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Title: Genetic Differentiation of Resident and Anadromous Rainbow Trout (Salmo gairdneri) in the Deschutes River Basin, Oregon

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Wild populations of rainbow trout (Salmo gairdneri) isolated above barriers to upstream migration are genetically differentiated from wild populations below barriers in the lower Deschutes River basin and from each other. Nonanadromous rainbow trout in the mainstem of the Deschutes River are differentiated from genetically more homogenous rainbow trout in the nonisolated tributaries. Gene diversity and likelihood analyses indicate that the greatest differences occur between rainbow trout in an isolated drainage, the White River, and rainbow trout in nonisolated drainages. These differences account for over 70% of the detectable biochemical genetic variation among groups in the Deschutes River basin. Differences among groups of rainbow trout from different tributaries and among groups of rainbow trout from isolated areas within tributaries represent significant but lesser proportions of the genetic differentiation among groups within the basin.

Analyses of morphological and biochemical differentiation among

native and nonnative rainbow trout suggest that White River rainbow trout may be remnants of an ancestral redband trout (Salmo sp.) population. Most White River populations are morphologically more similar to redband trout from the Oregon desert basins and native rainbow trout in the Deschutes River than to nonnative hatchery strains. White River populations have high frequencies of an allele for lactate dehydrogenase, LDH-4(100), uncommon in other populations in the Deschutes River basin and east of the Cascade Mountains, but lack the characteristic variation at other protein loci that would indicate they were derived from nonnative rainbow trout of coastal origins.

The lack of consistent patterns of differentiation between nonanadromous rainbow trout and rainbow trout presumed to be the progeny of the anadromous form indicate that some nonanadromous rainbow trout populations have probably evolved independently. Cluster analyses based on biochemical and morphological characters produced genetically similar groups that generally comprise populations within the same geographical area but not necessarily the same life history form. Consequently, a phenetic classification of rainbow trout into races by differences in anadromous behavior may not be not justified.

Genetic Differentiation of Resident and Anadromous Rainbow Trout (*Salmo gairdneri*) in the Deschutes River Basin, Oregon

by

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INTRODUCTION

Evolutionary theory emphasizes the importance of isolation in allowing genetic differences to accumulate within and among groups of organisms. Within species of the salmonid fishes different degrees of geographical and ecological isolation lead to genetic differentiation. Nearly all of the North American species are characterized by anadromous phenotypes, individuals that migrate, establish residence in salt-water and return to spawn in fresh-water (Rounsefell 1958). The tendency of anadromous fish to return to their natal streams to spawn results in potentially reproductively isolated groups and is a condition for genetic differentiation of fish from different streams. However, individuals of many salmonid fishes never establish salt-water residency, living out their lives within hundreds of yards of where they hatched or migrating only within streams (Rounsefell 1958, Cargill 1980). These fish survive in isolation above waterfalls, landlocked, or as nonanadromous phenotypes often sympatric with anadromous fish. Under conditions of restricted gene flow and limited population size, these groups may also become increasingly differentiated and uniquely adapted to local environments.

The identification and maintenance of such genetic diversity is essential to the efficient use and management of fishery resources (Behnke 1972, Larkin 1972, Thorpe et al. 1981). However, identification of genetic differences among populations is of limited

value in making appropriate decisions affecting the conservation and use of genetic variation in a fishery without estimates of the magnitude and source of the genetic diversity at different levels of organization within the geographical area comprising the fishery resource (Ryman 1983). Where the fishery resource includes both anadromous and nonanadromous fish in sympatry or parapatry, lack of this information makes such decisions difficult. Rainbow trout (Salmo gairdneri) include both anadromous and nonanadromous phenotypes throughout most of its range (Shapovalov and Taft 1954, Rounsefell 1958). Few authors have examined the distribution of genetic diversity within a drainage and included the diversity between anadromous rainbow trout (steelhead) and sympatric or parapatric nonanadromous (resident) populations as components of the total variation. For most drainages where both resident and steelhead rainbow trout occur, fishery resource managers must make decisions that potentially affect the genetic diversity of the species within the drainage based on conclusions from investigations that have examined genetic diversity at the regional level. These investigations often exclude resident rainbow trout (Allendorf 1975, Utter et al. 1980, Milner and Teel 1984, Milner et al. 1980, Wishard and Seeb 1983, Thorgaard 1983, Parkinson 1984, Schreck et al. 1986). Evidence from investigations of isolated populations of uncertain taxonomic status (Wilmot 1974, Gold 1977, Busack et al. 1980, Wishard et al. 1984), differences in migratory behavior (Neave 1944, Northcote et al. 1970, Chilcote et al. 1980), or admixtures of native and nonnative rainbow trout (Allendorf et al. 1980, Campton and Johnston

1985, Appendix B in this paper) suggests that levels of genetic differentiation of the species within a drainage may be considerable, but the pattern of diversity has not been quantified.

In this report, I examine biochemical genetic and morphological variation within a single drainage among isolated and nonisolated populations of rainbow trout (Salmo gairdneri). I have chosen to examine isolated and nonisolated populations rather than anadromous and nonanadromous populations, although they are related, for several reasons. First, the evolutionary dynamics of anadromous and nonanadromous behavior are only little understood. Lack of consistent taxonomic differences between the two forms in brown trout (Salmo trutta) (Ryman and Stahl 1981, Ryman 1983), Atlantic salmon (Salmo salar) (Ryman 1983), and rainbow trout (Behnke 1972, Allendorf and Utter 1979) over large geographical areas indicates that differentiation is the result of recent adaptations and not the evolution of a distinct phylogenetic line. Assuming such a pattern is valid for differentiation within smaller geographical areas, an analysis of genetic diversity that defines organizational levels by barriers to gene flow rather than life history differences provides a more consistent and complete picture of the differentiation within the drainage. I test this assumption and discuss evolution of life history forms in the Deschutes River basin with regard to their popular designation as races. Second, although the identification of individual life histories is possible for mature fish, it is extremely problematic in juvenile fish from streams inhabited by both steelhead

and resident rainbow trout (Nielson et al. 1985, Appendix C in this paper). Additionally, although the observation of steelhead and resident rainbow trout in a stream may suggest the segregation by life history phenotype of two randomly mating, sympatric populations, it does not confirm it. Neave (1944) documented inherited differences in meristic characters and migratory behavior between steelhead and resident rainbow in the Cowichan River, but evidence from other rivers is noticeably lacking.

This research is particularly timely. In the Columbia River, numbers of steelhead returning to spawn in tributaries have declined as a result of loss of spawning and juvenile rearing habitat, mortality at hydroelectric dams, and overfishing (Allen 1977, Raymond 1979, Netboy 1980). One solution is to remove extant barriers to upstream migration in order to increase the available habitat for steelhead. Where native resident rainbow trout have been isolated above barriers, such action would bring into sympatry populations of a species that have evolved separately. In jeopardy is the genetic diversity attributable to differences between isolated and nonisolated populations within the drainage. Clearly, estimates of the magnitude of genetic diversity distributed between isolated and nonisolated populations relative to the distribution of the remaining genetic diversity within organizational levels are essential for making decisions that potentially affect not just a single life history form but the genetic diversity of the whole species within the drainage.

METHODS

Study Area

The Deschutes River drains 26,700 square kilometers of northcentral Oregon. Anadromous salmonids once inhabited much of the basin, but since the 1950's, the Pelton-Round Butte Dam complex has limited salmon and steelhead spawning to the tributaries and mainstem of the lower 160 kilometers of river (Figure 1). Within this area, the White River is entirely blocked to upstream migration by waterfalls 3.4 kilometers from its mouth, although it does support populations of resident rainbow trout. Waterfalls on two tributaries, Jordan Creek and Tygh Creek, isolate resident rainbow trout from others within the White River. Steelhead have access to all of Bakeoven and Buck Hollow creeks, most of Trout Creek, and the lower portion of Nena Creek. A series of small waterfalls on East Foley Creek, a tributary in the headwaters of Trout Creek, and on Nena Creek isolate rainbow trout above the barriers from those below. The mainstem of the Deschutes River supports resident rainbow trout and juvenile steelhead.

Collection of Samples

Wild rainbow trout were collected from 22 locations above and below barriers within the lower Deschutes River basin (Figure 1). All age classes were included in collections made above barriers; rainbow trout collected from the mainstem were spawning adults; Samples from nonisolated locations in the tributaries were mostly juveniles but may have included adult resident rainbow trout. Nine

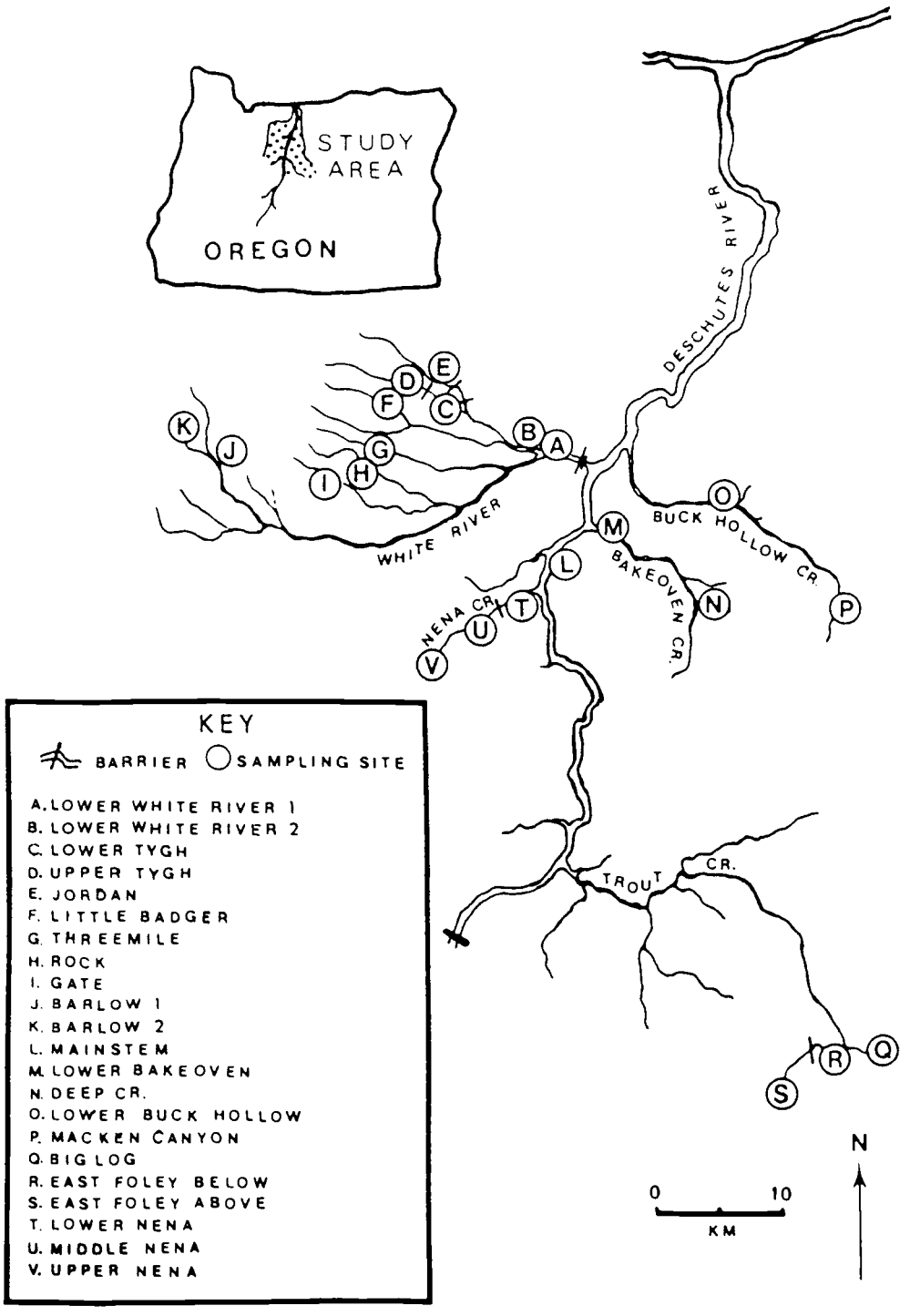

Figure 1. Map of lower Deschutes River with locations of sampling sites and barriers to upstream migration.

locations were sampled in more than one year. Four hatchery strains were also sampled. Two of the strains were founded from populations native to the river. The Deschutes strain was founded from the resident rainbow trout in the mainstem of the river; the Round Butte strain was founded primarily from steelhead that once spawned in Squaw Creek above the Pelton Dam (Kinunen and Moring 1978, Howell et al. 1985). The Oak Springs and the Cape Cod strains are not native to the drainage but have been released into various tributaries and may be presumed to represent other strains that also may have been released. Both strains were probably derived from McCloud River rainbow trout (Kinunen and Moring 1978, Dollar and Katz 1964). The common origin in the McCloud River and other coastal streams for many established strains of rainbow trout has also been documented by Needham and Behnke (1962), MacCrimmon (1971), and Busack and Gall (1980). Records provided by the Oregon Department of Fish and Wildlife of trout releases in the lower Deschutes River indicated the locations of populations with potential genetic admixtures of native and nonnative rainbow trout.

Electrophoresis

Fish collected for electrophoresis were frozen immediately on dry ice and stored for up to six months at -10C. Prior to electrophoresis, eyes, liver, and a portion of white muscle were extracted from each fish and placed in culture tubes. Tissue samples were homogenized with two drops of distilled water and centrifuged. Procedures for electrophoresis followed the methodology of Utter et al. (1974) and May (1975, 1979). Three buffer systems were used: (1)

RW - a tris, citric acid gel buffer at pH 8.5 and lithium hydroxide, boric acid tray buffer at pH 8.5 (Ridgway et al. 1970); (2) MF - a tris, boric acid, EDTA gel and tray buffer at pH 8.5 (Markert and Faulhaber 1965); and (3) AC - an amine citrate gel and tray buffer at pH 6.5 or 7.0 (Clayton and Tretiak 1972). Staining for enzyme activity followed methods outlined by Harris and Hopkinson (1976) and Allendorf et al. (1977). Table 1 lists the names, abbreviations, and numbers of loci expressed for the enzyme stains used. Nomenclature follows the system suggested by Allendorf and Utter (1979).

