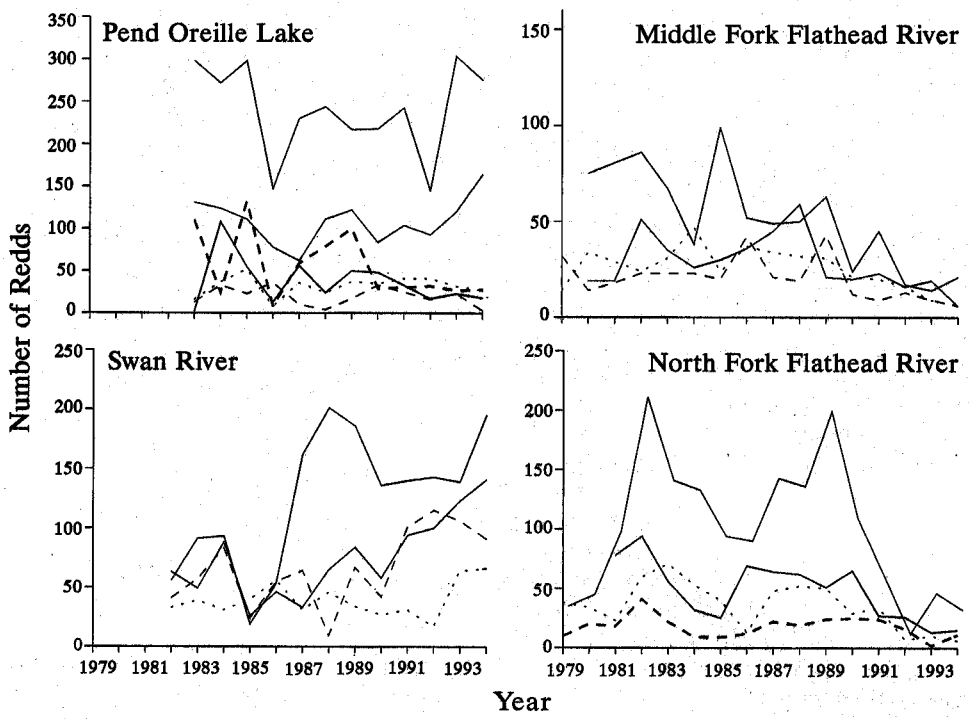

FIGURE 2.—Number of bull trout redds counted each year in streams of the North Fork Flathead River, Middle Fork Flathead River, Swan River, and Pend Oreille Lake basins. Each line represents counts from a single stream within the basin.

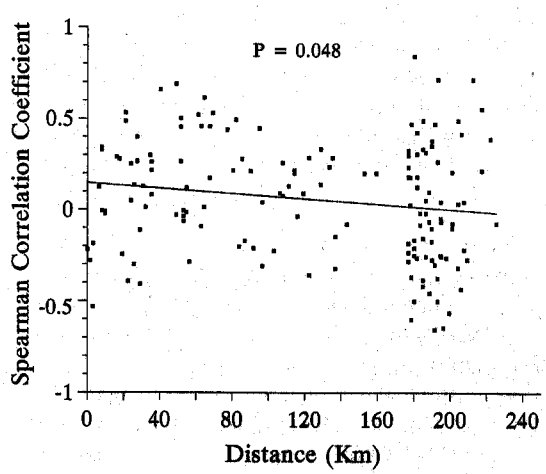

FIGURE 3.—Relationship of Spearman rank correlation coefficients for transformed bull trout redd counts and geographic distance between all possible pairs of streams. The fitted regression line and probability of slope = 0 are shown.

and five of the six streams in the Pend Oreille Basin were negatively correlated with year (Table 1).

The correlation analyses with transformed and untransformed redd counts produced virtually identical results. Therefore we present only the transformed results here. The association between distance and the correlation coefficients was weak ($r = 0.16$), but the negative regression coefficient was significant (Figure 3). A pattern was also evident in the frequency distributions of correlation coefficients with distance. The distributions for stream pairs less than 80 km apart and pairs between 80 and 160 km were significantly different from the distributions for pairs greater than 160 km apart or from the distribution of the randomized observations (Figure 4). In both cases our results indicate stronger positive correlations between closer streams.

