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[Article]

Fine-Scale Genetic Structure of Bull Trout at the Southern Limit of Their Distribution

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Abstract.—We used six polymorphic microsatellite loci to analyze the population genetic structure of bull trout *Salvelinus confluentus* in the Boise River, Idaho, and we compared our results with previous data from similarly sized river systems in western North America. Within the Boise River, we found low genetic variation within and significant differentiation among sample sites. Two cohesive groups of populations were associated with the two major subbasins in this system, which we attributed to long-term reduction of gene flow or distinct sources of colonization at this scale. We observed a significant pattern of isolation by distance in one subbasin and not in the other; this result suggests that the relative influences of gene flow and drift have differed between the two subbasins. Ecologically defined patches of suitable habitat were not good predictors of genetic variation among samples. Dams and other anthropogenic barriers have recently changed the potential for gene flow and genetic drift but were not associated with the major boundaries of genetic differentiation. There was some evidence of lost genetic variation in smaller patches that were physically isolated by both natural and anthropogenic barriers. We found a large range of within-population genetic variation and among-population genetic differentiation for bull trout from river basins across the species' range, but our estimates in the Boise River were the lowest (or among the lowest) observed. The relative roles of drift and gene flow appear to vary strongly at both fine and broad spatial scales. We cannot presume that the physical and ecological processes influencing the genetic population structure of bull trout in one region will accurately reflect those in another region; this may have important implications for conservation and management actions.

Genetic diversity is usually partitioned hierarchically across the range of a species. The fundamental processes controlling the distribution of genetic variation at neutral markers are genetic drift and gene flow. Factors influencing these processes include natural landscape features and habitat structure that control the size, geometry, interconnection, and dynamics of available habitats or habitat "patches" and local populations (Keyghobadi et al. 1999; Castric et al. 2001; Dunham et al. 2002; Costello et al. 2003). These effects can be modified by anthropogenic barriers, (e.g., dams or road culverts in aquatic systems) that disrupt established patterns of movement or the expression of distinct life histories and isolate populations to more limited areas (Morita and Yamamoto 2002; Yamamoto et al. 2004; Wofford et al. 2005). For coldwater salmonids that depend on distinct stream channel characteristics for spawning and early rearing, environmental conditions that define the size, distribution, and persistence of natal habitats may vary strongly along climatic, hydrologic, and geomorphic gradients (Montgomery et al. 1999). The manner in which genetic variation is distributed within and among populations then could be expected to vary with habitat patch structure and the natural and anthropogenic processes that influence it.

It seems likely that the dominant controls on the distribution of genetic variation will vary among regions with distinct landscapes and ecological (e.g., Hutchison and Templeton 1999) or management histories (Yamamoto et al. 2004; Wofford et al. 2005; Neville et al., in press). Fishes offer several relevant examples. Costello et al. (2003) found evidence of both contemporary (e.g., human constructed barriers) and historical (e.g., glacial and geomorphic constraints on colonization) effects on the distribution of genetic variation of bull trout

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Salvelinus confluentus in two river systems in British Columbia. Natural barriers, however, appeared to have greater influence on genetic structure in one basin than in the other. Similarly, Castric et al. (2001) and Poissant et al. (2005) found evidence for geographic variation in the effects of contemporary and historical factors on genetic differentiation of populations of brook trout *S. fontinalis*. Documenting variation in patterns of genetic differentiation is important if we are to avoid mismanagement based on the assumption that fine-scale genetic differentiation is homogeneous within distinct regions across a species' range.

Bull trout in the Boise River basin in southwestern Idaho offer an opportunity to evaluate several factors that influence genetic structure within a major river basin and among similar basins across a large part of the species' range in western North America. A number of studies have examined genetic structure of bull trout within individual river basins (Spruell et al. 1999; Kanda and Allendorf 2001; Neraas and Spruell 2001; Costello et al. 2003; Whiteley et al. 2004). Our work in the Boise River basin provides a useful comparison and contrast to this earlier work for four reasons. First, the Boise River is the largest network of interconnected habitats suitable for bull trout on the extreme southern limits of the species' range. There are enough populations distributed across a large enough area to resolve a meaningful pattern. Second, from previous work we understand the environmental controls on the distribution of suitable habitat, so we can define the geometry and interconnection of habitat that should constrain the size and dynamics of local populations (Rieman and McIntyre 1995; Dunham and Rieman 1999; Dunham et al. 2002). Third, the extreme southern location of the Boise River system also means that suitable habitats are strongly constrained by climate and stream temperature; as a result, the size and discontinuity of suitable habitats associated with local populations are probably more limited and extreme than those for populations that are more central in the species' range (Rieman and McIntyre 1995; Dunham and Rieman 1999; Dunham et al. 2001). Finally, four dams and several other natural and anthropogenic features that are known or potential barriers to upstream movements of bull trout allowed us to examine the effects of fragmentation on these populations.

In the work reported here, we addressed two general questions: (1) how is genetic variation partitioned within and among populations in the Boise River system, and can we attribute these patterns to either natural geographic or anthropogenic factors, and (2) how does fine-scale genetic structure differ among groups of populations within river basins distributed across the bull trout range? We use our results to consider the important differences in patterns of gene flow and population dynamics that may result from variation in river systems and population histories across the species' range.

Study Area

The study area and bull trout populations associated with it are described in detail elsewhere (Rieman and McIntyre 1995; Dunham and Rieman 1999). Briefly, the Boise River basin (Figure 1) represents one of the largest networks of mostly interconnected bull trout habitats (~5,700 km^2) on the extreme southern limits of the species' range.

Because of the species' southern location, habitats for bull trout were influenced only by alpine glaciation, as opposed to continental glaciation, which influenced populations in north-central range (Costello et al. 2003). Glacial retreat and subsequent colonization of currently occupied headwater habitats may have occurred earlier than in the more northern populations. The large-scale genetic associations for this region (Spruell et al. 2003) suggest that colonization probably occurred from a refuge associated with the nexus of the Boise, Snake, and Malheur rivers.

There are nominally three forks of the Boise River (North, Middle, and South); however, based on the geographic structure of the basin, there are two major subbasins (Figure 1). The North Fork joins the Middle Fork approximately 20 km upstream of the confluence with the South Fork. The majority of bull trout spawning habitat is near the headwaters of each of these basins, so populations in the South Fork are geographically distant from populations that are more closely located in the Middle and North forks. These two subbasins are isolated from the lower Boise and Snake rivers by dams constructed between about 50 and 100 years ago. A fourth dam was constructed in the upper Middle Fork subbasin nearly a century ago. These dams have created impassable barriers to upstream movements of bull trout. In addition, natural geomorphic features and more recent human development (i.e., road crossings) represent at least partial barriers to bull trout movements.

Bull trout exhibit a variety of life history patterns. Spawning and initial rearing are limited to cold headwater tributaries (Dunham and Reiman 1999). Juveniles rear in natal or nearby tributaries for several years. Some fish may remain in the tributary streams throughout life, but migratory individuals that move to main-stem rivers or reservoirs to mature are common. Philopatry and the association of water temperature with elevation and stream size suggest that local populations are essentially defined by patches or