Morphology

Randomly subsampled individuals from collections of rainbow trout from each of the main sampling locations were preserved in 10% formalin and stored in 40% isopropanol for morphological analysis. Data were collected for the following 12 meristic characters and spotting pattern: (1) scales above the lateral line, (2) scales in the lateral series, (3) dorsal fin pterygiophores, (4) anal fin pterygiophores, (5) pelvic fin rays, (6) pectoral fin rays, (7) branchiostegal rays, (8) gill rakers on the upper arch, (9) gill rakers on the lower arch, (10) pyloric caeca, (11) basibranchial teeth, and (12) vertebrae. Most individuals were examined twice. Methods are those of Hubbs and Lagler (1957) and Troutman (1981) with these exceptions. Counts of dorsal and anal fin pterygiophores were made on the row nearest the vertebral column; both pterygiophores and vertebrae were counted from radiographs. Spotting patterns were quantified by comparing each fish to one of

Table 1. International Union of Biochemistry enzyme names (1979), Enzyme Commission numbers, loci, tissue, and buffers used in this study. Tissues M, L, and E are muscle, liver, and eye, respectively. Descriptions of buffers are included in the text.

I.U.B. Enzyme Name	E.C. Number	Loci	Tissue	Buffer
Aconitate hydratase	4.2.1.3	AH	L	RW, AC
Adenosine deaminase	3.5.4.4	ADA-1	M, E	AC, MF
		-2	M, E	AC, MF
Alcohol dehydrogenase	1.1.1.1	ADH	L	AC
Creatine kinase	2.7.3.2	CK-1	M	RW
		-2	M	RW
Dipeptidase	3.4.13.11	DPEP-1	M, E	RW, MF
		-2	M, E	RW, MF
Glucosephosphate isomerase	5.3.1.9	GPI-1	M	RW
		-2	M	RW
		-3	M	RW
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH-1	M	RW, AC
Isocitrate dehydrogenase (NADP+)	1.1.1.42	IDH-3,4	L	AC
Lactate dehydrogenase	1.1.1.27	LDH-4	L, E	RW, MF
		-5	E	MF
Malate dehydrogenase	1.1.1.37	MDH-1,2	L	AC
		-3,4	M	AC
Malate dehydrogenase (NADP+)	1.1.1.40	ME-3	M	AC
		-4	L	AC
Mannosephosphate isomerase	5.3.1.8	MPI	M	MF
Phosphoglucomutase	2.7.5.1	PGM-1	L, M	AC
		-2	M	AC
Superoxide dismutase	1.15.1.1	SOD	L	RW
Tripeptide aminopeptidase	3.4.11.4	LGG	M, E	RW, MF

three phenotypes found among wild fish in the Deschutes River Basin (Figure 2). Phenotypes A and C represent extremes and were assigned values of 1 and 3, respectively. Phenotype B is a generalized spotting pattern found in rainbow trout east of the Cascade mountains (Behnke 1979) and was given a value of 2. Fish with intermediate phenotypes were assigned intermediate values.

Statistics

Statisical analysis of biochemical variation is based on isozyme frequencies for alternative enzymes. Alternative forms of these enzymes, coded by different deoxynucleic acid sequences that comprise synonymous genes occuring at the same locus, are treated as alleles (Allendorf and Utter 1979). Of the polymorphic loci examined in this study, breeding experiments have documented Mendelian inheritance for electrophoretic variations at ADA (Kobayaskhi et al. 1984), ADH (Allendorf 1975), G3PDH (Allendorf 1975, Stahl and Ryman 1982), IDH (Allendorf 1975, Ropers et al. 1973, Reinitz 1977), LDH (Utter et al. 1973), MDH (Bailey et al. 1970, May et al. 1979), slow loci for ME (Stoneking et al. 1979), PGM (Utter et al. 1973), and SOD (Cederbaum and Yoshida 1972, Utter et al. 1973). I assumed Mendelian inheritance in the absence of breeding experiments for variation at the remaining loci when it met the criteria of Allendorf and Utter (1979): (1) Patterns of electrophoretic variation conform to the known molecular structure of the protein; (2) Expression of electrophoretic variation is parallel in different tissues from the same fish; (3) Multiple tests of electrophoretic variation in a tissue from an individual show consistent phenotypes.

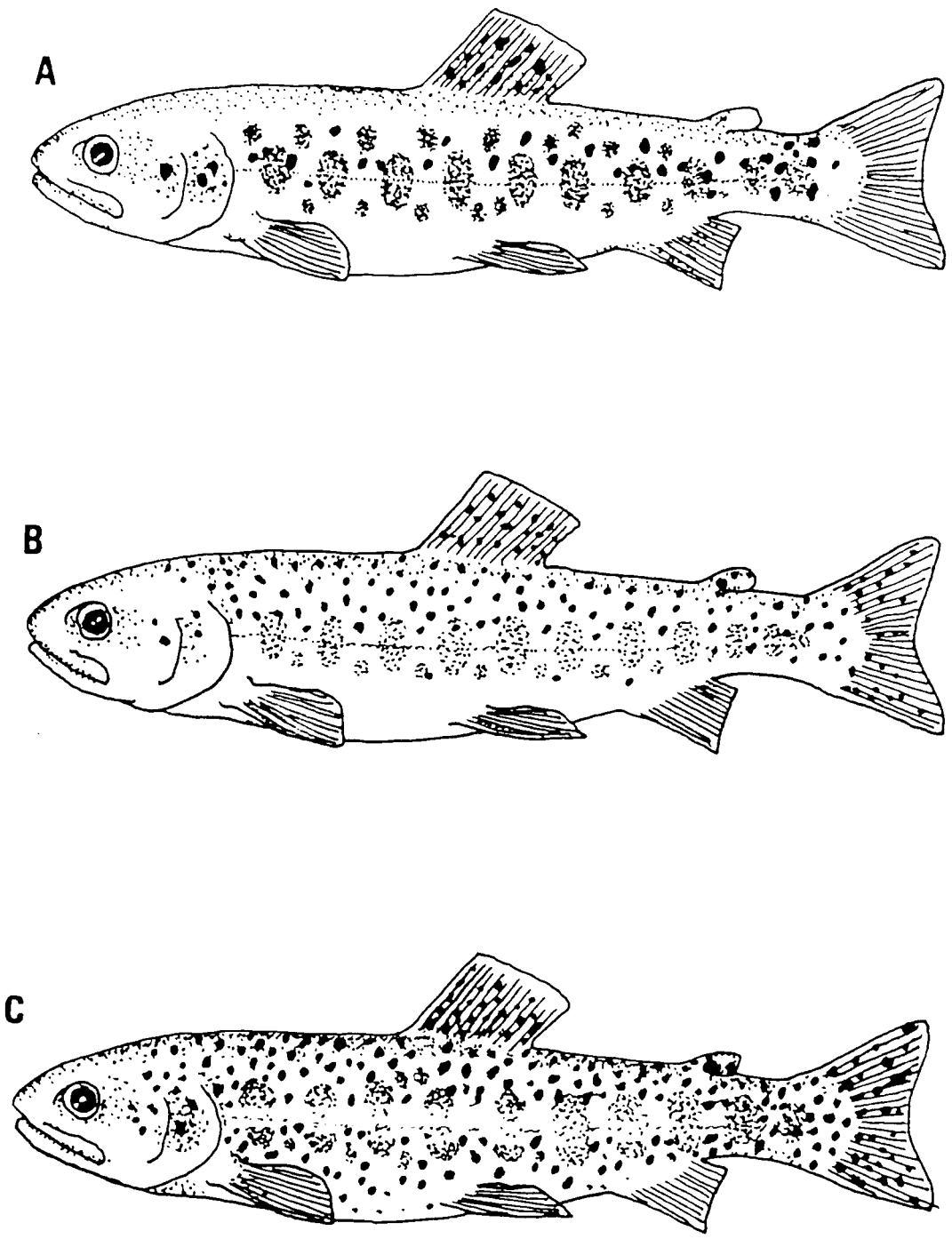

Figure 2. Generalized phenotypes used in analysis of spotting patterns.

I tested the hypothesis that each of the sample collections was drawn from a single, randomly mating unit by examining the observed distribution of genotypes at each locus for departures from the distribution expected under assumptions of Hardy-Weinberg equilibrium using a log likelihood ratio test (Sokal and Rohlf 1981). Tests were limited to those samples with expected values greater than one. Duplicated loci (IDH and MDH) were not included because expected values could not be calculated for a pair of loci. Average heterozygosities were calculated for all polymorphic loci using Hardy-Weinberg expectations and averaged over all loci. Polymorphic loci are those for which at least one sample had a frequency of the most common allele less than or equal to 0.95.

I based the analyses of biochemical genetic variation in the drainage on the organization of sampling locations into hierarchical levels (Figure 3). Gene diversity analysis compares the genetic diversity calculated for each level in the hierarchy to that expected of a single, panmictic population (Nei 1973, 1975, Chakraborty 1980, Chakraborty et al. 1982). The difference between the total diversity, if all sampling locations were part of a panmictic population, and the observed diversity within sampling locations is a measure of the absolute magnitude of genetic differentiation (D_{ST}) within the drainage. The relative measure of genetic differentiation (G_{ST}) is a ratio of D_{ST} to the total diversity and it estimates the proportion of genetic variation resulting from genetic differentiation within the drainage. This measure of population subdivision is comparable to the fixation index (F_{ST}) of Wright's F-statistics (Wright 1943). I

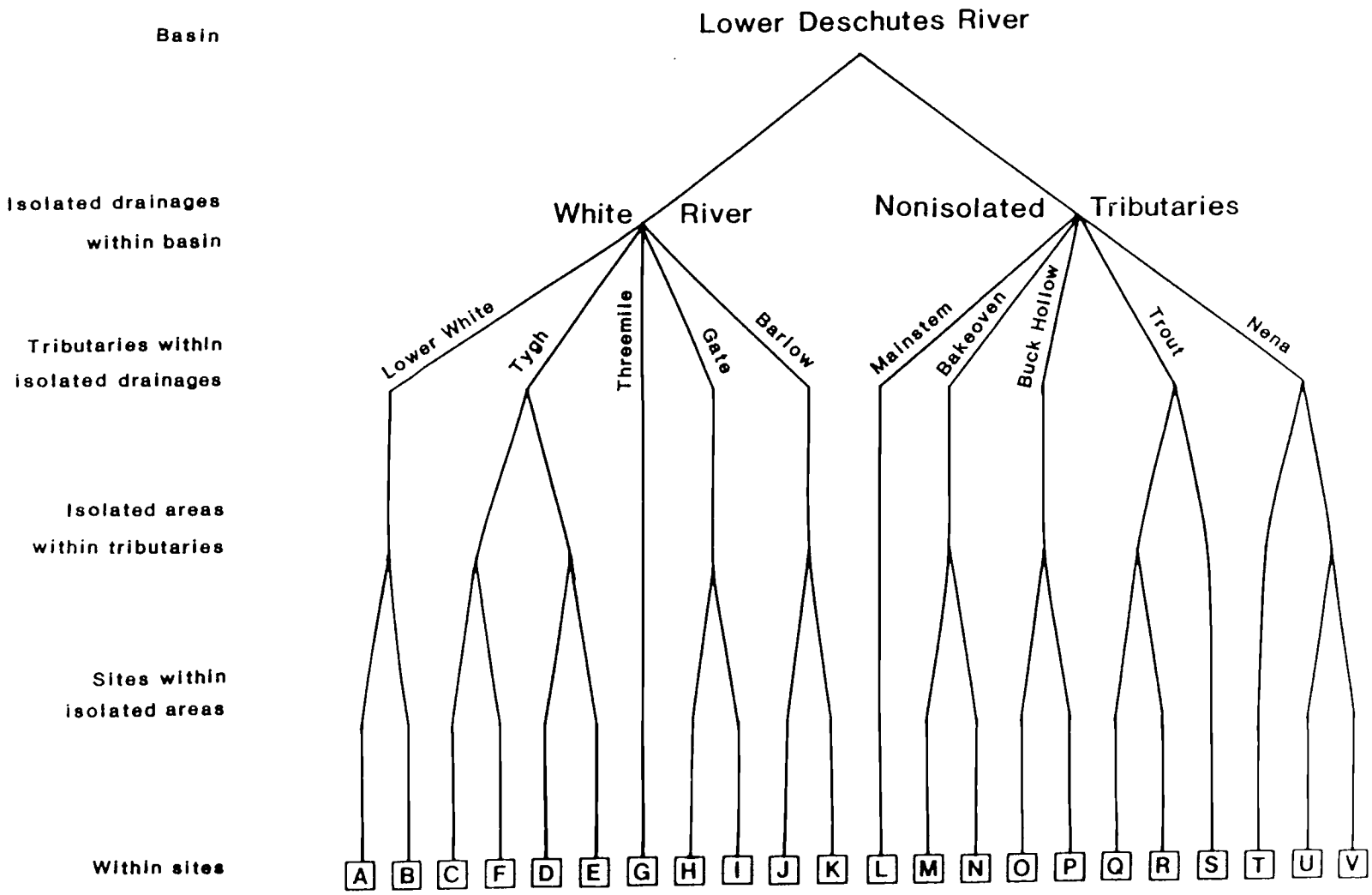

Figure 3. Hierarchy used in gene diversity analysis and log likelihood contingency table analysis of allelic heterogeneity in the lower Deschutes River basin. Sites correspond with locations in Figure 1.

decomposed relative and absolute measures of genetic differentiation further according to the following model:

$$H_T = H_S + D_{SA} + D_{AT} + D_{TD} + D_{DB}$$

where H_T = the total diversity,

H_S = the diversity within collection sites,

D_{SA} = the diversity among sites within isolated areas,

D_{AT} = the diversity among isolated areas within tributaries,

D_{TD} = the diversity among tributaries within isolated drainages,

and D_{DB} = the diversity between isolated drainages within the basin.