The PCA produced different results for the transformed and the raw redd counts. The analysis with transformed redd counts produced high loadings of consistent sign among several streams within basins but never among all streams (Table 2). The PCA did not show any obvious structure

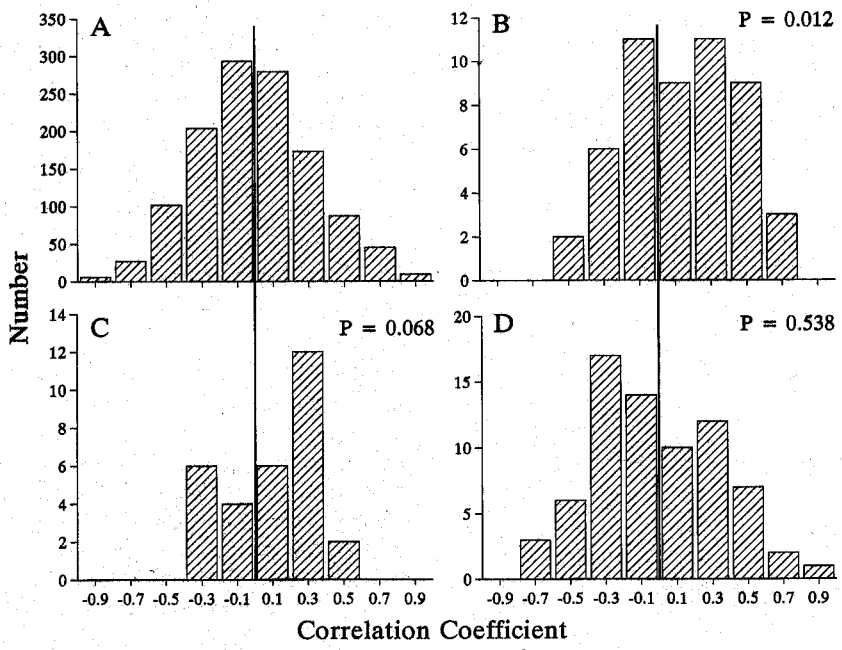

FIGURE 4.—Distribution of Spearman rank correlation coefficients for transformed bull trout redd counts (**A**) between all possible pairs of streams where the order of counts was randomized, and for pairs of streams separated (**B**) by less than 80km, (**C**) by 80–160 km, and (**D**) by more than 160 km. Probabilities for the Kolmogorov–Smirnov test for differences between each distribution and the random distribution are shown. Numbers on the *x*-axis represent the midpoints of the bins. The vertical line representing zero is shown to aid interpretation of the distributions.

in the transformed data associated with the basins. The PCA with the raw redd counts produced a strong pattern of association for streams within the two Flathead River basins. All of the streams supporting bull trout that share Flathead Lake as a common environment showed strong loadings of common sign on the latent variable represented in PC1 (Table 2).

We found strong correlations in annual discharge among the three Montana rivers (Flathead and Swan basins). We found little correlation between the Pack River (representing the Pend Oreille basin) and any of the other three rivers (Table 3).

Discussion

We found evidence of spatially influenced correlation in the number of bull trout redds and, presumably, in the abundance of spawning fish. Spatially influenced patterns in ecological characteristics are generally anticipated (Hanski 1989, 1991; Legendre 1993), and strong patterns of correlation in abundance related to distance have been documented for some taxa (Hanski 1991; Thomas 1991). Such patterns, however, are not well documented in salmonids. Milner et al. (1993) found correlation in abundance of trout among reaches within streams and among adjacent streams, but little association among streams throughout larger catchments. We similarly found correlation in interannual variation more likely among bull trout populations close to each other than among those far apart, but the patterns were not strong or consistent. The common trend for populations sharing Flathead Lake as a rearing environment suggest that both the temporal and spatial scale of analysis are important.

The magnitude and scale of environmental disturbance that influence critical life stages are likely to influence the patterns in temporal variation. We suspect that stream discharge and the frequency and timing of both low and high flows are important to interannual variation in reproductive success and early survival of bull trout. Weaver (1991) believed that low flows and dry channel segments blocked spawning movements of bull trout in some Flathead Basin streams, which lead to weak year-classes. High flows and bedload scour during the winter period of incubation are also known to influence early survival in other fall-spawning fishes

TABLE 2.—Principal component (PC) loadings for bull trout redd counts among 18 streams in the Flathead River, Swan River, and Pend Oreille Lake basins. Analyses were conducted on both transformed and raw counts; eigenvalues are given in parentheses. Loadings greater than 0.50 are indicated by an asterisk to help illustrate any pattern common among river and lake basins.