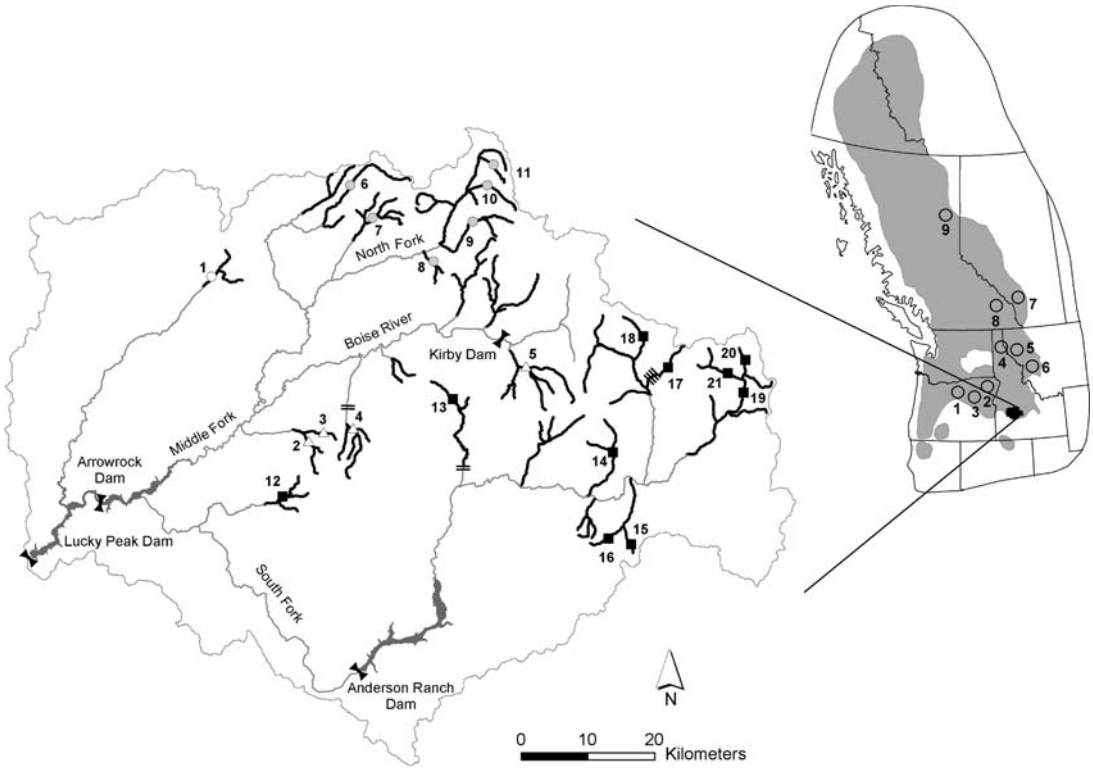

FIGURE 1.—The left-hand portion shows the Boise River basin, Idaho. The numbers, which correspond with those in Table 1, indicate bull trout sample sites (an open circle is used for Mores Creek, shaded circles for the North Fork, open triangles for the Middle Fork, and black squares for the South Fork). Four impassable dams are indicated by name. Potential culvert barriers are shown by double lines crossing the stream, and a potential geomorphic barrier is shown by four lines crossing the stream. Shaded stream segments are patches known to be occupied by bull trout (Dunham and Rieman 1999). In the right-hand portion, the shaded area indicates the bull trout's range; the numbered circles designate the river basins used in comparison with the Boise River basin to assess bull trout genetic variation, namely, (1) the Deschutes River, (2) Grande Ronde River, (3) John Day River, (4) Lake Pend Oreille, (5) lower Clark Fork River, (6) upper Clark Fork River, (7) Oldman River, (8) upper Kootenay River, and (9) Pine River.

networks of cold water distributed throughout the headwaters of the basin (Dunham and Rieman 1999; Dunham et al. 2002). If there is contemporary gene flow among these patches, it probably occurs through straying of migratory adults (Dunham and Rieman 1999; Rieman and Dunham 2000). Because the Boise River system is at the extreme southern limit of the species' range, we assume that natal habitats defining local populations will be more strongly constrained by climate, producing a discontinuity of suitable habitats that are smaller and more patchy than habitats more central to the species' range.

Methods

Sampling.—As the foundation for our study, we used habitat patches delineated by Dunham and Rieman (1999) to identify the stream networks we assumed would define local populations across the Boise River basin (Figure 1). We collected fin tissue from small (<150 mm), premigratory (following Dunham and Rieman 1999) bull trout in discrete stream segments (100–1,000 m) distributed among a subset of occupied patches in each of the subbasins of the larger river network. We restricted the sample to small fish to ensure analysis of individuals from their natal patches. We minimized the likelihood of sampling siblings or single age-classes by distributing collection efforts across size-classes and age-classes and across multiple sites in the selected streams.

Most sample collections were made in a single year. In four streams (Roaring River and Rattlesnake, Emma, and Sheep creeks), we collected the sample across multiple years. When these collections were treated separately by year, several exact tests for genic and genotypic differentiation (see below) were statistically significant, but only the results for Rattlesnake Creek

TABLE 1.—Sample information, average expected heterozygosity (H_S), total number of alleles, mean allelic richness, and inbreeding coefficient F_{IS} values for bull trout populations from the Boise River basin, Idaho.

Sample number	Location	N	H_S	Total number of alleles	Mean allelic richness	F_{IS}
Mainstem Boise River						
1	Mores Creek	16	0.278	11	1.8	−0.172
Middle Fork						
2	Sheep Creek	26	0.212	12	1.8	−0.012
3	East Fork Sheep Creek	25	0.253	12	1.8	−0.024
4	Roaring River	39	0.180	12	1.6	−0.019
5[a]	Yuba River	30	0.288	14	2.1	0.067
North Fork						
6	Crooked River	38	0.096	9	1.3	0.025
7[a]	Bear Creek and River	27	0.239	13	1.8	−0.127
8	Lodgepole Creek	51	0.216	12	1.8	−0.133
9	Johnson Creek	30	0.239	13	1.9	0.033
10	Ballentyne Creek	38	0.250	13	1.9	0.109
11	McLeod Creek	42	0.238	13	1.9	−0.083
South Fork						
12	Rattlesnake Creek	39	0.204	12	1.7	0.031
13	Elk Creek	29	0.111	9	1.4	−0.064
14[a]	Skeleton Creek	36	0.204	11	1.6	0.194
15	Boardman Creek	30	0.196	10	1.6	0.089
16	Smoky Dome Creek	28	0.198	10	1.6	−0.107
17	Emma Creek	52	0.099	9	1.3	0.022
18	Johnson Creek	33	0.247	10	1.7	−0.158
19	Big Smoky Creek	29	0.196	12	1.7	−0.090
20	Upper Big Smoky Creek	35	0.205	10	1.5	−0.065
21	West Fork Big Smoky Creek	37	0.246	10	1.6	0.127

* Samples from two or more locations were pooled for analysis.

were significant when we used the sequential Bonferroni method to correct for multiple tests (Rice 1989) or when we used Fisher's method to combine *P*-values across multiple loci. Although there was evidence that allele frequencies differed at several loci in these among-year comparisons, we combined the data from multiple years in all four cases because this should be the most accurate estimate of allele frequencies in those streams (Waples 1989).

Our samples were intentionally distributed in patches associated with tributaries above and below the four dams: Kirby Dam, constructed in 1906; Arrowrock Dam, constructed in 1915; Anderson Ranch Dam, completed in 1950; and Lucky Peak Dam, completed in 1954 (Figure 1). Immediately after construction, all of these dams blocked upstream fish passage, but in the mid-1990s a fish ladder was constructed to pass bull trout over Kirby Dam. In addition to these unequivocal barriers, two of our samples (Roaring River, Elk Creek) were located above road culverts that have been at least partial barriers to upstream movement for the past 20–40 years (Figure 1). A third sample, Emma Creek, was located above a debris fan that appears to be a barrier to upstream movement during the time of adult migration in most years (B.E.R., unpublished observations). Natural geomorphic processes occurring after alpine glaciation created the Emma Creek fan, but we have not determined its age. It was not possible to sample immediately below these barriers (to test for direct effects of disruption in gene flow) because the barriers were at or below the boundaries of the local patch (i.e., there were no juvenile bull trout immediately below the barrier).

We collected and analyzed tissue for 710 individuals from 21 samples in 20 streams (Table 1) and from 15 patches (Table 2). A sample consisted of collections from several sites within a single stream. In the Yuba River, Bear Creek and River, and Skeleton River samples, we pooled fish collected from multiple tributary streams within the patch. Samples for the Yuba River required pooling from the most distant sites (maximum = 8 km) and largest number of tributary streams (five).