The mainstem of the lower Deschutes River was considered a separate tributary within a system of nonisolated tributaries. Analyzing the White River system and the system of nonisolated tributaries separately using the same model but without D_{DB} provided a comparison of the genetic infrastructure of the two systems. Each polymorphic locus was analyzed and averages were calculated based on all loci.

I tested hypotheses of allelic homogeneity at different levels of organization using the log likelihood ratio test (G test) in a nested contingency table analysis following the hierarchy in Figure 3. This analysis partitioned the total heterogeneity into within and among-group components in a manner analogous to analysis of variance and allowed calculation of standardized measures (G test statistic/degrees of freedom summed over all loci) for comparing heterogeneity at each organizational level (Smouse and Ward 1978). Both native and introduced hatchery strains were also included in a nested form in the analysis. I used a similar analysis to examine

differentiation between resident rainbow trout in the mainstem of the Deschutes River and rainbow trout below barriers in the nonisolated tributaries. Prior to both gene diversity analysis and tests of allelic heterogeneity at different heirarchical levels, I tested for allelic heterogeneity between years within sites. To avoid low expected values in tests of heterogeneity, only those loci with mean allelic frequencies of the common allele less than 0.95 were included and rare alleles were combined with more frequent classes. Modified significance levels were calculated by dividing the significance level by the number of loci to account for the increase in Type I error when making multiple comparisons (Cooper 1968).

Lack of knowledge of the relative importance of genetic and environmental components of morphological variation in each population precludes parallel analyses of the distribution of morphological genetic variation among and within organizational levels. Although the environmental component of morphological variation may confound interpretation of genetic differences, morphological and biochemical analyses should reflect congruent patterns of differentiation, but not necessarily degrees of differentiation, when they involve tests of evolutionary hypotheses (Buth 1984). A genetic component has been determined for number of scales (Neave 1944, Winter et al. 1980), fin rays (MacGregor and MacCrimmon 1977), branchiostegal rays (MacGregor and MacCrimmon 1977), gill rakers (Smith 1969), vertebrae (Winter et al. 1980), and numbers of pyloric caeca (Bergot et al. 1976, Blanc et al. 1979). I presumed a genetic basis for differences

in spotting pattern in the absence of controlled experiments based on its value in taxonomic studies of related trouts (Needham and Gard 1959, Quadri 1959, Bulkley 1963, Gold 1977, Behnke 1979).

I tested for morphological differentiation and compared the patterns of morphological differentiation to patterns of biochemical genetic differentiation. Rainbow trout from different locations were examined for morphological differences using analysis of variance. Tukey's studentized range method was used to test for a difference in means between all pairs of samples for each morphological character; character means were tested simultaneously using Hotelling's T^2 test. Canonical variates were generated by stepwise discriminant analysis to remove correlation among characters and maximize the differences among sampling locations. I constructed phenograms of genetic similarity to analyze biochemical and morphological differentiation in a heirarchical manner based on characteristics of the data and the clustering algorithm rather than on an imposed heirarchy. Phenograms of wild and hatchery samples were derived by the unweighted pair-group method using arithmetic averages (UPGMA) algorithm (Sneath and Sokal 1973). Cluster analysis of biochemical data was based on a matrix of Nei's genetic distance values (Nei 1972, 1978); cluster analysis of morphological data was based on a matrix of the Euclidean distance between canonical means. I examined the relationship of morphological and biochemical data by testing for correlation between morphological and Nei's genetic distance values and visually examining the phenograms for congruence.

RESULTS

Electrophoresis

I identified 14 polymorphic loci for further analysis. Isozyme frequencies and sample sizes for these loci are summarized in Appendix A. Rare alleles (<5.0%) occurred at six additional loci: ADA-2, CK-1, LDH-5, GPI-1, TAPEP, PGM-1. No variation occurred at four loci. All alleles have been observed in other populations of rainbow trout, except for the GPI-2(25) allele, which was unique to two populations in the White River, and the ADA-1(92) allele, which was unique to the nonnative hatchery strains.

Hardy-Weinberg Equilibrium

I failed to reject the hypothesis that each of the sample collections was drawn from a single, randomly mating unit. Genotypic distribution conformed to that expected under Hardy-Weinberg equilibrium with three exceptions. An excess of heterozygotes for LDH-4 occurred in samples from Deep Creek in 1985; a deficiency of heterozygotes occurred for AH in samples from East Foley Creek in 1984 (the result of poor resolution of the stained enzyme) and in middle Nena Creek in 1984. This number of departures from the Hardy-Weinberg distribution would be expected at the 5% significance level for the 96 comparisons. I concluded that each of the locations could be treated as a separate local population.

Allelic Heterogeneity Between Years

Allelic frequencies did not vary significantly between years within sites. Table 2 summarizes the results of the log likelihood

Table 2. Log likelihood contingency table analysis of allelic heterogeneity between years within sampling locations and among sampling locations. G = log likelihood ratio test statistic; df = degrees of freedom. One, two, or three asterisks indicate that the probability of a greater G value is less than 0.05, 0.01, or 0.001.

	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM	
Source of Variation	df/a	G/b	df	G	df	G	df	G	df	G	df	G	df	G
Total	17	74.07***	34	47.77	17	34.60*	17	71.83***	17	18.78	17	18.77	119	265.82***
Among sites	8	63.24***	16	22.43	8	25.18**	8	54.07***	8	12.10	8	13.80	56	190.81***
Within sites (between years)	9	10.83	18	25.35	9	9.43	9	17.76	9	6.68	9	4.96	63	75.01
Mainstem	1	0.00	2	3.12	1	0.72	1	0.55	1	0.54	1	0.27	7	5.20
Bakeoven (mouth)	1	2.11	2	0.67	1	2.32	1	1.73	1	0.32	1	0.01	7	7.15
Bakeoven (Deep Cr)	1	0.69	2	5.51	1	0.07	1	4.92	1	1.76	1	0.29	7	13.24
Buck Hollow (Lower)	1	0.01	2	2.64	1	1.80	1	0.84	1	0.32	1	2.33	7	7.95
Buck Hollow (Macken)	1	0.32	2	1.08	1	0.72	1	0.43	1	2.01	1	0.01	7	4.56
East Foley (above)	1	7.20*	2	8.13	1	0.52	1	3.06	1	1.21	1	0.07	7	20.18*
Big Log	1	0.34	2	0.57	1	0.06	1	1.68	1	0.06	1	1.91	7	4.61
Nena (Middle)	1	0.00	2	1.03	1	0.26	1	0.12	1	0.17	1	0.02	7	1.59
Nena (Lower)	1	0.16	2	2.61	1	2.96	1	4.45	1	0.31	1	0.05	7	10.54

contigency table analysis. The only significant difference occurred within the population in East Foley Creek in 1984 at the AH locus. Because a significant deficiency of heterozygotes at that locus in that sample was the result of poor electrophoretic resolution, data for AH in the 1984 sample from East Foley Creek were not included in any additional analyses. For all other sites, data from both years were combined.

Average Heterozygosities

Average heterozygosities range from 0.019 in the upper Tygh Creek population to 0.107 in the Oak Springs strain (Table 3). I could not test for significant differences among populations because calculation of the sampling variance for estimates of heterozygosity requires the assumption of linkage equilibria, which I did not test (Nei 1973). Several patterns are obvious, however. Most values are consistent with previous estimates for rainbow trout (Allendorf and Utter 1979). With the exception of the lower White River and Rock Creek populations, all populations in the White River have lower levels of genetic variation than those in the nonisolated tributaries. White River populations also have fewer rare alleles and more loci with extreme frequencies of the common allele than those in the unisolated tributaries. Low levels of heterozygosity, fewer rare alleles, and more loci fixed for a single allele should occur in small, isolated populations, which are subject to inbreeding and random genetic drift. The lower White River and Rock Creek are the only locations included in this study to have received direct introductions of hatchery rainbow trout in recent years; lower Tygh

Table 3. Average heterozygosity, number of rare alleles, and number of loci with frequencies of the common allele greater than 0.95.

Population	Average Heterozygosity	Number of rare alleles	Number of loci with $P < 0.95$
White River			
Lower White River	0.068	7	18
Lower Tygh Creek	0.059	5	19
Jordan Creek	0.051	7	20
Upper Tygh Creek	0.019	3	23
Little Badger Creek	0.044	2	21
Threemile Creek	0.052	8	22
Rock Creek	0.063	8	19
Gate Creek	0.046	5	21
Barlow Creek	0.049	8	21
Average	0.051	5.9	20.4
Unisolated Tributaries			
Mainstem	0.081	7	18
Bakeoven Creek	0.077	15	18
Buck Hollow Creek	0.078	12	19
Big Log Creek	0.063	8	19
East Foley Creek (below falls)	0.060	3	20
East Foley Creek (above falls)	0.069	10	19
Lower Nena Creek	0.070	7	20
Middle Nena Creek	0.081	5	18
Upper Nena Creek	0.076	4	17
Average			
All	0.073	7.9	18.7
Below barriers	0.072	8.8	18.0
Above barriers	0.075	6.3	19.0
Native Hatchery Strains			
Round Butte	0.075	8	19
Deschutes	0.080	5	19
Average	0.078	6.5	19.0
Nonnative Hatchery Strains			
Cape Cod	0.073	6	19
Oak Springs	0.107	3	16
Average	0.090	4.5	17.5

Creek was the site of introductions from 1934 to 1938; nonnative rainbow trout were released into Jordan Creek in 1925. The slightly greater levels of genetic variation in these populations, especially the highly isolated Jordan Creek, may reflect gene flow from hatchery strains. In contrast, the unusually low level of genetic variation in the upper Tygh Creek population occur after an apparently long period of isolation above waterfalls within the White River and reduced population sizes. I found no evidence of reduced heterozygosities in either native or introduced hatchery populations.

Gene Diversity Analysis

In a randomly mating population, 100% of the total genetic variation would occur among individuals within sites; G_{ST} would be zero. Within the Deschutes River basin, 87.6% of the genetic variation occurs within sites; G_{ST} is 0.124, indicating that 12.4% of the total genetic variation is distributed among subpopulations within the drainage (Table 4). This level of genetic differentiation lies at the upper end of the range for moderately differentiated populations based on similar analyses of different organisms (Hartl 1980). Decomposition of G_{ST} indicates that the most important component of genetic differentiation is the subdivision of the basin into the White River system and remaining, nonisolated areas. This accounts for 8.8% of the total genetic diversity and 71.1% of the genetic diversity distributed among subpopulations. Differences among tributaries are a small but significant component of genetic differentiation within the drainage. The differences between isolated populations within tributaries and among sites also contribute minor amounts.

Table 4. Distribution of genetic diversty in the lower Deschutes River basin based on biochemical genetic data for rainbow trout from 22 locations. Averages are calculated from all loci.

	Absolute Gene Diversity		Relative Gene Diversity				
Locus	Total	Within Sites	Isolated drainages within basin	Tributaries within isolated drainages	Isolated areas within tributaries	Sites within isolated areas	Within Sites
ACO	0.4294	0.3906	0.0012	0.0510	0.0182	0.0198	0.9096
ADA1	0.0014	0.0014	0.0000	0.0000	0.0000	0.0000	1.0000
ADH	0.0132	0.0129	0.0000	0.0076	0.0000	0.0152	0.9773
AGP1	0.0218	0.0214	0.0000	0.0183	0.0000	0.0000	0.9817
IDH3&4	0.4614	0.4555	0.0041	0.0033	0.0009	0.0043	0.9872
LDH4	0.4805	0.3216	0.3174	0.0110	0.0012	0.0008	0.6693
MDH1&2	0.0133	0.0129	0.0000	0.0150	0.0075	0.0075	0.9699
MDH3&4	0.0869	0.0838	0.0046	0.0196	0.0000	0.0104	0.9643
ME3	0.0115	0.0110	0.0087	0.0000	0.0087	0.0261	0.9565
ME4	0.0080	0.0078	0.0125	0.0000	0.0000	0.0125	0.9750
GPI2	0.0123	0.0112	0.0081	0.0650	0.0000	0.0163	0.9106
GL1	0.1106	0.1065	0.0145	0.0054	0.0027	0.0136	0.9638
PGM2	0.0164	0.0154	0.0122	0.0183	0.0000	0.0305	0.9390
SOD	0.1368	0.1294	0.0044	0.0197	0.0007	0.0292	0.9459
Average							
Basin	0.0751	0.0659	0.0878	0.0199	0.0053	0.0106	0.8763
Unisolated Tributaries	0.0755	0.0740		0.0132	0.0026	0.0040	0.9801
White River	0.0561	0.0513		0.0410	0.0143	0.0303	0.9144

The pattern of genetic differentiation in the White River system differs from that in the system of nonisolated tributaries. The White River system is more differentiated (G_{ST} = 0.086) than the system of nonisolated tributaries (G_{ST} = 0.02). Qualitatively, the White River system is moderately differentiated and the system of nonisolated tributaries is little differentiated (Hartl 1980). Greater differentiation of the White River occurs at all levels of comparison. The differences among tributaries account for the greatest proportion of genetic divergence in both systems. However, the relative importance of this level of organization is much greater for the system of nonisolated tributaries than for the White River system. Differentiation at this geographical level explains approximately 66% of the total differentiation within the nonisolated tributaries and 48% of the total differentiation within the White River.