	Transformed redd counts		Raw redd counts	
Stream	PC1 (5.01)	PC2 (2.84)	PC1 (6.44)	PC2 (2.86)
North Fork Flathead River basin				
Big	−0.231	−0.759*	0.603*	−0.098
Coal	0.777*	0.100	0.790*	0.419
Whale	0.424	0.577*	0.829*	0.159
Trail	−0.670*	−0.273	0.786*	−0.408
Middle Fork Flathead River basin				
Morrison	0.588*	−0.257	0.783*	0.367
Granite	−0.534*	−0.122	0.601*	−0.131
Lodgepole	−0.467	0.278	0.571*	−0.272
Ole	0.279	0.252	0.771*	0.006
Swan River basin				
Elk	−0.377	0.124	−0.416	0.108
Goat	0.263	0.644*	−0.389	0.243
Squeezer	−0.372	0.249	−0.777*	−0.190
Lion	−0.449	0.528*	−0.859*	0.126
Pend Oreille Lake basin				
East Fork	0.858*	−0.444	0.566*	0.693*
Johnson	−0.239	0.642*	0.093	−0.543*
Trestle	0.931*	0.274	−0.072	0.868*
Grouse	0.229	0.260	0.248	0.057
North Gold	0.649*	−0.247	−0.114	0.305
Gold	0.354	0.187	−0.420	0.713*
Proportion of total variance explained				
	0.28	0.16	0.36	0.16

TABLE 3.—Matrix of Spearman rank correlation coefficients of mean annual flow for the Middle Fork Flathead, North Fork Flathead, Swan, and Pack rivers in western Montana and northern Idaho. The sample size is shown in parentheses.

River	Swan	Middle Fork Flathead	North Fork Flathead
Middle Fork Flathead	0.83 (21)		
North Fork Flathead	0.75 (21)	0.88 (21)	
Pack	0.03 (13)	−0.08 (13)	−0.07 (13)

(Wickett 1958; Seegrist and Gard 1972). Bedload scour resulting from rain-on-snow events may be an important factor for bull trout populations in the region of this study (Rieman and McIntyre 1993). The correlations in discharge among the four rivers also indicate that hydrologic events occur over a scale consistent with the pattern we observed.

We found no compelling evidence that common events in the lake environments contributed to the spatial pattern in interannual variation. In the PCA with transformed data, common high loadings were sometimes evident among several streams within the lake basin but never among all streams. The raw data, however, produced a strong pattern for all streams associated with Flathead Lake, indicating that the lake environment is important in long-term trends. The recent expansion of a population of introduced lake trout *Salvelinus namaycush* in Flathead Lake has been associated with the declining bull trout numbers (T. Weaver, Montana Department of Fish Wildlife and Parks, personal communication). Long-term coexistence of bull trout and lake trout is questionable (Donald and Alger 1992). We suspect that the lake environments contribute to variability among bull trout populations on time scales consistent with changes in overall lake productivity or the processes influencing fish community structure (i.e., predation, competition, forage availability), but that interannual variability in those characteristics is relatively minor. In general, year-class strength in fishes is believed to be strongly influenced by environmental conditions at spawning or early in life (Shepherd and Cushing 1980; Rothschild and DiNardo 1987). Because spawning and initial rearing (2 or 3 years) occur in streams before migration to a lake (Bjornn 1957; Fraley and Shepard 1989), we believe it more likely that year-class variation is related to the stream environments. Any synchrony in interannual abundance among populations is probably the result of similar conditions among streams, whereas patterns over longer time scales may be associated with both lake and stream environments.

We found evidence of correlation influenced by distance, but we think it is striking that the pattern was so weak. The major variation in stream conditions that seem likely to influence populations should occur with annual climatic events that probably influence entire basins in a similar way. We anticipated a much stronger pattern. Although there was a clear tendency for more positive correlations with closer populations, we did not find a prevalence of strong (i.e., $r > 0.6$) correlations, and negative correlations were common. We propose three alternative explanations for the weak pattern.