Microsatellites.—All DNA extraction, polymerase chain reaction (PCR), and microsatellite visualization methods were performed as described in Spruell et al. (1999) and Neraas and Spruell (2001). We extracted DNA from each fin clip by standard methods and used nine microsatellite loci (Spruell et al. 1999; Neraas and Spruell 2001): *Ssa311*, *Ssa456*, *Ots101*, *Fgt3, Sco19, Ogo2, Bt73, Sfo18,* and *Oneμ7*. Six of these loci were polymorphic in this system (Table 3). We visualized fluorescently labeled PCR products on acrylamide gels using an Hitachi FMBIO II fluorescent imager and used a MapMarker LOW (BioVentures) ladder and

TABLE 2.—Patch number, tributaries contained within patches, and patch size for bull trout in the Boise River basin, Idaho. Numbers in parentheses correspond to those in Table 1. The area of the polygon defining the watershed boundaries of the stream network contained within a patch was used as a measure of patch size (Dunham and Rieman 1999).

Patch number	Location within patches	Area (km^2)
1	Mores Creek (1)	1,000
2	Sheep Creek (2) and East Fork Sheep Creek (3)	4,065
3	Roaring River (4)	5,482
4	Yuba River (5)	12,108
5	Crooked River (6)	6,941
6	Bear Creek and River (7)	2,965
7	Lodgepole Creek (8) and Johnson Creek (North Fork; 9)	6,904
8	Ballentyne Creek (10) and McLeod Creek (11)	13,500
9	Rattlesnake Creek (12)	2,375
10	Elk Creek (13)	3,542
11	Skeleton Creek (14)	5,377
12	Boardman Creek (15) and Smoky Dome Creek (16)	5,127
13	Emma Creek (17)	2,737
14	Johnson Creek (South Fork; 18)	13,714
15	Big Smoky Creek (19, 20) and West Fork Big Smoky Creek (21)	22,637

individuals of known genotypes as standards for scoring.

Sample sizes for each locus varied (Table 3). The DNA yield was inconsistent, apparently because of our use of denatured ethanol for some of the samples; *Sco19* was influenced most strongly by the reduced DNA yield. In Elk Creek, this locus could be used for only eight individuals, but sample sizes from other locations generally exceeded 15 (Table 3). We retained *Sco19* in our analysis to maximize the number of independent alleles and reduce the coefficient of variation of estimates of genetic distance (Kalinowski 2002).

Bull trout hybridize with nonnative brook trout that also occur in some streams in the Boise River basin. Five individuals (one in the Crooked River and four in the Bear River) contained microsatellite alleles indicative of brook trout (P.S., unpublished data). We

TABLE 3.—Bull trout allele frequencies at 21 sample locations in the Boise River basin, Idaho. Sample sizes (*N*) represent the number of successfully amplified individuals for each sample at each locus. Blank spaces indicate absence of the allele at that location.

	Oneμ7			*Bt73*				*Fgt3*				
Location	**218*	**244*	*N*	**138*	**140*	**144*	*N*	**157*	**163*	**175*	**183*	*N*
Main-stem Boise River												
1. Mores Creek	0.469	0.531	16	0.094		0.906	16	0.833	0.167			15
Middle Fork												
2. Sheep Creek	0.609	0.391	23	0.071		0.929	23	0.975	0.025			20
3. East Fork Sheep Creek	0.580	0.420	25	0.080		0.920	25	0.980	0.020			25
4. Roaring River	0.500	0.500	39		0.179	0.821	39	0.949	0.051			39
5. Yuba River	0.740	0.260	25	0.023	0.159	0.818	25	0.923	0.077			26
North Fork												
6. Crooked River	0.500	0.500	34			1.000	34	0.985	0.015			34
7. Bear Creek and River	0.537	0.463	27	0.083		0.917	27	0.840	0.160			25
8. Lodgepole Creek	0.538	0.463	40			1.000	40	0.909	0.091			33
9. Johnson Creek	0.455	0.545	22	0.023		0.977	22	0.917	0.083			18
10. Ballentyne Creek	0.516	0.484	32	0.033		0.967	32	0.845	0.155			29
11. McLeod Creek	0.568	0.432	37	0.051		0.949	37	0.946	0.054			37
South Fork												
12. Rattlesnake Creek	0.513	0.487	39		0.053	0.947	39	0.986	0.014			36
13. Elk Creek	0.550	0.450	20			1.000	20	1.000				28
14. Skeleton Creek	0.361	0.639	36		0.015	0.985	36	0.879	0.091	0.030		33
15. Boardman Creek	0.207	0.793	29			1.000	29	0.817		0.183		30
16. Smoky Dome Creek	0.542	0.458	24			1.000	24	0.826		0.174		23
17. Emma Creek	0.188	0.812	48			1.000	43	1.000				49
18. Johnson Creek	0.469	0.531	32			1.000	32	0.848		0.152		33
19. Big Smoky Creek	0.333	0.667	27			1.000	27	0.845		0.017	0.138	29
20. Upper Big Smoky Creek	0.528	0.472	35			1.000	35	0.811			0.189	33
21. West Fork Big Smoky Creek	0.471	0.529	36			1.000	36	0.985		0.015		37

confirmed that these individuals were hybrids by use of paired interspersed nuclear-element PCR (Spruell et al. 2001). These five fish appeared to be first-generation hybrids and were excluded from subsequent analyses (Allendorf et al. 2001).

Variation within and among samples.—Allele frequencies, deviations from Hardy–Weinberg (HW) expectations, linkage disequilibrium, mean allelic richness (where each locus was corrected for the smallest sample size; Table 3), observed (H_O) and expected heterozygosity (H_E) per locus and population, mean within-population expected heterozygosity (H_S), pairwise exact tests for genic and genotypic differentiation, *F*-statistics, and pairwise genetic differentiation index (F_{ST}) estimates were calculated using GENEPOP version 3.4 (Raymond and Rousset 1995) and FSTAT version 2.9.3.2 (Goudet et al. 1996; Goudet 2001). We used θ for estimates of F_{ST} (Weir and Cockerham 1984). We generated 95% confidence intervals for multilocus F_{ST} estimates by bootstrap sampling over loci (Goudet et al. 1996). We used F_{ST} instead of a microsatellite-specific genetic distance index (R_{ST}) because F_{ST} estimates are more conservative when relatively few (<20) microsatellite loci are used and when populations have diverged recently (Gaggiotti et al. 1999). Markov chain methods in GENEPOP were used to test for deviations from HW proportions, linkage disequilibrium, and genic and genotypic divergence in allele frequencies or genotypic frequencies among populations for all loci and population pairs. We used permutation procedures implemented by GENETIX version 4.0 (Belkhir 1999) to test the significance of pairwise F_{ST} estimates using 1,000 permutations. For pairwise exact tests for genic and genotypic differentiation, we used the binomial likelihood function of Chapman et al. (1999) to estimate the likelihood of obtaining as many or more significant tests as actually obtained by chance.

We used PHYLIP (Felsenstein 1992) to calculate Cavalli-Sforza and Edwards' (1967) genetic distance (CSE) with the GENDIST module and to construct a UPGMA (unweighted pair-group method with arithmetic averages) dendrogram using the NEIGHBOR module. We used CONSENSE to generate a consensus tree from bootstrap values from 1,000 replicate data sets created in SEQBOOT. We used CSE to analyze genetic divergence between populations because it is drift based, does not assume any models of mutation, and performs well in simulations of microsatellite data (Takezaki and Nei 1996).

We tested different hierarchical arrangements of population samples to consider whether genetic structure was associated with the geographic structure of the river network. We used an analysis of molecular variance (AMOVA; Excoffier et al. 1992) performed with ARLEQUIN version 2.001 (Schneider et al. 2000) to test three geographical arrangements of populations. Arrangement 1 pooled samples into three groups, each

TABLE 3.—Extended.