Individual loci contribute to differentiation within the lower Deschutes River at different levels of organization. Except for LDH-4, G_{ST} values at each locus are comparable, ranging from 0 to 0.09, which is expected under a model of neutral selection (Allendorf and Phelps 1981). The most important contribution is the differentiation of White River populations from the others at the LDH-4 locus, accounting for 31.7% of the total genetic diversity at that locus. The DPEP locus also contributed to the differences between isolated drainages. The AH locus accounted for little of the differences between isolated drainages but contributed greatly to the differentiation of tributaries within isolated drainages, as did the GPI2 locus and the MDH-3,4 locus. The PGM-2, SOD, and ME-3 loci

accounted for most of the differences between sites within isolated areas. Genetic diversity at the IDH-3,4 locus was almost entirely concentrated within sites and contributed little to differentiation within the basin.

Allelic Heterogeneity Among Groups of Populations

Only six loci, AH, IDH-3,4, LDH-4, MDH-3,4, DPEP, and SOD met the minimum expected value criteria for testing. At almost every level of organization, I rejected the hypothesis that no differences in allelic frequencies occurred among populations forming groups (Table 5). Exceptions were at the level of differences between sites within tributaries. I found no evidence of allelic heterogeneity within the lower White River and Barlow Creek in the White River system or within Bakeoven Creek and Buck Hollow Creek in the system of nonisolated tributaries.

Ranking and comparing the standardized measure of heterogeneity (G/df) calculated at each level reveals considerable differences in the magnitude and distribution of allelic heterogeneity. Two comparisons show significantly greater heterogeneity than any others: the comparison of White River populations with the populations in the nonisolated tributaries (G/df = 176.81) and the comparison of introduced and native hatchery strains (G/df = 71.47). In both cases, allelic differences at the LDH-4 locus are the major source of allelic heterogeneity. Populations in the White River and introduced hatchery populations are characterized by high frequencies of the LDH-4(100) allele; native hatchery populations and wild populations in the

Table 5. Log likelihood contingency analysis of allelic heterogeneity among sampling locations. G = log likelihood ratio test statistic; df = degrees of freedom. One, two, or three asterisks indicate that the probability of a greater G value is less than 0.05, 0.01, or 0.001.

Source of Variation	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM		Standardized Measure (G/df)
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	
Total Basin	25	378.03***	50	263.56***	25	1478.94***	25	331.38***	25	158.31***	25	279.68***	175	2889.89***	16.51
Between hatchery and wild	1	16.83***	2	7.39	1	55.90***	1	55.50***	1	15.02***	1	53.16***	7	203.80***	29.11
Within hatchery and wild	24	361.20***	48	256.18***	24	1423.04***	24	275.88***	24	143.28***	24	226.52***	168	2686.09***	15.99
Hatchery	3	107.98***	6	36.42***	3	271.00***	3	114.33***	3	17.36**	3	88.53***	21	635.61***	30.27
Between origins	1	101.64***	2	16.44**	1	251.99***	1	82.72***	1	6.62	1	40.87***	7	500.28***	71.47
Within origins	2	6.34	4	19.98**	2	19.01***	2	31.61***	2	10.74*	2	47.66***	14	135.34***	9.67
Native	1	5.45	2	11.02*	1	19.01***	1	8.12*	1	10.36***	1	0.02	7	53.99***	7.71
Nonnative	1	0.89	2	8.96	1	0.00	1	23.49***	1	0.38	1	47.64***	7	81.35***	11.62
Wild	21	253.23***	42	219.76***	21	1152.04***	21	161.55***	21	125.92***	21	137.98***	147	2050.48***	13.95
Between isolated drainages	1	28.09***	2	58.53***	1	1077.68***	1	3.07	1	69.50***	1	0.78	7	1237.64***	176.81
Within isolated drainages	20	225.14***	40	161.23***	20	74.36***	20	158.48***	20	56.42***	20	137.21***	140	812.84***	5.81

Table 5 (continued). Log likelihood contingency analysis of allelic heterogeneity among sampling locations.

Source of Variation	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM		Standardized Measure
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	(G/df)
White River	10	167.83***	20	131.98***	10	48.29***	10	95.91***	10	28.11*	10	118.07***	70	590.20***	8.43
Among Tributaries	4	56.10***	8	50.19***	4	46.10***	4	36.32***	4	11.71	4	43.48***	28	243.90***	8.71
Within Tributaries	6	111.73***	12	81.79***	6	2.19	6	59.60***	6	16.41	6	74.58***	42	346.30***	8.25
Lower White	1	5.77	2	0.74	1	0.08	1	1.08	1	0.00	1	0.03	7	7.70	1.10
Tygh	3	78.71***	6	67.64***	3	0.00	3	53.66 **	3	11.66	3	44.95***	21	256.62***	12.22
Between isolated areas	1	74.56***	2	6.21	1	0.00	1	0.21	1	5.81	1	1.57	7	88.36***	12.62
Within isolated areas	2	4.14	4	61.43***	2	0.00	2	53.45***	2	5.85	2	43.39***	14	168.27***	12.02
Tygh (below)	1	4.14	2	25.92***	1	0.00	1	21.76***	1	5.85	1	13.96***	7	71.64***	10.23
Tygh (above)	1	0.00	2	35.51***	1	0.00	1	31.69***	1	0.00	1	29.43***	7	96.63***	13.80
Gate	1	20.54***	2	7.24	1	2.11	1	4.79	1	4.75	1	29.14***	7	68.56***	9.79
Barlow	1	6.72	2	6.17	1	0.00	1	0.06	1	0.00	1	0.47	7	13.42	1.92

Table 5 (continued). Log likelihood contingency analysis of allelic heterogeneity among sampling locations.

Source of Variation	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM		Standardized Measure
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	(G/df)
Unisolated tributaries	10	57.31***	20	29.24	10	26.07*	10	62.57***	10	28.31**	10	19.14	70	222.64***	3.18
Among tributaries	4	45.42***	8	16.96	4	21.51**	4	35.97***	4	2.57	4	12.21	28	134.63***	4.81
Within tributaries	6	11.89	12	12.29	6	4.56	6	26.60**	6	25.75**	6	6.93	42	88.01***	2.10
Bakeoven	1	0.30	2	1.50	1	2.52	1	4.29	1	0.15	1	0.15	7	8.91	1.27
Buck Hollow	1	0.80	2	1.00	1	0.61	1	3.84	1	0.12	1	0.24	7	6.60	0.94
Trout	2	9.58*	4	8.53	2	0.01	2	5.92	2	8.21	2	2.05	14	34.30**	2.45
Between isolated areas	1	9.05*	2	1.88	1	0.00	1	4.30	1	0.34	1	1.92	7	17.49*	2.50
Within isolated areas	1	0.53	2	6.65	1	0.01	1	1.61	1	7.88*	1	0.14	7	16.82*	2.40
Trout (below)	1	0.53	2	6.65	1	0.01	1	1.61	1	7.88*	1	0.14	7	16.82*	2.40

Table 5 (continued). Log likelihood contingency analysis of allelic heterogeneity among sampling locations.

Source of Variation	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM		Standardized Measure
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	(G/df)
Nena	2	1.21	4	1.27	2	1.41	2	12.55*	2	17.26**	2	4.48	14	38.19***	2.73
Between isolated areas	1	0.96	2	1.14	1	1.41	1	0.25	1	7.60*	1	0.06	7	11.42	1.63
Within isolated areas	1	0.25	2	0.13	1	0.00	1	12.30***	1	9.66*	1	4.42	7	26.76***	3.82
Nena (above)	1	0.25	2	0.13	1	0.00	1	12.30***	1	9.66*	1	4.42	7	26.76***	3.82

mainstem and nonisolated tributaries are characterized by frequencies of the alternate alleles ranging from 0.333 to 0.70 (Figure 4). Tests of allelic heterogeneity at other loci for these comparisons, however, do not show parallel results.

Analysis of standardized measures for comparisons within the White River and within the system of nonisolated tributaries at a given level confirm the results of the gene diversity analysis. First, levels of heterogeneity are consistently greater in the White River than in the nonisolated tributaries of the Deschutes River, indicating greater differentiation. Standardized measures for differences among tributaries are greater for the White River (G/df = 8.7) than for the nonisolated tributaries of the Deschutes River (G/df = 4.8). Values for differences within tributaries are also greater for the White River (G/df = 8.3) than the system of nonisolated tributaries (G/df = 2.1). In almost all tributaries in the White River, standardized measures for comparisons of sites are of the same magnitude as measures for differences among tributaries. Second, differences among tributaries are relatively more important in the organization of genetic diversity within the nonisolated tributaries than within the White River. The ratio of the standardized measures for among-group comparisons to within-group comparisons, used in a manner analogous to an F-statistic to examine differences in genetic dispersion (Smouse and Ward 1978), indicates that the nonisolated tributaries of the Deschutes River form more discrete clusters than tributaries of the White River. This ratio is 1.06 (8.71:8.25) for the among-tributaries to within-tributaries comparison for the White

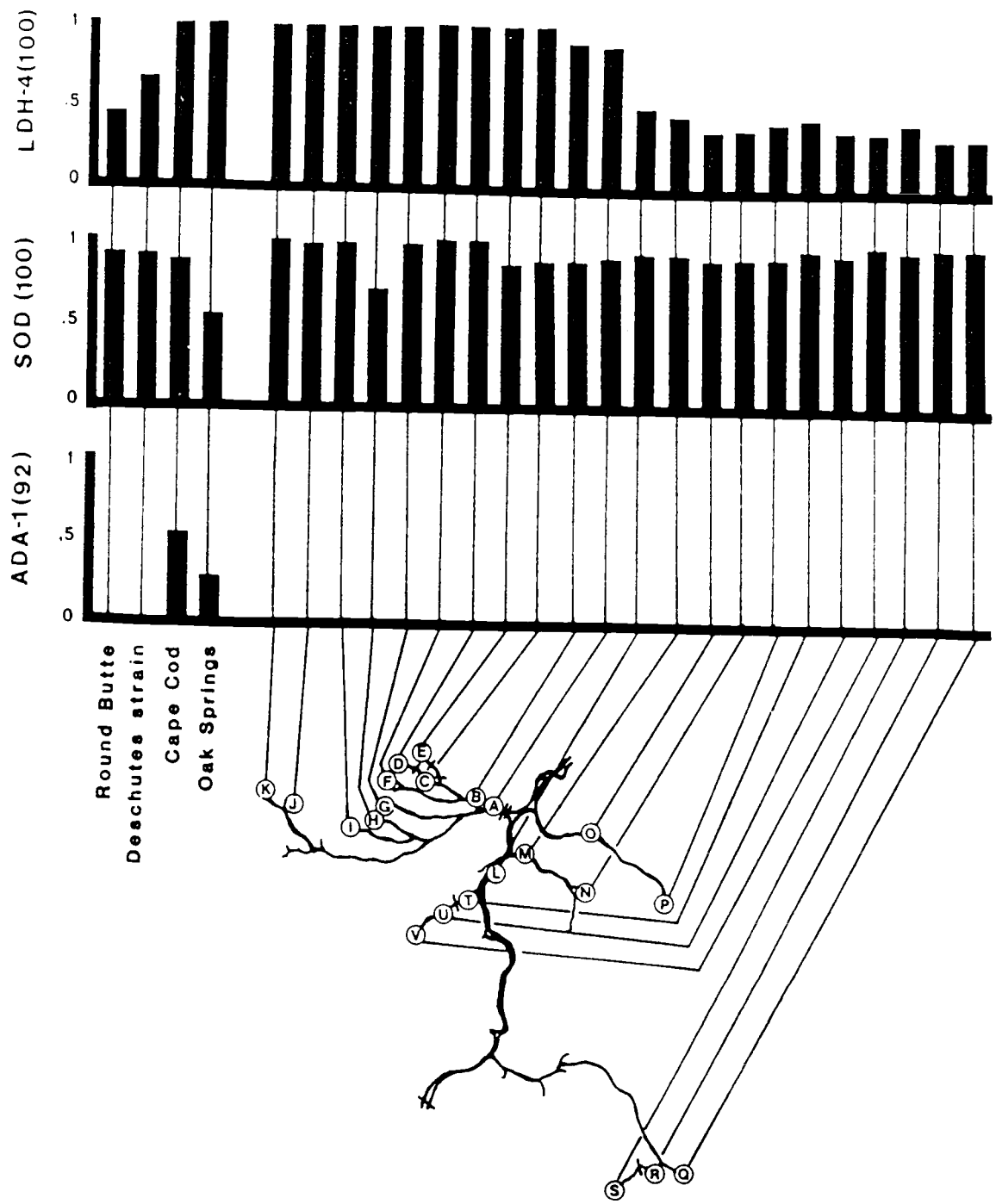

Figure 4. Distribution of allelic frequencies for rainbow trout in the lower Deschutes River basin at three loci that separate native rainbow trout east of the Cascade Mountains and nonnative rainbow trout of coastal origins. Populations A to K are in the White River; L to V are in the unisolated tributaries. Names of individual sampling sites are in Figure 1.

River and 2.29 (4.81:2.1) for the same comparison in the nonisolated tributaries of the Deschutes River.

A major component of the allelic heterogeneity within the system of nonisolated tributaries of the Deschutes River is differentiation of the resident rainbow trout in the mainstem of the Deschutes River from the populations in the tributaries. I rejected the hypothesis of allelic homogeneity between resident rainbow trout in the mainstem of the Deschutes River and the populations below barriers in the nonisolated tributaries. Significant differences occurred at four of the six loci examined and the sum of the tests (Table 6). Significant allelic heterogeneity also occurred among the tributaries at three of the six loci and the sum of tests. However, the magnitude of heterogeneity among tributary populations is significantly less (G/df = 2.5) than the heterogeneity between tributary populations and the mainstem population (G/df = 9.1), which is comparable to the that among isolated populations in the White River.