First, heterogeneity in habitat availability or condition may minimize the influence of common disturbance. Populations in some habitats will respond to an environmental signal while others re-

spond weakly or not at all. It is thought that small populations of animals or those in marginal habitats are more likely to be regulated by environmental rather than demographic (population) processes (Saunders et al. 1990). In essence, small populations and those in less suitable habitats are more likely to respond to environmental variation because they have fewer refuges or less local habitat diversity to buffer such change. The lack of strong correlation among populations may reflect the availability of relatively complex habitats or a relatively weak large-scale environmental signal in relation to that habitat condition. Some streams may respond to minor climatic events differently by virtue of aspect, elevation, or other physiographic characteristics (King 1989; Pupacko 1993). It may also be that the period of record is simply too short to observe environmental disturbances large enough to influence many populations at the same time. We could not evaluate the influence of habitat characteristics on magnitude of variation or correlation in these data, but such work could be important. Habitat disruption or increased environmental variation resulting from land-use management might well lead to increased synchrony among populations.

Second, heterogeneity in life history pattern among populations may dampen the signal of common year-class variation. Variation in life history among local populations could arise through differences in local environments. Bull trout mature between age 5 and 7, and annual or alternate-year repeat spawning is possible (Block 1955; Pratt 1985; Fraley and Shepard 1989). Early growth in the natal stream influences both the age of initial migration and the age of maturity in other salmonids (Thorpe 1986; Gross 1991), including the closely related Arctic char *Salvelinus alpinus* (Jonsson and Hindar 1982; Hindar and Jonsson 1993; Milbrink et al. 1993). Differences or variation in stream productivity should contribute to variation in life history. If reproductive isolation exists among streams because of homing or physical barriers (i.e., separate lake basins) local adaptation and genetic drift could also contribute to genetically based variation in life history patterns.

Third, sampling error may overwhelm the common signal among streams. Biologists have tried to minimize error by repetitive sampling (to ensure complete spawning) and by complete stream sampling or identification of representative reaches (Pratt 1985; Weaver 1992). The redds are also characteristically large (often 1 m or more in length) and easily seen because streamflows at the time of survey (late September through early October) are generally low and the water is clear. Despite the apparent utility and a wide application of the method, we found no clear evaluation of potential sampling error. The recognition of redds might be influenced by the variation in streamflow and water clarity, by the age of redds (older redds can be obscured by the growth of algae or bedload movement), or by substrate size and condition (the characteristic pit may not be obvious in coarse or highly diverse substrates). The number of redds counted might be biased because spawning was incomplete at the time of survey or because adults used stream reaches other than those surveyed. It is possible that imprecision or some nonsystematic bias in the estimates obscures the true pattern in adult number under such circumstances (Rothschild and DiNardo 1987). Redd counts are an important tool for fishery managers and can provide important information for questions such as those addressed here. Unfortunately long-term data sets based on careful monitoring programs are rarely maintained. Expansion of existing monitoring programs could be valuable, but there is also a need for a study of the error associated with the method.

The nature of the spatial pattern and the underlying processes have important implications for management and conservation of the species. Asynchrony among local populations can provide stability to the regional population and help to minimize the risks of regional extinction. The lack of strong correlation also shows that redd counts in a limited number of index areas may not be good indicators of trends in all local populations. To understand the dynamics of regional populations it will be important to maintain extensive monitoring programs. Our analysis suggests that interannual correlation in redd number or rate of change is influenced by distance, but even within basins the patterns are not strong. Accordingly, conservation management should favor maintenance of multiple local populations relatively close together to facilitate dispersal and demographic support or individual populations and patches large enough and stable enough to insure local persistence in the face of environmental variability. The presence of diverse habitats and life histories may play an important role in stabilizing regional populations. If habitat condition contributes both to the magnitude and correlation in variation among local populations, continued habitat disruption will lead not only to continued loss or restriction of local populations but also to reduced stability and increased risk in the regional popu-

lations. The declining trend observed in all of the Flathead Lake streams shows that even well-dispersed regional populations are not immune to environmental change. Changes such as those occurring in Flathead Lake could lead to the simultaneous extinction of many local populations. Conservation management of species like bull trout must incorporate the maintenance and replication of multiple populations at both local and regional scales.

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