	Sco19				*Ssa311*			*Ots101*		
Location	**200*	**204*	**206*	*N*	**112*	**120*	*N*	**100*	**112*	*N*
Main-stem Boise River										
1. Mores Creek		1.000		14	0.250	0.750	16	0.188	0.813	16
Middle Fork										
2. Sheep Creek	0.067	0.633	0.300	15	0.040	0.960	25		1.000	25
3. East Fork Sheep Creek	0.250	0.386	0.364	22	0.083	0.917	24		1.000	24
4. Roaring River	0.013	0.934	0.053	38	0.026	0.974	39		1.000	39
5. Yuba River	0.079	0.763	0.158	19	0.283	0.717	30	0.083	0.917	30
North Fork										
6. Crooked River		0.980	0.020	25		1.000	33		1.000	33
7. Bear Creek and River	0.059	0.735	0.206	17	0.019	0.981	27	0.019	0.981	27
8. Lodgepole Creek	0.045	0.750	0.205	22	0.021	0.979	47	0.021	0.979	47
9. Johnson Creek	0.100	0.650	0.250	10	0.071	0.929	28	0.017	0.983	30
10. Ballentyne Creek	0.109	0.717	0.174	23	0.076	0.924	33	0.029	0.971	34
11. McLeod Creek	0.275	0.650	0.075	20	0.077	0.923	39	0.013	0.988	40
South Fork										
12. Rattlesnake Creek	0.145	0.605	0.250	38	0.014	0.986	37		1.000	37
13. Elk Creek		0.937	0.063	8	0.017	0.983	29		1.000	29
14. Skeleton Creek		0.554	0.446	28		1.000	36		1.000	36
15. Boardman Creek		0.853	0.147	17	0.161	0.839	28		1.000	29
16. Smoky Dome Creek		0.833	0.167	18	0.056	0.944	27		1.000	28
17. Emma Creek		0.845	0.155	42	0.010	0.990	48		1.000	49
18. Johnson Creek		0.786	0.214	28	0.242	0.758	33		1.000	33
19. Big Smoky Creek	0.036	0.785	0.179	28	0.052	0.948	29		1.000	29
20. Upper Big Smoky Creek		0.609	0.391	33	0.095	0.905	35		1.000	35
21. West Fork Big Smoky Creek		0.636	0.364	32	0.129	0.871	37		1.000	37

corresponding to the three forks of the Boise River. Arrangement 2 consisted of two groups: all the sites from the South Fork and all remaining sites from the North and Middle forks. Arrangement 3 placed Rattlesnake Creek with the Middle and North Fork group instead of the South Fork group. Rattlesnake Creek is a tributary that joins the South Fork below Anderson Ranch Dam and appears to be more similar genetically to Middle and North Fork sites than to South Fork sites above Anderson Ranch Dam (see below). This final analysis represented an a posteriori arrangement that best partitioned genetic variation. Mores Creek was not included in these analyses because it is geographically removed from each of the three forks of the Boise River (Figure 1).

We tested for associations between genetic and geographic distances among samples to consider the potential influence of geographic distance on the distribution of genetic variation. Given the apparent influence of interpatch distance on the persistence of bull trout (Dunham and Rieman 1999), we hypothesized that gene flow would be more likely to occur among samples in close proximity. Using the program IBD (Isolation by Distance; Bohonak 2003), we used Mantel IBD tests for both CSE and pairwise F_{ST}. Tests were performed with and without log transformation of geographic distances. We estimated the distance between all possible pairs of samples using a geographical information system. The distance between any two samples was calculated as the distance along the stream network between the lower bounds of the stream reaches where sampling occurred.

We tested for an association between habitat patch size and measures of genetic variation to consider the potential influence of habitat patch geometry on genetic diversity. Because patch size should limit population size, we hypothesized that smaller patches would show reduced genetic variation. Patch size was defined as the area of the polygon defining the watershed boundaries of the stream network encompassed in the patch (Table 2; Dunham and Rieman 1999). We regressed H_S and total number of alleles on patch area after arcsine transformation of H_S. We averaged both H_S and total number of alleles when there was more than one site within a single patch, because F_{ST} was greater than zero in each case and thus sites within patches were not drawn from a single panmictic population. We performed this analysis for the entire basin as a whole and within each of the two major genetic assemblages we observed (see below).

We could not test for the influence of barriers on genetic variation directly, because bull trout do not occur immediately upstream and downstream of barriers in this system. Instead, the influence of barriers had to be inferred by comparing genetic variation and genetic distance among populations that were presumably above isolated barriers with those that were not.

Comparison among regions.—We compiled published data on genetic variation from seven similarly sized river basins across the species' range (Figure 1) to quantitatively compare our results from the Boise River basin with recent work from more central and northern basins within the range of bull trout. These include the Deschutes, Grande Ronde, and John Day rivers (Spruell et al. 2003); Clark Fork River (Spruell et al. 1999; Neraas and Spruell 2001; Whiteley et al. 2004); and Oldman, Pine, and Kootenay rivers (Costello et al. 2003). We divided the data from the Clark Fork River into three subbasins that are approximately the same size as the Boise River basin. The first group included tributaries of Lake Pend Oreille and Clark Fork tributaries downstream from Cabinet Gorge, a geomorphic feature that appears to have been a natural barrier to gene flow in that system (Neraas and Spruell 2001). The second group contained tributaries to the lower Clark Fork River (upstream from Cabinet Gorge and downstream from the confluence with the Flathead River); the third group contained tributaries to the upper Clark Fork River (the Bitterroot and Blackfoot rivers and Rock and Rattlesnake creeks).

We compared genetic diversity among basins based on estimates of H_E, mean number of alleles, and pairwise F_{ST}. We used data from all nine microsatellite loci in the Boise River (including the three monomorphic loci) to adjust estimates of H_S and number of alleles, because all nine loci are variable elsewhere in the species' range. We compared mean values of H_E, mean number of alleles, and F_{ST} for each basin using an analysis of variance (ANOVA), and we performed Tukey post hoc analysis for pairwise comparisons ($\alpha = 0.05$) with the Statistical Package for the Social Sciences 11 (SPSS).

Results

Within-Sample Variation

Genetic variation within each of the 21 samples was generally low (Table 1). Average H_S ranged from 0.096 to 0.288, but most samples were between 0.190 and 0.250. Mean allelic richness ranged from 1.3 to 2.1 (Table 1). Bull trout from the two sites most likely to be directly affected by dams (Mores Creek and Yuba River) did not have reduced genetic variation and in fact estimates from these sites were among the highest we observed. The three sites putatively above barriers (Elk and Emma creeks and Roaring River), along with

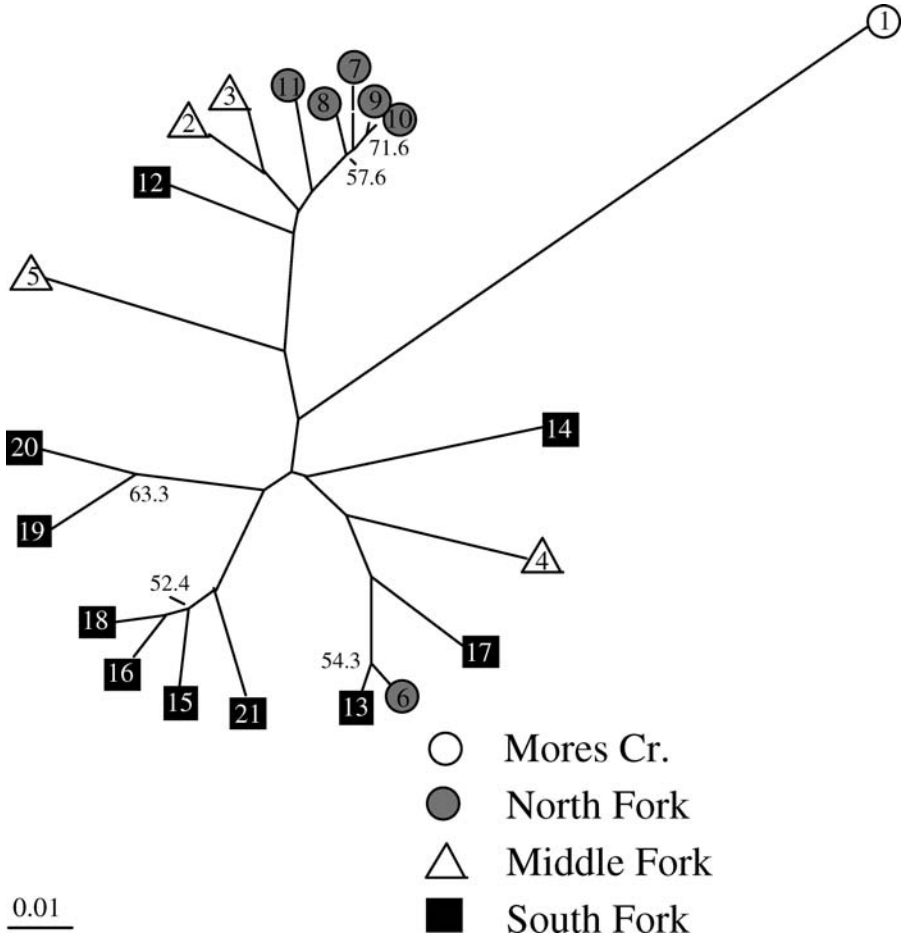

FIGURE 2.—Dendrogram based on genetic distances (Cavalli-Sforza and Edwards 1967) for bull trout populations in the Boise River basin, Idaho. The numbers within symbols correspond to the sample sites in Table 1 and Figure 1. Bootstrap values greater than 50% are shown at their respective nodes.