Biochemical Genetic Similarity

Two features of the phenogram of biochemical genetic similarity are important (Figure 5). First, the populations included in this study form three distinct and easily interpretable groups. The first group (Custer A) includes only the two introduced hatchery populations. The second group (Cluster B) includes only the White River populations. Two subclusters are present within the White River. One subcluster comprises the two populations isolated above waterfalls in Tygh Creek system and Rock Creek. The second subcluster

Table 6. Log likelihood contingency analysis of allelic heterogeneity between ananadromous rainbow trout from the mainstem and rainbow trout from unisolated locations in tributaries of the lower Deschutes River. G = log likelihood ratio test statistic; df = degrees of freedom. One, two, or three asterisks indicate the probability of a greater G value is less than 0.05, 0.01, or 0.001.

Source of Variation	AH		IDH-3,4		LDH-4		MDH-3,4		DPEP		SOD		SUM		Standardized Measure
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	(G/df)
Total	10	57.31	20	29.24	10	26.07*	10	62.57***	10	28.31**	10	19.14	70	222.65***	3.18
Between mainstem and unisolated tributaries	1	14.64***	2	12.99**	1	16.37***	1	19.01***	1	0.85	1	0.02	7	63.89***	9.13
Within mainstem and unisolated tributaries	9	42.67***	18	16.25	9	9.70***	9	43.56***	9	27.461**	9	19.12	63	158.76***	2.52
Unisolated tributaries	9	42.67***	18	16.25	9	9.70***	9	43.56***	9	27.461**	9	19.12	63	158.76***	2.52

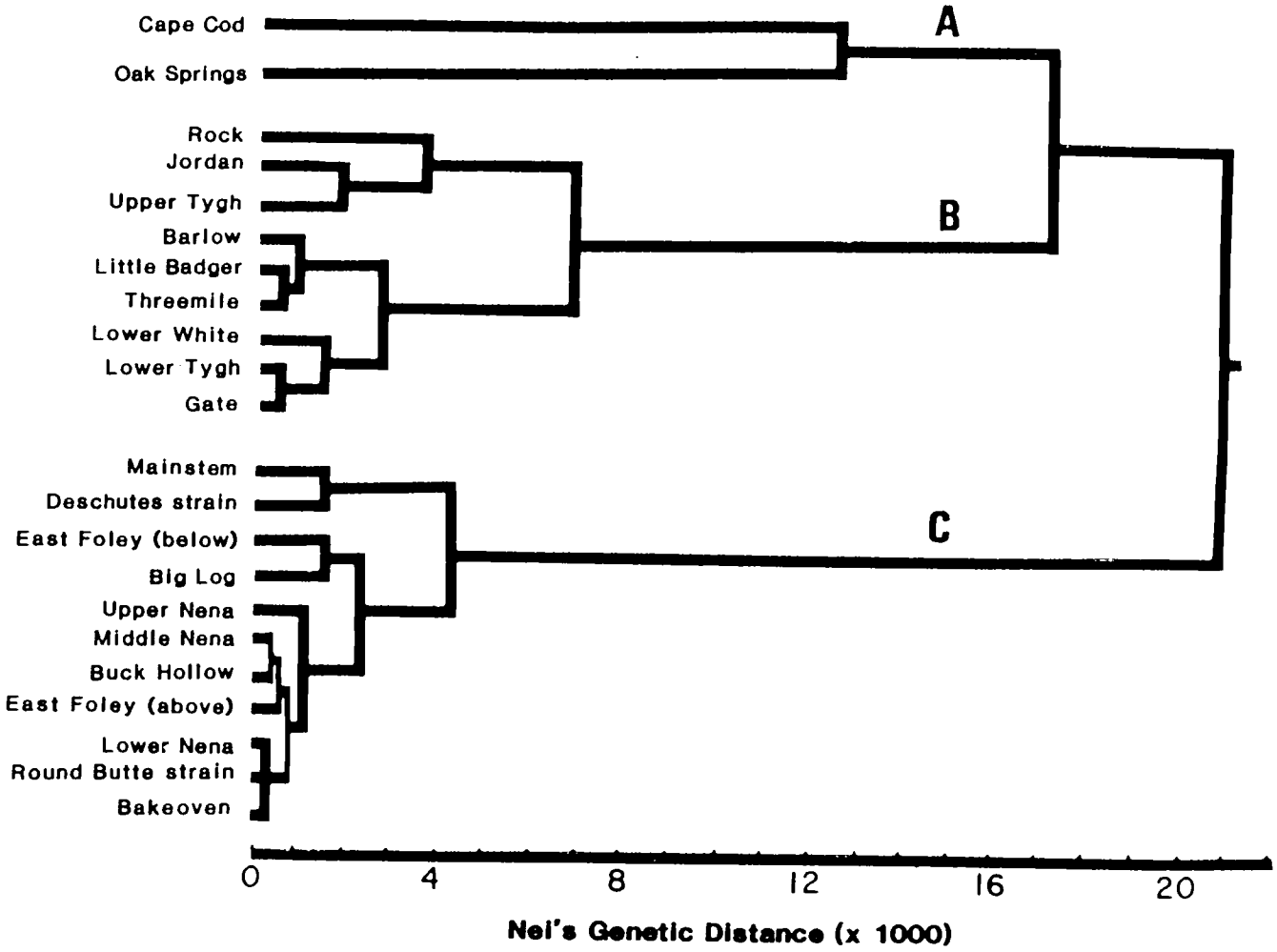

Figure 5. Phenogram of biochemical genetic similarity of hatchery and wild rainbow trout. A, B, and C denote the three main clusters.

comprises populations from the lower part of the White River system and populations from small, isolated, headwater streams. The third group (Cluster C) includes all the hatchery and wild populations native to the nonisolated tributaries of the Deschutes River. Within this group, the populations from the tributaries form a rather homogenous subcluster. No patterns are obvious, except for the similarity of populations in East Foley Creek below the barrier and Big Log Creek, which are geographically proximate and nonisolated. Rainbow trout above barriers in Nena Creek and East Foley Creek are neither most similar to each other nor most similar to the populations directly below barriers. However, the wild resident rainbow trout population in the mainstem of the Deschutes River and the hatchery strain that was derived from it clearly form a second subcluster that diverges from the first group.

The second important feature of the phenogram is the apparent similarity between the rainbow trout in the White River and the introduced hatchery populations. This partially reflects their nearly identical allelic frequencies at the LDH-4 locus. It is also an artifact of the UPGMA algorithm. When allelic frequencies for rainbow trout at sites within tributaries without significant allelic heterogeneity (the lower White River, Barlow Creek, Bakeoven Creek, and Buck Hollow Creek) are not combined, the UPGMA algorithm assigns the White River and nonisolated tributary populations of the Deschutes River to the same group. Other algorithms also produced dissimilar results. Nei's genetic distance between Cluster A and Cluster B using the unweighted average is 0.01740; between Cluster B and Cluster C, it

is 0.01792. Consequently, although the White River populations are more similar to the introduced hatchery strains using this algorithm, it is probably more realistic to consider each of these clusters as an equally distinct and differentiated group.

Morphology

Significant differences were detected among rainbow trout populations from different locations by analysis of variance for every character except basibranchial teeth. Weakly developed basibranchial teeth were present in one trout each from Little Badger Creek, Threemile Creek, and the mainstem of the Deschutes River. Analysis of pairwise tests of univariate and multivariate means (Table 7) suggests morphological homogeneity of several groups. Univariate means were significantly different in 166 of the 190 test of all possible pairs of populations; multivariate means were significantly different in 175 of the 190 comparisons (Table 8). Nonsignificant tests resulted from comparisons of Threemile, Gate, and Barlow creeks in the White River system, all sites above and below falls in Nena and Trout creeks, and wild and hatchery populations of rainbow trout from the nonisolated tributaries of the Deschutes River.

Canonical Variate and Cluster Analysis of Morphological Similarity

Six characters provided the best discrimination among populations in the stepwise discriminant analysis. These are scales above the lateral line, scales in the lateral series, branchiostegal rays, pyloric caeca, vertebrae, and spotting pattern. The first three canonical variates account for 85% of the total dispersion based on

Table 7. Means, standard errors, and sample sizes (N) for 12 morphological characters, proportion of sample with basibranchial teeth, and means for six canonical variates (CV).

SAMPLE	N	SCALES ABOVE LATERAL LINE	SCALES IN LATERAL SERIES	DORSAL FIN PTERYGIOPHORES	ANAL FIN PTERYGIOPHORES	PELVIC FIN RAYS	PECTORAL FIN RAYS
LOWER WHITE	20	30.20 (.53)	143.20 (1.70)	13.10 (.12)	12.45 (.17)	9.80 (.12)	14.20 (.12)
LOWER TYGH	19	32.58 (.47)	139.90 (1.63)	12.68 (.13)	12.37 (.11)	9.63 (.11)	14.21 (.16)
UPPER TYGH	20	32.70 (.40)	144.11 (1.42)	12.65 (.11)	12.15 (.08)	10.15 (.11)	14.70 (.15)
JORDAN	19	29.42 (.45)	128.26 (1.75)	12.90 (.13)	12.26 (.15)	9.47 (.14)	14.21 (.12)
LITTLE BADGER	20	34.95 (.40)	149.35 (1.19)	13.05 (.15)	12.20 (.09)	9.60 (.11)	14.35 (.13)
THREEMILE	20	35.05 (.41)	145.85 (1.41)	13.00 (.13)	12.35 (.13)	9.40 (.11)	13.70 (.11)
ROCK	20	33.70 (.45)	141.70 (1.33)	13.70 (.13)	12.70 (.11)	9.90 (.07)	14.50 (.14)
GATE	19	34.58 (.73)	146.95 (2.11)	12.95 (.16)	12.58 (.14)	9.79 (.10)	13.68 (.15)
BARLOW	20	37.65 (.53)	150.95 (1.57)	12.75 (.12)	12.15 (.15)	9.60 (.13)	13.70 (.16)
MAINSTEM	20	31.80 (.45)	140.15 (1.35)	12.95 (.11)	12.45 (.11)	9.80 (.12)	14.20 (.19)
BAKEOVEN	15	34.47 (.31)	145.53 (2.01)	12.93 (.15)	12.47 (.13)	9.93 (.07)	14.00 (.14)
BUCK HOLLOW	15	33.93 (.49)	150.13 (1.64)	13.27 (.15)	12.53 (.19)	9.80 (.11)	13.93 (.21)
NENA (ABOVE)	10	31.40 (.40)	150.00 (2.64)	13.10 (.18)	12.60 (.16)	10.50 (.17)	14.10 (.23)
NENA (BELOW)	5	31.40 (1.03)	154.80 (1.46)	13.60 (.25)	12.40 (.25)	10.80 (.37)	14.40 (.25)
BIG LOG	10	31.60 (.50)	147.40 (1.99)	12.40 (.16)	12.20 (.25)	9.60 (.16)	13.20 (.94)
EAST FOLEY (ABOVE)	10	31.60 (.45)	142.80 (1.94)	12.80 (.20)	12.10 (.13)	9.60 (.16)	13.50 (.17)
DESCHUTES STRAIN	15	29.87 (.49)	135.60 (1.51)	13.20 (.15)	12.40 (.19)	9.73 (.15)	13.80 (.11)
OAK SPRINGS STRAIN	15	30.60 (.64)	135.71 (1.91)	13.87 (.19)	12.87 (.17)	9.73 (.15)	14.60 (.13)
CAPE COD STRAIN	15	28.93 (.51)	130.27 (1.45)	13.07 (.21)	12.67 (.16)	9.93 (.07)	14.07 (.18)
ROUND BUTTE STRAIN	20	32.35 (.60)	145.45 (1.76)	12.90 (.16)	12.25 (.14)	9.95 (.09)	13.65 (.11)

Table 7. Continued.

SAMPLE	BRANCHIOSTEGAL RAYS	GILL RAKERS UPPER ARCH	GILL RAKERS LOWER ARCH	PYLORIC CAECA	VERTEBRAE
LOWER WHITE	11.25 (.16)	7.20 (.14)	11.05 (.15)	40.45 (1.47)	63.00 (.32)
LOWER TYGH	11.37 (.16)	7.05 (.18)	11.68 (.17)	41.17 (1.73)	63.00 (.24)
UPPER TYGH	10.90 (.10)	7.60 (.11)	12.55 (.21)	33.55 (1.08)	62.85 (.20)
JORDAN	11.37 (.16)	6.95 (.18)	11.21 (.20)	35.42 (1.27)	63.84 (.16)
LITTLE BADGER	10.80 (.12)	7.30 (.13)	12.30 (.18)	35.05 (1.08)	62.60 (.13)
THREEMILE	10.90 (.16)	7.20 (.12)	11.95 (.11)	41.15 (1.43)	62.75 (.31)
ROCK	11.45 (.14)	7.35 (.11)	11.95 (.14)	52.10 (1.78)	63.20 (.25)
GATE	10.63 (.16)	7.00 (.13)	11.53 (.43)	39.00 (1.03)	63.21 (.21)
BARLOW	10.60 (.11)	6.85 (.17)	11.80 (.17)	38.20 (1.32)	62.65 (.24)
MAINSTEM	11.75 (.16)	7.35 (.33)	11.70 (.32)	49.70 (2.80)	63.40 (.27)
BAKEOVEN	11.20 (.15)	7.40 (.21)	12.47 (.17)	40.40 (1.45)	64.07 (.18)
BUCK HOLLOW	11.53 (.19)	7.53 (.19)	12.33 (.21)	39.93 (1.29)	64.53 (.22)
NENA (ABOVE)	11.00 (.15)	7.50 (.22)	12.30 (.15)	40.44 (2.18)	63.80 (.20)
NENA (BELOW)	11.20 (.37)	7.00 (.32)	11.80 (.49)	40.60 (3.61)	64.20 (.37)
BIG LOG	10.90 (.18)	7.10 (.18)	11.50 (.22)	39.40 (1.95)	65.00 (.15)
EAST FOLEY (ABOVE)	10.90 (.18)	7.10 (.23)	11.90 (.23)	37.40 (1.05)	64.40 (.22)
DESCHUTES STRAIN	10.93 (.12)	7.13 (.17)	11.47 (.19)	54.33 (2.33)	62.80 (.24)
OAK SPRINGS STRAIN	11.53 (.22)	7.47 (.19)	11.47 (.17)	53.40 (1.36)	61.87 (.32)
CAPE COD STRAIN	10.33 (.27)	7.80 (.18)	11.47 (.27)	55.87 (2.47)	62.33 (.25)
ROUND BUTTE STRAIN	11.70 (.15)	7.50 (.12)	12.25 (.14)	43.90 (1.02)	63.30 (.21)

Table 7. Continued.

SAMPLE	SPOTTING INDEX	BASI-BRANCHIAL TEETH	CV I	CV II	CV III	CV IV	CV V	CV VI
LOWER WHITE	2.40 (.13)	0.00	-0.32	0.76	-0.04	0.98	0.32	0.40
LOWER TYGH	2.37 (.16)	0.00	-0.04	0.36	0.33	-0.25	0.51	0.26
UPPER TYGH	2.90 (.07)	0.00	1.35	1.04	0.74	0.49	0.38	0.17
JORDAN	2.63 (.11)	0.00	-0.91	2.61	0.29	-0.63	0.52	-0.18
LITTLE BADGER	2.25 (.19)	0.05	1.77	-0.50	0.36	0.48	0.37	-0.44
THREEMILE	2.55 (.11)	0.05	1.12	-0.45	0.81	-0.20	0.04	0.19
ROCK	2.00 (.10)	0.00	-0.89	-1.01	0.05	-0.80	-0.14	0.49
GATE	2.37 (.14)	0.00	1.37	-0.22	0.41	0.06	-0.36	-0.17
BARLOW	2.60 (.17)	0.00	2.48	-1.07	1.00	-0.34	-0.11	-0.05
MAINSTEM	1.70 (.13)	0.05	-1.47	-0.51	-0.67	-0.44	0.26	0.23
BAKEOVEN	2.00 (.17)	0.00	0.79	-0.17	-0.69	-0.69	-0.22	-0.18
BUCK HOLLOW	2.07 (.12)	0.00	0.94	0.00	-1.46	-0.39	-0.17	0.35
NENA (ABOVE)	1.90 (.23)	0.00	0.38	0.10	-1.15	1.13	-0.46	0.04
NENA (BELOW)	1.80 (.37)	0.00	0.60	-0.11	-1.78	1.29	-0.48	0.28
BIG LOG	2.00 (.00)	0.00	0.58	0.81	-1.44	0.24	-1.06	-0.02
EAST FOLEY (ABOVE)	2.00 (.15)	0.00	0.38	0.94	-0.86	0.08	-0.53	-0.43
DESCHUTES STRAIN	1.47 (.13)	0.00	-2.43	-0.66	0.21	0.33	-0.50	-0.32
OAK SPRINGS STRAIN	1.33 (.13)	0.00	-2.69	-1.35	0.26	0.30	0.81	-0.37
CAPE COD STRAIN	2.27 (.21)	0.00	-2.55	0.18	1.83	0.48	-1.03	0.14
ROUND BUTTE STRAIN	1.45 (.11)	0.00	-0.58	-0.75	-1.18	0.14	0.57	-0.25

Table 8. P values from Hotelling's T square test (above diagonal) and morphological characters with significantly different means ($P < .05$) in comparisons between populations by Tukey's test (below diagonal).

LOWER WHITE		.0065	.0000	.0001	.0000	.0000	.0000	.0007	.0000	.0001	.0000	.0000	.0010	.0665	.0032	.0021	.0005	.0000	.0003	.0000
LOWER TYGH	1		.0000	.0000	.0000	.0008	.0075	.0101	.0000	.0163	.0009	.0022	.0122	.0005	.0011	.0708	.0002	.0001	.0000	.0023
UPPER TYGH	1,9	-		.0000	.0003	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0017	.0006	.0000	.0000	.0000	.0000	.0000	.0000
JORDAN	2	1,2	1,2, 5,9		.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0006	.0002	.0002	.0047	.0000	.0000	.0000	.0000
LITTLE BADGER	1,9	1,2	-	1,2, 9,12		.0011	.0000	.0178	.0200	.0000	.0006	.0000	.0019	.0039	.0000	.0001	.0000	.0000	.0000	.0000
THREEMILE	1	1	1,5, 6,10	1,2	-		.0000	.2113	.1516	.0000	.0738	.0322	.0010	.0030	.0007	.0217	.0000	.0000	.0000	.0000
ROCK	1,10	3,10	3,5, 10,13	1,2, 3,10	10	3,10		.0000	.0000	.0337	.0009	.0001	.0023	.0027	.0002	.0001	.0000	.0014	.0000	.0002
GATE	1	-	6	1,2	-	-	3,7, 10		.2774	.0002	.0221	.0040	.0125	.0052	.0064	.0051	.0000	.0000	.0000	.0000
BARLOW	1,2	1,2, 7	1,5. 6	1,2, 7,12	1	1	1,2, 3,7, 10	1		.0000	.0056	.0012	.0007	.0040	.0006	.0020	.0000	.0000	.0000	.0000
MAINSTEM RESIDENTS	10,13	7,10, 13	10,13	1,2, 10,13	1,2, 7,10	1,7, 10,13	3	1,7, 10,13	1,2, 7,10, 13		.0003	.0004	.0020	.0101	.0009	.0068	.1112	.0102	.0000	.0097
BAKEOVEN	1,9	-	12,13	1,2, 9	12	12	3,10	-	1,10 12	1		.3748	.0098	.0072	.0056	.0146	.0000	.0000	.0000	.0017
BUCK HOLLOW	1,9, 12	2,12	12,13	1,2, 9	12	12	2,10, 12	7,12	1,7, 10,12	2	-		.0246	.0164	.0477	.1355	.0001	.0000	.0000	.0001
UPPER NENA	5,9	2,5	13	2,5	1,5	1,5	10	1,5	1,5	2,5	1	-		.5871	.0674	.3097	.0248	.0004	.0003	.0038
LOWER NENA	5	2,5	13	2,5	5	5	2,5	5	1,5	2,5	-	-	-		.0979	.1770	.0226	.0118	.0022	.0003
BIG LOG	12	12	6,12, 13	2,6	1,2	1,12	3,6, 10,12	1,12	1,10, 12	12	-	-	5	5		.5783	.0008	.0015	.0000	.0006
FAST FOLEY	12	12	6,12, 13	-	1,12	1,12	3,10	1	1,10, 12	-	-	-	5	5	-		.0010	.0001	.0000	.0010
DESCHUTES STRAIN	10, 13	1,10, 13	1,2, 10,13	10,13	1,2, 10,13	1,2, 10,13	1	1,2, 10,13	1,2, 10,13	7	1,2, 10	2,10, 12	1,2, 5,10	2,5, 10	2,10, 12	10,12		.0482	.0392	.0013
OAK SPRINGS STRAIN	3,10, 13	3,10, 13	3,4, 10,13	3,10, 12,13	1,2. 3,10, 13	1,2, 3,10, 13	1,12	1,2,3, 7,10, 12,13,	1,2,3 4,7, 10,13	3,12	1,2, 3,10, 12	2,10, 12	1,2, 5,10, 12	2,5, 10, 12	2,3, 6,10, 12	3,10, 12	-		.0035	.0000
CAPE COD STRAIN	2,7, 10	1,2, 7,10	1,2, 10	7,10, 12	1,2, 10	1,2, 10	1,2, 7	1,2, 10	1,2, 10	1,2, 7	1,2, 7,10, 12	2,7, 10,12	1,2, 10,12	2,10, 12	2,10, 12	2,10, 12	13	3,7, 13		.0000
ROUND BUTTE HATCHERY	9,13	13	6,7, 10,13	1,2, 9,10, 13	1,7, 10,13	1,5, 7,13	3,10	7,13	1,7, 8,13	-	-	12	-	-	12	-	2,10	2,3, 10,12	1,2,7, 10,13	

1 = Scales above lateral line
2 = Scales along lateral series
3 = Dorsal rays
4 = Anal rays
5 = Pelvic rays
6 = Pectoral rays
7 = Branchiostegal rays
9 = Gill rakers (lower arch)
10 = Pyloric caeca
12 = Vertebrae
13 = Spotting pattern

these six characters (Figure 6). Canonical variate I represents a gradient from coarse-scaled to fine-scaled forms of rainbow trout. Canonical variates II and III are primarily contrasts of characters that separate different groups of the fine-scaled form.

Several patterns are apparent. First, all populations in the nonisolated tributaries of the Deschutes River, except for the mainstem resident rainbow trout, are morphologically very similar to each other. These populations are characterized by fine scales, moderate numbers of pyloric caeca, and a generalized spotting pattern. The mainstem resident rainbow trout population differs from these by having fewer scales, a greater number of pyloric caeca, and fewer vertebrae. Second, populations in the White River are morphologically dissimilar forms of fine-scaled rainbow trout. One group, composed of rainbow trout from the lower White River and Tygh Creek system, is very similar to the rainbow trout in the nonisolated tributaries of the Deschutes River, except for having fewer pyloric caeca and heavier spotting. A second group, consisting of the Threemile Creek, Barlow Creek, Little Badger Creek, and Gate Creek populations is characterized by very fine scales, low numbers of pyloric caeca, low numbers of branchiostegal rays, and heavy spotting. The most divergent populations are the Upper Tygh Creek and Jordan Creek populations, which are isolated above barriers within the White River. Upper Tygh Creek is differentiated from the others by low pyloric caecal counts and heavy spotting; Jordan Creek is differentiated by coarse scales and low pyloric caecal counts. Rainbow trout in Rock Creek are moderately fine-scaled but have high numbers of pyloric

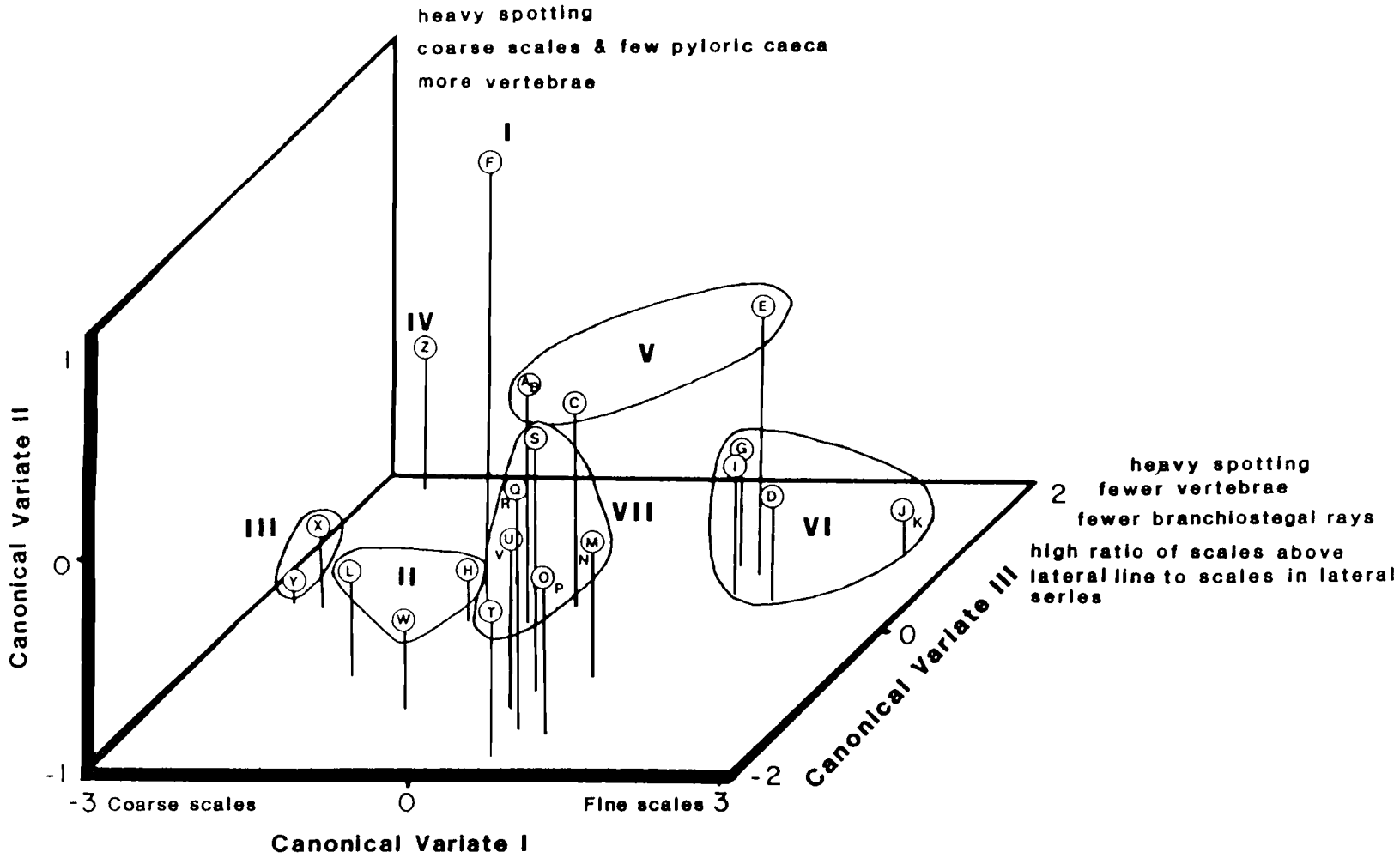

Figure 6. Distribution of populations along the first three canonical variates of morphological variation. Sites for each population correspond with Figure 1. Populations A to K are in the White River; L to V are in the unisolated tributaries; W = Round Butte Hatchery strain; X = Deschutes strain; Y = Oak Springs strain; Z = Cape Cod strain. Roman numerals refer to clusters in Figure 7.

caeca. Third, hatchery strains are morphologically dissimilar. The nonnative and Deschutes strains are characterized by coarser scales, greater numbers of pyloric caeca, and lighter spotting than other populations. The Cape Cod strain is differentiated from these by heavy spotting. The Round Butte steelhead strain are a lightly spotted, fine-scaled rainbow trout.