Crooked River, had the lowest genetic variation (Table 1).

Four of 81 exact tests for deviation from HW proportions were statistically significant, the same number expected by chance ($\alpha = 0.05$). There was no pattern either for certain loci or for certain populations to yield significant *P*-values. Seven of 174 exact tests for linkage disequilibrium were significant; eight were expected by chance ($\alpha = 0.05$). Four significant comparisons were between *One*μ*7* and another locus. However, each comparison was with a different locus and in a different geographic location; *Fgt3* and *Sco19* showed evidence of linkage disequilibrium in three upper South Fork sites. These loci have not shown evidence of linkage disequilibrium in previous studies, and thus are probably not located close together on the same chromosome (Spruell et al. 1999; Neraas and Spruell 2001). Population subdivision or low effective population size also may have caused the observed association.

We did not find evidence for differentiated populations within the Bear and Skeleton Creek samples (no significant heterozygote deficit). The Yuba River sample deviated significantly from HW expectations at *Ssa311* ($P = 0.025$; one-tailed test for heterozygote deficit), and the inbreeding coefficient (F_{IS}) was equal to 0.436 at this locus, indicating a heterozygote deficit. A positive F_{IS} value (0.360) was also found for *Ots101* in this sample, but the one-tailed *P*-value for the exact test for HW proportions was not significant ($P = 0.165$). The other four loci had negative F_{IS} values for this sample, indicating an excess of heterozygotes. One site within the Yuba River (Grouse Creek) had a disproportionately high occurrence of the

TABLE 4.—Pairwise genetic differentiation index values (F_{ST}; above diagonal) and counts of significant genic and genotypic tests of bull trout allele frequency differences (below diagonal: genic/genotypic) between Boise River, Idaho, sample sites for six microsatellite loci. For pairwise F_{ST} estimates, significant values are in bold italics ($P < 0.05$) or marked with an asterisk ($P < 0.001$). For tests of genic and genotypic differentiation, the binomial likelihood method (Chapman et al. 1999) was used to correct for multiple tests, where the likelihood of one or more significant tests was 0.27 and the likelihood of two or more significant tests was 0.03 (in bold italics). Sample numbers (SNs) correspond to those in Table 1.

	Mores Creek	Middle Fork				North Fork						South Fork			
SN	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1		***0.125****	***0.179****	***0.077****	***0.065***	***0.107***	***0.071****	***0.074****	***0.084***	***0.052***	***0.098***	***0.134****	***0.101***	***0.175****	***0.096****
2	***3/3***		0.013	***0.079****	***0.060****	***0.109***	0.004	0.013	−0.012	0.006	0.015	−0.006	0.052	***0.047***	***0.152****
3	***3/3***	0/0		***0.164****	***0.093****	***0.210****	***0.056***	***0.064***	0.017	***0.048***	0.024	0.020	***0.142****	***0.062***	***0.186****
4	***3/3***	***2/2***	***2/2***		***0.105****	***0.028***	***0.043****	***0.045****	***0.061***	***0.045****	***0.072****	***0.069****	0.021	***0.141****	***0.123****
5	***2/2***	***1/2***	***3/3***	***3/2***		***0.160****	***0.073****	***0.081***	***0.063***	***0.059****	***0.069***	***0.096****	***0.105****	***0.179****	***0.193****
6	***4/4***	1/1	***3/3***	1/1	***4/4***		***0.064****	***0.054***	***0.084***	***0.057***	***0.097****	***0.090****	−0.014	***0.175****	***0.145****
7	***3/3***	1/1	***2/2***	***2/3***	***2/3***	***3/3***		−0.012	−0.011	−0.014	0.016	0.013	0.034	***0.045***	***0.104***
8	***3/3***	0/0	***2/2***	***2/1***	***3/3***	***2/2***	0/0		−0.013	−0.018	0.014	0.010	0.028	***0.047***	***0.095***
9	***2/2***	0/0	0/0	***2/2***	***2/2***	***2/1***	0/0	0/0		−0.020	−0.003	−0.014	0.042	0.014	***0.083***
10	***3/3***	1/0	***2/2***	***2/2***	***3/3***	***2/2***	0/0	0/0	0/0		0.002	0.010	0.028	***0.045***	***0.082***
11	***3/3***	0/1	1/1	***2/2***	***3/3***	***3/3***	0/1	0/0	0/0	0/0		0.002	***0.058***	***0.079***	***0.119****
12	***5/5***	1/1	1/1	***2/2***	***3/2***	1/1	***2/2***	1/1	0/0	***1/2***	1/1		***0.049***	***0.036***	***0.122****
13	***3/3***	0/0	1/1	1/1	***1/2***	0/0	1/1	1/1	0/1	1/1	0/1	1/1		***0.132***	***0.141****
14	***4/4***	***1/2***	***4/4***	***2/2***	***4/4***	***2/2***	***2/3***	1/1	***2/2***	***2/2***	***3/3***	***2/2***	***2/2***		***0.097***
15	***4/4***	***2/3***	***4/4***	***4/4***	***3/3***	***4/3***	***4/4***	***3/3***	***2/2***	***2/2***	***4/4***	***4/4***	***3/3***	***3/3***	
16	***4/4***	1/1	***2/2***	***2/2***	***4/4***	***2/2***	1/1	1/1	1/1	1/1	***2/2***	***2/2***	1/1	***2/3***	1/1
17	***6/6***	***3/3***	***4/4***	***4/4***	***6/6***	***2/2***	***3/3***	***2/2***	***3/3***	***4/3***	***3/3***	***3/3***	1/1	***3/3***	***2/2***
18	***4/4***	***2/2***	***4/4***	***4/4***	***3/3***	***3/3***	***3/3***	***2/2***	***2/2***	***3/3***	***4/4***	***3/3***	***2/2***	***3/2***	1/1
19	***5/5***	***2/2***	***4/4***	***3/3***	***4/4***	***2/2***	***3/3***	***1/2***	1/1	1/1	***2/3***	***2/2***	***1/2***	***2/2***	1/1
20	***4/4***	0/1	***2/2***	***4/3***	***4/4***	***2/2***	***4/4***	***2/3***	***2/2***	***2/2***	***2/2***	***2/2***	***2/2***	***2/2***	***3/3***
21	***4/5***	***2/2***	***3/3***	***3/3***	***5/5***	***3/3***	***3/2***	***2/2***	1/1	***2/2***	***3/3***	***2/2***	***2/2***	***2/2***	***3/3***

*Ssa311*112* allele. When the five fish from this site were removed from the analysis, the sample conformed to HW proportions but allele frequencies changed only slightly (data not shown). Although the result from *Ssa311* in the Yuba River sample suggests that some population subdivision may be present upstream from Kirby Dam, the effect on our analysis was presumed to be slight because removing the Grouse Creek sample had a negligible effect on allele frequencies.

Among-Sample Variation

We found evidence for significant genetic differentiation among sample locations. Many pairwise F_{ST} estimates differed significantly from zero, and many counts of significant genic and genotypic tests differed by more loci than expected by chance (Table 4). The likelihood that one or more tests out of a total of six tests (one test for each locus) for genic or genotypic differentiation were significant by chance was 27%, whereas the likelihood for two or more significant tests was 3%. Therefore, we considered two or more significant loci per pairwise population comparison as statistically significant (Table 4).

The allele frequency data (Table 3) supported two geographically cohesive genetic groups in the Boise River basin. These groups corresponded to the South Fork and the combined Middle and North forks, with the exception that Rattlesnake Creek, a South Fork tributary (Figure 1), was part of the Middle and North Fork genetic group. The alleles *Fgt3*175* and **183* only occurred in the upper South Fork; *Ots101*100* and *Bt73*138* only occurred in the Middle Fork, North Fork, and Mores Creek (Table 3). Several alleles were limited to the Middle Fork, North Fork, and one or two South Fork locations. For example, *Sco19*200* occurred throughout the North and Middle forks but only in Rattlesnake and Big Smoky creeks within the South Fork; *Bt73*140* occurred in Rattlesnake and Skeleton creeks in the South Fork but only in the Roaring and Yuba rivers in the Middle Fork. Similarly, *Fgt3*163* occurred only in Rattlesnake and Skeleton creeks in the South Fork but throughout the Middle and North forks. The *Fgt3*183* allele occurred in the main stem of Big Smoky Creek at moderate frequency (Table 3) but was absent from all other samples, including the West Fork of Big Smoky Creek, a second major tributary to Big Smoky Creek.

The AMOVA arrangement with the two a posteriori defined groups (arrangement 3) produced the strongest significance for among-group variance (Table 5). Arrangement 2 was weaker but also significant. Arrangement 1 was not significant.

The South Fork group and the Middle and North Fork group were apparent in the UPGMA dendrogram

TABLE 4—Extended.

	South Fork				
SN	16	17	18	19	20
1	***0.077****	***0.201****	***0.052***	***0.091****	***0.120****
2	***0.032***	***0.205****	***0.053***	***0.073***	0.010
3	***0.103***	***0.254****	***0.097****	***0.121****	***0.043***
4	***0.046***	***0.140****	***0.078****	***0.068****	***0.098****
5	***0.083****	***0.310****	***0.059***	***0.152****	***0.093****
6	***0.045***	***0.153****	***0.091***	***0.072***	***0.115***
7	0.015	***0.147****	***0.044***	***0.039***	***0.033***
8	0.010	***0.137****	***0.038***	***0.029***	***0.032***
9	0.015	***0.130****	0.021	0.023	−0.005
10	0.011	***0.128****	***0.026***	***0.028***	0.024
11	***0.048***	***0.165****	***0.056***	***0.057***	***0.045***
12	***0.040***	***0.138****	***0.060****	***0.049***	0.015
13	0.022	***0.165****	***0.064***	***0.062***	***0.073***
14	***0.079***	***0.119****	***0.079****	***0.048***	0.021
15	***0.078***	***0.051***	***0.041***	***0.027***	***0.092****
16		***0.156****	0.015	***0.038***	***0.042***
17	***2/2***		***0.135****	***0.043***	***0.129****
18	1/1	***3/3***		***0.039***	***0.025***
19	***2/2***	1/1	***2/2***		***0.043***
20	1***/2***	***3/3***	1/1	***2/2***	
21	***2***/1	***4/4***	***3/2***	***2/2***	1/1

(Figure 2). The South Fork samples formed one group, and the majority of the samples from the Middle and North forks formed a second group. As expected from the allele frequencies, Rattlesnake Creek clustered with the Middle and North Fork group. There were several instances where the cluster analysis appeared to be influenced by genetic drift and reduced within-population genetic variation rather than gene flow mediated by geographic proximity. Two Middle and North Fork locations (Roaring and Crooked rivers) clustered with sites from the South Fork (Figure 2) that also had reduced variation (Table 1) and a high frequency of common alleles (Table 3). Mores Creek (Figures 1, 2), the one site separated by Arrowrock Dam from the remainder of the system, was also separated by a long branch and occurred at an intermediate location on the dendrogram. Bootstrap support for the dendrogram was generally low, as expected when there is variation among loci in depicting patterns of genetic structure.

Tests for IBD in the entire Boise River basin were highly significant for both CSE (Figure 3a) and pairwise F_{ST} ($r = 0.20$, $P \leq 0.004$; data not shown). When we removed samples presumably isolated by barriers (Yuba and Roaring rivers and Emma, Elk, and Mores creeks), the patterns were strengthened (Figure 3b). Log transformation highlighted the pattern of reduced differentiation among geographically proximate sites but did not significantly change the results of tests for IBD (data not shown). When we considered IBD only within the two major genetic groups (the Middle-North forks–Rattlesnake Creek, hereafter the Middle and North Fork group, versus the South Fork group), we found a significant relationship with CSE for the Middle and North Fork group (Figure 3c) but not for the South Fork group (Figure 3d). The IBD based on F_{ST} was not significant for the Middle and North Fork group ($r = 0.34$, $P \leq 0.052$) or the South Fork group ($r = 0.14$, $P \leq 0.235$; data not shown). Results did not change with the removal of above-barrier samples.

We found a weak trend for larger patches to have greater levels of genetic variation, but the relationship between patch area and H_E or total number of alleles was not significant ($P > 0.05$; Figure 4). This was the case when we considered the entire basin as a whole and when we considered each of the genetically differentiated groups separately.

Comparison among Regions

We found significant differences in mean heterozygosity, number of alleles, and pairwise F_{ST} among the river basins we considered (Figure 5). In each case, our observations for the Boise River populations either

TABLE 5.—Results from an analysis of molecular variance examining bull trout genetic versus geographic structure in the Boise River, Idaho. For geographical arrangement 1, the three groups correspond to each of the river's three forks (South, Middle, North). In arrangement 2, the Middle and North forks are combined into one group and the South Fork is the second group. Arrangement 3 is the same as arrangement 2, except that Rattlesnake Creek (Table 1) is included with the Middle and North forks, instead of the South Fork.

Geographical arrangement	Number of groups	Variance component	Percentage of variation	*P*-value
1. Three forks	3	Among groups	0.8	0.177
		Among samples within groups	3.6	<0.001
		Within sites	95.6	<0.001
2. Middle and North forks versus South Fork	2	Among groups	1.8	0.02
		Among samples within groups	3.1	<0.001
		Within sites	95.1	<0.001
3. Middle and North forks (including Rattlesnake Creek) versus South Fork	2	Among groups	2.7	0.002
		Among samples within groups	2.7	<0.001
		Within sites	94.7	<0.001