Cluster analysis of population means at all canonical variates reveals several important features of morphological divergence (Figure 7). First, White River populations are more differentiated than populations in the nonisolated tributaries of the Deschutes River. Second, most populations of rainbow trout are morphologically more similar to other populations in the same system than to populations from other systems. With the exception of the mainstem rainbow trout population, all populations in the system of nonisolated tributaries of the Deschutes River form a single, exclusive cluster. Similarly, with the exception of rainbow trout in Jordan Creek and Rock Creek, all populations in the White River system also form a single, exclusive cluster. These two clusters form another cluster of wild, fine-scaled rainbow trout. Third, morphologically similar populations within both the White River and the system of nonisolated tributaries are usually geographically related. This is particularly obvious in the system of nonisolated tributaries. The Buck Hollow Creek population is most similar to the population in nearby Bakeoven Creek; populations in the two streams in Trout Creek are most similar to each other; all these tributaries drain the eastern side of the Deschutes River basin and the populations in them are more similar to each other

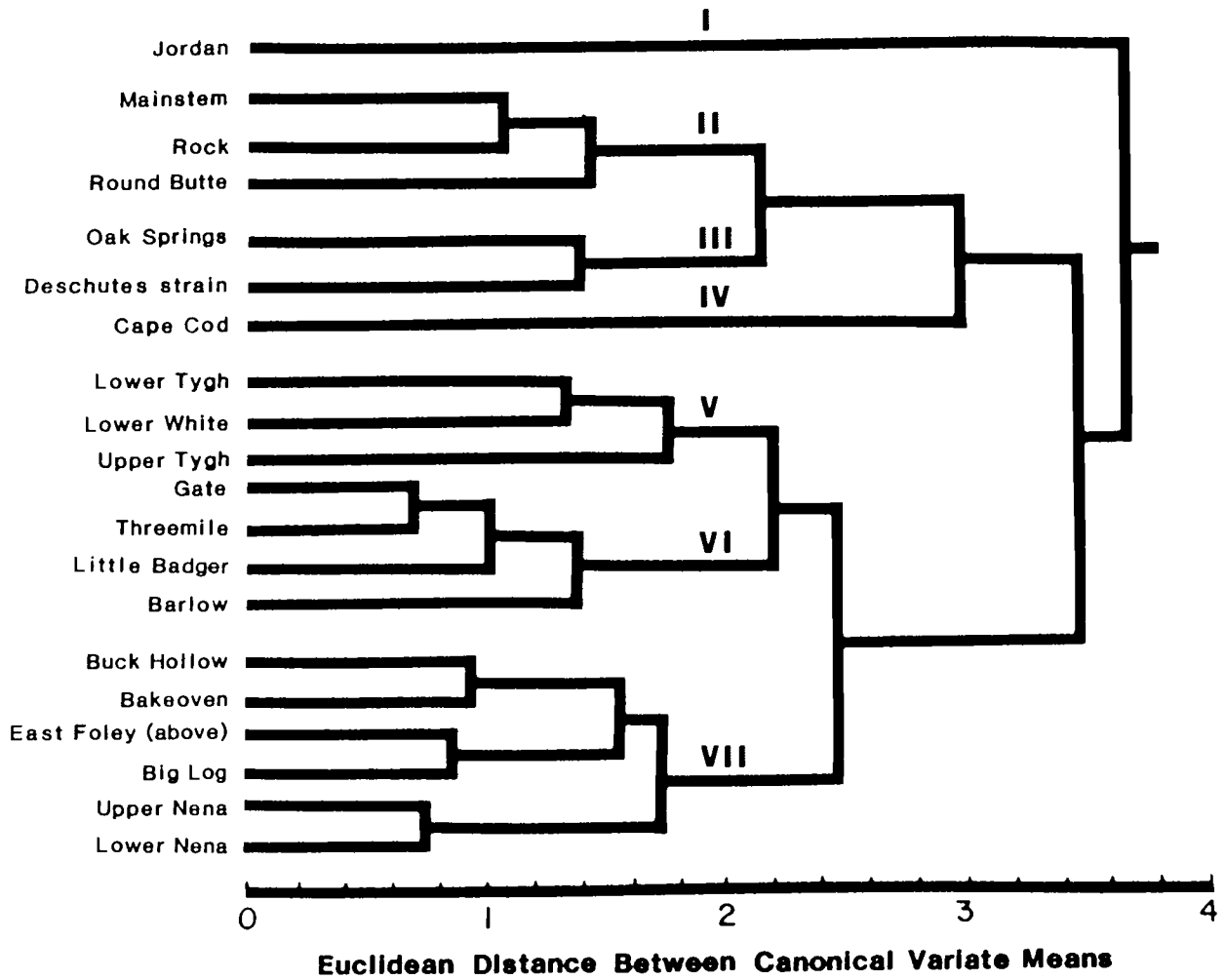

Figure 7. Phenogram of morphological similarity of hatchery and wild rainbow trout. Roman numerals correspond with clusters in Figure 6. Sites within tributaries are combined to simplify viewing.

than to populations in Nena Creek, which drains the western side of the basin.

Congruence of Morphological and Biochemical Genetic Data

Nei's genetic distance and canonical Euclidean distance were significantly correlated ($t = 7.61$, 188 df, $P < 0.001$). The coefficient of determination, however, is small ($r^2 = 0.24$), indicating that only one-fourth of the total variation is attributable to genetic distance. Biochemical and morphological phenograms are remarkably similar, however. Both phenograms assign populations in White River and nonisolated tributaries of the Deschutes River to separate clusters. The similarity among rainbow trout in Little Badger, Threemile, and Barlow creeks is evident in both analyses, as is the similarity of populations in the lower White River and lower Tygh Creek and the homogeneity of tributary populations (excluding the mainstem) in the nonisolated tributaries. Differentiation of the mainstem population from other populations in the nonisolated tributaries of the Deschutes River is evident in both analyses but the assignment of that population to a cluster of similar populations differs. The dissimilarity of introduced hatchery populations to native populations is more evident in the phenogram of biochemical genetic similarity than in the phenogram of morphological similarity.

CONCLUSIONS

In a basin with extensive barriers to migration isolation may occur among rainbow trout at different levels of geographical organization. In the Deschutes River basin, barriers occur between areas within tributaries and between drainages within the basin. Of the components of genetic diversity examined in this study, the most important is the differentiation attributable to differences among rainbow trout in isolated drainages. Patterns of morphological and biochemical differentiation indicate an evolutionary divergence of rainbow trout in the White River and the nonisolated tributaries of the Deschutes River that did not occur among other isolated populations within the basin.

Evolutionary Relationships Among Populations

The genetic divergence of rainbow trout in the White River and nonisolated tributaries of the Deschutes River may reflect the single or combined results of three basic evolutionary forces: the stochastic effects of small population size, gene flow, and natural selection. Where rainbow trout are isolated above barriers, the strong selection against downstream migrants that pass over the barrier should result in a reduction in the tendency to migrate downstream (Northcote 1981). The greatest detectable genetic difference between isolated and nonisolated populations of rainbow in the Deschutes River occurs at the LDH-4 locus between White River rainbow trout populations and those in the nonisolated tributaries below. Northcote et al. (1970) demonstrated a difference in allelic

frequencies at this locus, as well as meristic differences, between populations of rainbow trout above and below falls in British Columbia. Differences in migratory behavior for these trout have a genetic basis in rheotaxis (Northcote 1969, 1981) that is correlated with differences between LDH-4 isozymes in the two populations (Northcote and Kelso 1981). Functional and physiological differences between the isozymes are also correlated with superior swimming performance (Tsuyuki and Williscroft 1973, 1977). These observations may be used to support the notion of a selective advantage of the LDH4-(76) allele in the populations of resident rainbow trout.

I found no evidence of a pattern in the distribution of LDH-4 alleles among isolated and nonisolated populations in the Deschutes River or among resident rainbow trout populations that would indicate that selection for nonanadromous behavior explains the electrophoretically detectable differences among populations, although other, unknown selective pressures may be responsible (Figure 4). Populations above barriers in the nonisolated tributaries are characterized by high frequencies of the LDH-4(76) allele similar to the populations below the barriers. Populations in the White River are characterized by high frequencies of the LDH-4(100) allele. The frequency of the LDH4-(76) allele is significantly greater than zero in only the lower White River population. The resident rainbow trout in the mainstem of the river are characterized by nearly equal frequencies of the two alleles.

The lack of variation at the LDH-4 locus in the White River populations is not typical of rainbow trout populations east of the

Cascade Range. A sharp cline exists between coastal and inland rainbow trout populations in the Columbia and Fraser Rivers for allelic frequencies at the LDH-4 and SOD loci. Inland populations are characterized by high levels of variation at the LDH-4 locus and relatively little variation at the SOD locus. Allelic frequencies at the LDH-4 locus and SOD locus in populations from the nonisolated tributaries are typical of inland rainbow trout populations. Coastal populations are characterized by very little variation at the LDH-4 locus and relatively more variation at the SOD locus (Huzyk and Tsuyuki 1974, Allendorf 1975, Milner et al. 1980, Schreck et al. 1986).

I hypothesized two possible origins for the genetic divergence of White River and Deschutes River rainbow trout populations: (1) White River rainbow trout are remnant populations of a rainbow trout-like ancestral population. The atypical allelic frequencies in the White River may be representative of an ancestral population that was protected by isolation above waterfalls or may reflect stochastic effects of small, fluctuating population sizes or parallel evolution in similar environments. (2) White River rainbow trout are the descendants of rainbow trout from another basin, most likely coastal, that were released into the system. I believe that biochemical, morphological, and geological evidence favor the first hypothesis. However, not enough data are available to choose between possible scenarios for the first hypothesis. Also, the extremely high frequencies of the LDH-4(100) allele that characterize both coastal

and White River rainbow trout may obscure any biochemical evidence of polyphyletic origins of White River rainbow trout.

White River rainbow trout populations are morphologically similar to populations in the nonisolated tributaries of the Deschutes River and dissimilar to nonnative, hatchery rainbow trout. That White River populations occupy vastly different thermal and hydrological environments (Schroeder and Lindsay 1985) yet share common morphological characteristics is evidence of a strong genetic component to morphological similarities. A sharp cline in scale counts and a cline in pyloric caecal counts exist between coastal rainbow trout and inland rainbow trout. Coastal rainbow trout generally have coarse scales and relatively more pyloric caeca than fine-scaled inland rainbow trout (Behnke 1979, Schreck et al. 1986). Behnke (1979, 1981) hypothesized that the morphological similarity among inland rainbow trout reflects a post-glacial invasion of the Columbia River basin and Oregon desert basins by a rainbow trout-like redband trout (Salmo sp.), replacing the native cutthroat trout (Salmo clarki) in areas not isolated by waterfalls. The Deschutes River was probably invaded during this period. Fossil material of redband trout is present in Fossil Lake, an ephemeral pond that is the remnant of Fort Rock Lake (Allison and Bond 1983). Access to this Oregon desert basin would have been possible via the Deschutes River prior to the Pleistocene lava flows that now separate the drainages (Allison 1940, 1979). Redband trout may also have invaded the White River. No cutthroat trout inhabit the White River (Schroeder and Lindsay 1983). White River rainbow trout are characterized by fine scales and low

numbers of pyloric caeca with two exceptions. Rainbow trout from Jordan Creek have coarse scales and very low pyloric ceacal counts; rainbow trout from Rock Creek are fine-scaled but have pyloric caecal counts greater than those for other White River populations. One particular group of populations from remote, headwater streams - Little Badger, Threemile, Barlow, and Gate creeks - is particularly distinguished by redband morphologies. Samples from two of these populations contained trout with basibranchial teeth, a primitive trait also characteristic of redband trout. This suggests that isolation in the White River has protected remnant populations of the redband trout that invaded Fort Rock Lake via the Deschutes River at the end of the last glacial epoch.

The systematics of redband trout are unresolved (Wishard et al. 1984). Redband trout also occur in the headwaters of the Sacramento River. These trout are generally morphologically similar to the redband trout in the Columbia River and Oregon Desert basins but lack the characteristic variation at the LDH-4 locus (Utter and Allendorf 1977, Gold 1977, Behnke 1979). Behnke (1981) has hypothesized that the Sacramento form evolved from an invasion of a different rainbow trout-like ancestor. White River rainbow trout may also represent remnants of a different form of redband trout. Wilmot (1974) found no variation at the LDH-4 locus in 51 individuals from a remnant population of redband trout that has persisted in the Fort Rock Basin. Allelic frequencies at other loci are also similar to those found in populations from the White River. Disjunct populations of other

species, such as Richardsonius balteatus, Cottus bairdi, and Catostomus columbianus, isolated above waterfalls in tributaries of the Columbia River and related drainages, are also more similar to each other than to differentiated populations below falls. These populations may represent remnants of an older ichthyofauna (Hubbs and Miller 1948, Bisson and Bond 1971) or reflect parallel evolution (Smith 1966).