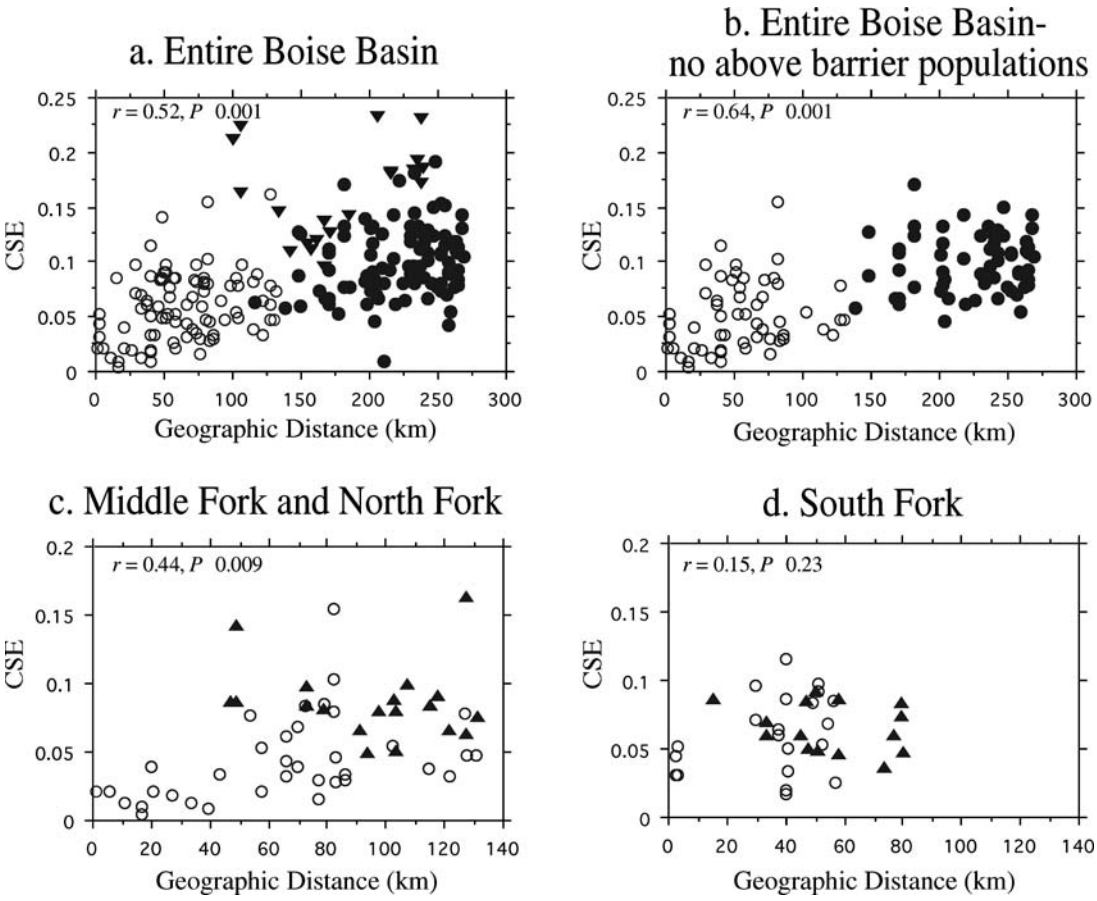

FIGURE 3.—Isolation-by-distance analysis of bull trout populations in the Boise River basin, Idaho. Pairwise Cavalli-Sforza and Edwards (1967) genetic distance (CSE) is plotted against geographic distance for **(a)** all populations, **(b)** all populations except those above dams and putative natural barriers, **(c)** Middle and North Fork subbasin populations, and **(d)** South Fork subbasin populations. Comparisons among populations within the same subbasin (the South Fork group or the Middle and North Fork group) are shown as open circles; comparisons among populations from different subbasins are shown as filled circles. In **(a)** the triangles represent Mores Creek samples, in **(c)** Yuba and Roaring River samples, and in **(d)** Elk and Emma Creek samples. The results of Mantel tests (r and P) are shown for each panel.

were, or were among, the lowest estimated for the species.

Discussion

Distribution of Genetic Variation

Our hierarchical analysis indicated that most of the genetic differentiation of bull trout populations in the Boise River was partitioned between the two major subbasins (the South Fork and the Middle and North forks). Despite low polymorphism at the microsatellite loci used, this pattern was supported by the geographic distribution of specific alleles, the AMOVA results, and the two major groups that were apparent in the dendrogram. This pattern of genetic differentiation of the two major subbasins reflected the physical structure of the Boise River basin.

The results of tests for IBD for the entire basin (Figure 3a, b) provided further support for the differentiation of the two major subbasins. The trend in the between-basin population pairs was relatively flat compared with the within-basin population pairs (Figure 3b). The overall pattern was strongly influenced by the difference between subbasins. We found no evidence of IBD in the South Fork but a clear pattern of IBD in the Middle and North Fork group. Thus, a balance between gene flow and drift apparently has been influential in the Middle and North forks, whereas drift has been more dominant in the South Fork and between the two subbasins (e.g., Hutchison

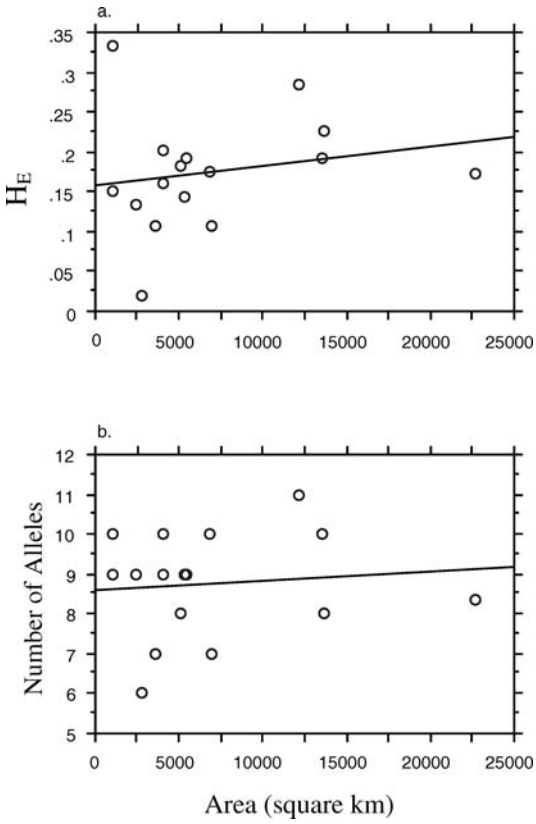

FIGURE 4.—Relationships between patch area and **(a)** expected heterozygosity (H_E) and **(b)** the total number of alleles for bull trout in the Boise River basin, Idaho. Neither relationship was significant.

and Templeton 1999). It appears that there has been relatively little connectivity and perhaps a very different history of landscape and population structure between the two subbasins.

The pattern of IBD in the Middle and North Fork group indicated that gene flow has been relatively strong among sites in close proximity in this subbasin. These results support the contention that contemporary gene flow between nearby populations has been important, even when those populations have been separated by thermally unsuitable habitats. Straying of adult salmonids is generally expected to decline with distance from the natal habitat (Dunham and Rieman 1999; Rieman and Dunham 2000; Castric and Bernatchez 2004; Quinn 2005), providing a plausible mechanism for our observation and those found in studies of closely related species (e.g., Bouza et al. 1999; Carlsson and Nilsson 2000; Castric et al. 2001; Castric and Bernatchez 2003).

The apparent distinction of the South Fork suggested that different or more heterogeneous processes have been important in the colonization or subsequent structuring in this part of the basin. The general patterns indicated that drift has been more important, but the South Fork also appeared to be genetically differentiated into two groups (upper and lower; Figure 2) based on the presence of two unique alleles at *Fgt3* and the absence of several alleles at other loci in some tributaries (Table 3). We suspect a past disruption of gene flow associated with a sharp geomorphological boundary (i.e., a natural barrier now opened by recent fluvial processes) just upstream of Skeleton Creek (C. Luce, U.S. Forest Service, Rocky Mountain Research Station [RMRS], Boise, Idaho, personal communication); however, more localized reductions of within-population genetic variation in several tributaries (Emma, Skeleton, and Elk creeks) could also be important. It is also possible that the South Fork may have a different colonization history than the Middle and North forks. Exchange of bull trout between the headwaters of the South Fork and the immediately adjacent headwaters of the upper Salmon River could have occurred through headwater transfer (B.E.R., personal observation). In other work, we sampled bull trout from the upper Salmon River basin to determine if the *Fgt3* alleles found only in upper South Fork sites were also present in the Salmon River. We found that *Fgt3*175* occurred at high frequency (0.833) in the upper Salmon River, consistent with the possibility of historical gene flow between the upper South Fork and the Salmon River (A.R.W., unpublished data).

Given the emerging evidence of geographic constraints on genetic variation for other salmonids, we hypothesized that the geometry and size of habitats might also be important controls on the patterns of genetic variation within the subbasins we sampled. Our results provided little evidence of a patch-size effect, despite geographic isolation imposed by the discontinuity of thermally suitable habitats (e.g., Dunham and Rieman 1999). We see three possible explanations. First, the extant habitat patches are only remnants of what were larger and less geographically isolated habitats in relatively recent times. Climate change over the last century has probably warmed streams in the Boise River (and other systems; Rieman et al. 1997), shrinking the size of thermally suitable stream networks (or patches). This relatively recent loss simply may not have been extreme or long enough to be expressed in local genetic diversity. Second, gene flow among populations may have been high enough to limit the loss of local genetic variation. Finally, the results may have been due to low power caused by low marker polymorphism. It is possible that more variable

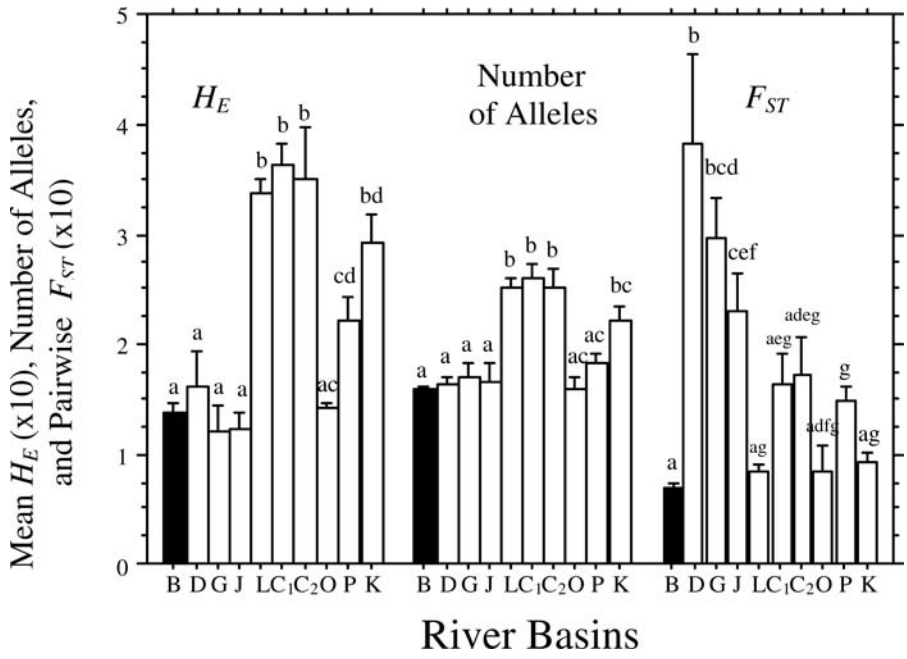

FIGURE 5.—Mean (+SE) expected heterozygosity (H_E), number of alleles, and genetic differentiation index (F_{ST}) of bull trout populations in the Boise River basin, Idaho (B; $N = 21$ populations) and in eight other river basins in northwestern North America, namely, the Deschutes River (D; $N = 5$; Spruell et al. 2003), Grande Ronde River (G; $N = 11$; Spruell et al. 2003), John Day River (J; $N = 10$; Spruell et al. 2003), Lake Pend Oreille (L; $N = 10$; Neraas and Spruell 2001), lower Clark Fork River (C_1; $N = 7$; Neraas and Spruell 2001), upper Clark Fork River (C_2; $N = 5$; Whiteley et al. 2004), Oldman River (O; $N = 3$; Costello et al. 2003), Pine River (P; $N = 14$; Costello et al. 2003), and upper Kootenay River (K; $N = 14$; Costello et al. 2003). Means sharing the same letter do not differ significantly (Tukey post hoc analysis: $P > 0.05$).

markers along with more extensive sampling within patches would reveal a stronger pattern.

Although we found streams that were potentially isolated above human or natural barriers (Elk and Emma creeks and Roaring River) had among the lowest levels of observed genetic variation, we were surprised by the lack of evidence of restricted gene flow across the far more obvious barriers imposed by the major dams constructed in the Boise River basin over the last century. For example, bull trout in the Yuba River have been isolated by Kirby Dam for approximately 100 years, before a fish ladder was constructed. Even so, that sample had among the highest levels of genetic variation we observed. For the IBD analysis of the Middle and North Fork group, comparisons that included Yuba River samples tended to have greater values (Figure 3c), suggesting that genetic differentiation in this river may be more than can be explained by geographic isolation alone, but this provides only weak evidence for an effect of this dam on genetic diversity. These results, along with the substructure implied by the differentiation of the Grouse Creek samples, suggest to us that the area above Kirby Dam has been sufficiently large and diverse to support one or more populations of at least moderate effective population size. The effects of drift and isolation simply have not been strong enough to observe within the elapsed period.

Our results for Mores Creek were also counterintuitive. We found an unexpectedly high level of genetic variation in Mores Creek, which has been geographically and physically isolated from any other bull trout habitats in the basin since the construction of Arrow Rock Dam (Figure 1). Before human development, Mores Creek was probably the downstream-most Boise River tributary that contained thermally suitable habitat for bull trout. Because of its limited headwater elevation, this habitat is and probably always has been quite small and geographically removed from others in the basin. Bull trout have been collected only sporadically (16 fish total) in sampling spanning more than 3 years. Based on patch size and apparent isolation, we would not expect bull trout to persist in Mores Creek (Dunham and Rieman 1999) or to retain significant genetic variation there. Despite this, Mores Creek still had the highest H_S observed in any of the samples.

We suspect that fish in Mores Creek are actually the

progeny of bull trout that were entrained at Arrowrock Dam and were unable to return upstream at maturity. Entrainment of juvenile bull trout through Arrowrock Dam has been demonstrated with radio tagging (T. Salow, U.S. Bureau of Reclamation [BOR], personal communication). Given the lack of spawning habitat in the tailrace of the dam, we believe that some of the fish may have migrated to Mores Creek as the only alternative spawning habitat below Arrowrock Dam. We would not expect the heterozygosity observed in Mores Creek samples to persist in a very small population that had been isolated for an extended period. We might expect greater genetic variation to be retained in a population supported by forced dispersal from multiple upstream populations. In essence, the bull trout in Mores Creek could represent a demographic "sink" (Pulliam 1988) maintained by forced dispersal from a source of fish upstream of Arrowrock Dam. In this case, the construction of two dams would have accentuated, rather than eliminated, gene flow into a single population—a situation that may also have occurred with the construction of dams elsewhere (Neraas and Spruell 2001).

Comparison among Regions

The comparison among regions suggested that fine-scale genetic structure varies dramatically across the bull trout's range. Our results also suggest that the history of colonization (e.g., Poissant et al. 2005), the subsequent gene flow and drift effects caused by landscape constraint (e.g., Costello et al. 2003), and the influence of anthropogenic fragmentation (e.g., Yamamoto et al. 2004) have differentially affected the ultimate genetic structure of populations and the distribution of genetic diversity. Other studies have found that populations at range extremes have reduced within-population variation (e.g., Beebee and Rowe 2000; Schwartz et al. 2003; Vucetich and Waite 2003; Stamford and Taylor 2004) and increased among-population genetic differentiation (e.g., Vrijenhoek et al. 1985; Hutchison 2003) relative to core populations. Our results were consistent with these other studies in terms of reduced within-population variation but provided an example in which fine-scale population differentiation at the range periphery appeared to be reduced relative to populations closer to the range core.

More detailed analyses with higher-resolution molecular data sets will be necessary to confirm these patterns and to explore likely causes of the variation we observed among river basins. We are particularly interested in the role of natural fragmentation on the evolution of dispersal and gene flow (e.g., Heino and Hanski 2001). If in fact F_{ST} is substantially lower in the Boise River basin, one hypothesis worth consideration is that more dynamic geomorphic processes, coupled with smaller and patchier populations, have actually led to increased dispersal in this system, whereas factors such as natural barriers may have a greater effect on reducing gene flow in other portions of the species' range (e.g., Costello et al. 2003).

Conclusions

Within the Boise River basin, we found relatively low levels of genetic variation overall but significant differentiation among groups of samples in the two major subbasins of this system. We found support for the model of IBD in one subbasin but not the other, indicating the apparent effects of differential drift and gene flow across this river system. Ecologically defined patches of suitable habitat were not good predictors of genetic variation within samples. We also observed reduced genetic variation above several anthropogenic or natural barriers but did not detect an effect of large dams on genetic diversity.

Patterns of genetic variation were complex and inconsistent both between subbasins within the Boise River and among basins across the species' range. Molecular genetic analyses of bull trout have tended to find more variation within populations and greater differentiation among sites or streams (Spruell et al. 1999; Taylor et al. 1999, Kanda and Allendorf 2001; Neraas and Spruell 2001; Costello et al. 2003; Spruell et al. 2003; Whiteley et al. 2004).

The distribution of genetic variation is an important consideration for conservation management. These patterns reflect the summation of factors influencing colonization, dispersal, and gene flow and their interactions with the landscapes and geomorphic processes shaping the habitats available to the species. As shown by our data, we cannot presume that the genetic population structure in one region will accurately reflect that of another region because the relevant temporal and spatial scales for biological and physical processes may vary substantially across the species' range. It may be necessary to develop conservation management strategies that are as diverse as the systems we hope to manage.

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