The stochastic effects associated with small, fluctuating population sizes and the geographical isolation may also explain the genetic differentiation of the White River populations. The disparate frequency of the LDH-4 alleles could have occurred at a colonization event or as a result of random genetic drift. Many of these streams are small and the genetic structures of populations in them would be easily effected by flood, drought, and or volcanic activity. Lower average heterozygosity, fewer rare alleles, and more loci with extreme frequencies of the common allele in the White River populations and especially in the upper Tygh Creek population are evidence that such stochastic processes could have occurred. The White River has been subjected to volcanic activity relatively recently in its geological history: the debris fan that forms the south flank of Mt. Hood, the eastern slope of which is the glacial headwaters of the White River, was deposited only 2,000 years ago. The chaotic structure of the flows of this last major eruption, as well as previous ones, indicate that hot lava flowed down a snow and ice-clad volcano and generated mudflows that are found in many nearby river valleys (McKee 1972). The impact of such catastrophies on fish populations as well as the

unstable environment they create should have been considerable.

Human introductions of rainbow trout into the White River system may also explain the differentiation of those populations from the populations of rainbow trout in the nonisolated tributaries of the Deschutes River. Meristics or allelic frequencies that are characteristic of coastal populations or intermediate between coastal and inland populations of rainbow trout have been used as evidence of nonnative ancestries of rainbow trout in some tributaries of the Columbia River (Allendorf et al. 1980, Campton and Johnston 1985, Appendix B in this paper). I found consistent evidence of introgression between nonnative and native rainbow trout in only those populations known to have received hatchery introductions. Morphological analyses of the wild rainbow trout populations included in this study do not show evidence of nonnative ancestries for most populations. Canonical variate analysis suggests that these populations form two groups of fine-scaled rainbow trout: populations in the nonisolated tributaries and several White River populations fit the morphological profile of middle Columbia River rainbow trout; divergent populations in White River populations may best fit the morphological profile of the redband trout of the Oregon desert basins (Behnke 1979, Schreck et al. 1986). The rainbow trout in Jordan Creek, which have low scale counts, and Rock Creek, which have moderate scale counts and relatively more pyloric caeca than other White River populations, probably reflect introgression of nonnative strains.

Although allelic frequencies for LDH-4 in White River rainbow trout populations are characteristic of coastal rainbow trout, allelic frequencies at other diagnostic loci do not support a hypothesis of nonnative ancestry for all populations (Figure 4). Variation at the SOD locus is not significantly different between the White River and the populations in the nonisolated tributaries of the Deschutes River, although by comparison, variation is significantly greater in the nonnative hatchery populations than in the native hatchery populations (Table 5). Greater variation does occur at the SOD locus in those populations known to have received hatchery introductions, although only the Rock Creek population has an unusually high level of variation. White River populations also lack variation at a third diagonistic locus, ADA-1. Variation at this locus has been used as a genetic marker to infer interbreeding of nonnative and native rainbow trout populations in a tributary of the upper Deschutes River basin (Appendix B in this paper).

Characteristics of the genetic population structure of White River rainbow trout and the hydrography of the drainage do not support a hypothesis of nonnative ancestry. Had significant hybridization occurred between nonnative and native rainbow trout, the addition of new genetic material should increase the average heterozygosities of the populations. Only those populations that have received direct introductions of nonnative rainbow trout have average heterozygosities noticeably greater than the mean for all White River populations. Additionally, it appears unlikely that gene flow from nonnative rainbow trout that have strayed from the sites of introduction can

explain the genetic divergence. Average G_{ST} for the White River indicates a significant level of genetic divergence. Estimates of genetic divergence may be used to infer effective population size or proportions of straying (Allendorf and Phelps 1981). Although stochastic effects of limited effective population size are probably contributing to divergence within the White River, the presence of impassable waterfalls and seasonal barriers to migration (Schroeder and Lindsay 1983, 1985) suggest local isolation of many of these populations. It is improbable that under such conditions the rate of gene flow could have been great enough to shift the frequency of the LDH-4(76) allele from that characteristic of inland rainbow trout to near zero in eight of the nine populations unless these streams were barren of native rainbow trout populations.

Evolution of Races

Most popular racial characteristics are based on those traits that maximize the differences between otherwise similar individuals. Consequently, these characteristics may not represent the whole genome (Hartl 1980). Racial characteristics in the Salmonidae are based on life history differences. Differences in time of return to natal streams for anadromous rainbow trout have led to the designation of winter and summer races; differences in anadromous behavior have led to the designation of resident and steelhead races.

A phenetic definition of race is a group of individuals who are genetically more similar to each other than to others from other groups (Hartl 1980). Biochemical and morphological phenograms do not

show that resident populations of rainbow trout in the Deschutes River are more similar to each other than to steelhead populations. Assuming the phenetic criterion and that the characters I examined are representative of the whole genome, the classification of rainbow trout into races by differences in anadromous behavior is not justified.

I found no evidence that the resident rainbow trout within the Deschutes River basin represent a single phylogenetic line. No synapomorphic biochemical or morphological homologies describe the resident rainbow trout populations. Not all populations of isolated rainbow trout are relicts of an ancestral resident population that is different from one that gave rise to steelhead populations in the drainage. This is consistent with the results of other studies conducted over larger geographical areas (Behnke 1972, Allendorf and Utter 1979). Based on this evidence, I believe that nonanadromous populations have evolved independently within the drainage, often from steelhead populations.

These conclusions are based on the assumption that I correctly identified resident and steelhead populations. The resident rainbow trout in the mainstem of the Deschutes River, known as "redsides" (Bond 1973), have traditionally been considered and are presently managed as a separate, resident race. However, spawning areas and times may overlap substantially with those for steelhead in some years. Male hatchery steelhead that do not migrate develop typical redside appearance and have been observed spawning with female steelhead (Fessler 1972). Evidence from karyotypic and reassociation

properties of DNA show no difference between resident and steelhead rainbow trout in the Deschutes River (Wilmot 1974, Gharrett 1975).

Based on biochemical, morphological, and population characteristics, I believe that the resident rainbow trout in the mainstem of the Deschutes River constitute a uniquely differentiated population that is sympatric with other less differentiated populations of the rainbow trout in the Deschutes River. The nonanadromous behavior of these trout have been documented by tagging and breeding studies (Aho and Fessler 1975). Spawning resident rainbow trout may be distinguished from adult steelhead by size (Rybock 1975). In samples collected in 1986 from one location, I found equal numbers of males and females, many of which were ready to spawn - evidence that this is not a pseudopopulation of residual male steelhead that do not migrate to the ocean.

Phenograms of morphological and biochemical similarity suggest that mainstem rainbow trout are genetically differentiated and more reproductively isolated than rainbow trout in nonisolated locations of Deschutes River tributaries. These rainbow trout are differentiated from rainbow trout in the other nonisolated locations at four of the six loci examined. The degree of allelic heterogeneity is similar to that among smaller and more isolated populations in the White River and suggests a relatively long period of reproductive isolation or differential response to selection.

I inferred that the samples I examined from other nonisolated populations are largely or wholly the progeny of steelhead. However,

the evidence is circumstantial. I was unable to distinquish sympatric individual progeny of resident and steelhead rainbow trout in these tributaries (Appendix C). Low levels of allelic heterogeneity among populations from the tributaries, which are many kilometers apart and in different environments, can be explained by a more recent divergence from a common ancestor, which is not supported by homologies, or by the homogenizing effects of gene flow. Levels of allelic heterogeneity among resident populations, which are geographically near and nonisolated, within the White River and Nena Creek are much greater (Table 5). This indicates that populations spawning in the tributaries are migratory and most likely anadromous. While collecting samples in the tributaries, I observed few rainbow trout greater than 230mm in length. Analysis of otoliths from rainbow trout that were sampled indicates that they were largely two years old or younger (Currens unpublished data). Most wild steelhead in the Deschutes River migrate to the ocean after one to three years in freshwater and at a length of less than 260 mm (Howell et al. 1985).

Parapatric populations in the system of nonisolated tributaries are also differentiated from each other. Rainbow trout above barriers in East Foley Creek are differentiated from those below at the AH locus; rainbow trout at two locations above barriers in Nena Creek are differentiated from those below at a single, different locus, DPEP, and from each other at the DPEP and MDH-3,4 loci. These differences in allelic frequencies at one or two loci support the inference that these populations are isolated, although without knowledge of the effective population size, it is impossible to determine whether the

lack of greater differences reflects recent isolation or irregular immigration. Consequently, selection for nonanadromous behavior may not be complete.

Selection by downstream barriers on migratory rainbow trout is clearly important for most of the populations I examined. Whether the nonanadromous behavior in the mainstem population evolved under similar selective pressures or sympatrically with anadromous populations is unknown. One possible hypothesis is that nonanadromous behavior developed in lacustrine populations of redband trout in glacial impoundments at the end of the last glacial epoch. Anadromous populations spawned in the rivers, leading to differentiation of the two forms. When water levels in the lakes dropped, some resident rainbow trout took up existence in the streams while others became landlocked and survived in intermittent streams flowing into the dessicated lakes. Behnke (1979, 1981) has inferred ancestral lacustrine existence from differences in gill raker counts. I compared the number of gill rakers in rainbow trout from the tributaries, the mainstem of the Deschutes River, Buck Creek and Bridge Creek (two intermittent streams in the Fort Rock basin) to data published by Behnke (1979) from collections of rainbow trout made by Snyder in 1904 from Buck Creek. I found no significant differences among the groups.

Implications for Resource Management

I founded my research on the assumption that meeting the need to identify and maintain genetic diversity of a species within a given

geographical area requires knowledge of how evolution has proceeded. I have presented evidence that a major component of evolution within a drainage is related to historical or extant isolation of parapatric and sympatric populations. Isolated populations may be relict forms of the species, be uniquely adapted to particular environments, or neither. Isolated or partially isolated populations provide a system of experiments in evolution for the species that is more efficient than that possible by a large, nonisolated population (Li 1955). Meffe (1986) noted that systems of isolated populations will maximize the variation among populations and maintain potentially unique phenotypes for the greatest flexibility in management. Practically, management and maintenance of a complex system of isolated, partially isolated, and sympatric populations of rainbow trout may be impossible. Alternatively, genetic surveys that are based on only nonisolated populations or a single life history form are incomplete and of limited value in making decisions which affect the genetic diversity of the whole species. Gene diversity analysis provides a quantitative estimate of the distribution of genetic diversity among and within groups at hierarchical levels and can be used to compliment other heirarchical analyses, such as cluster analysis, or analyses based on other kinds of genetic data.

The distribution of genetic diversity within the Deschutes River basin suggests that isolated drainages and systems of nonisolated tributaries should be managed as individual units. Special consideration is then possible for relict or unique populations in isolated drainages and sympatric populations in nonisolated waters.

Additionally, the differences in genetic infrastructure between systems of nonisolated and isolated drainages indicate that genetically discrete stocks inhabit much smaller geographical areas in an isolated drainage. Consequently, management units within the two systems should not be defined by the same geographical level. Finally, management decisions that potentially affect the genetic diversity within drainages should be made on the basis of all available biochemical genetic, morphological, and life history data and should incorporate both phenetic and evolutionary analyses. Biochemical genetic data alone may detect significant genetic differentiation of populations that is associated with random effects of small population size but that does not reflect differentiation for life history traits, morphological features, or aesthetic, economic, or adaptive potentials that would justify unique management consideration. Similarly, inferences of nonnative origins or hybridization of wild and nonnative rainbow trout that are based on biochemical genetic markers at few loci without corraborative evidence from other kinds of genetic data can lead to erroneous management practices. The unfortunate consequences could be the unintentional loss of a valuable and irreplaceable resource.

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APPENDICES

APPENDIX A

Isozyme Frequencies and Allele Sample Sizes for Polymorphic Loci in Deschutes River Rainbow Trout.

Table 9. Isozyme frequencies and allele sample sizes for polymorphic loci in Deschutes River rainbow trout. The number above a column is the relative mobility of that allele. Negative mobilities indicate cathodal migration.

		AH				ADA-1		
LOCATION	YEAR	N	100	83	66	N	100	92
MAINSTEM	1984	146	.562	.432	.007	148	1.000	
	1986	96	.563	.438		106	1.000	
BAKEOVEN (MOUTH)	1984	76	.684	.316		80	1.000	
	1985	50	.800	.160	.040	60	1.000	
BAKEOVEN (DEEP CR.)	1984	118	.678	.322		120	1.000	
	1985	128	.727	.242	.031	136	1.000	
BUCK HOLLOW (LOWER)	1984	66	.621	.379		150	1.000	
	1985	92	.630	.359	.011	98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	24	.625	.250	.125	50	1.000	
	1985	98	.561	.439		96	1.000	
BIG LOG	1984	40	.900	.100		40	1.000	
	1985	96	.865	.135		100	.990	.010
EAST FOLEY (BELOW)	1984	28	.821	.179		30	1.000	
EAST FOLEY (ABOVE)	1984	64	.688	.313		64	1.000	
	1985	78	.872	.128		88	.989	.011
NENA (LOWER)	1984	8	.625	.375		40	1.000	
	1985	98	.694	.306		100	1.000	
NENA (MIDDLE)	1984	26	.615	.385		42	1.000	
	1985	92	.620	.337	.043	92	1.000	
NENA (UPPER)	1984	78	.654	.346		86	1.000	
WAPINITIA	1984	0				32	1.000	
LOWER WHITE (SITE 1)	1984	46	.891	.109		58	1.000	
(SITE 2)	1984	26	.654	.346		26	1.000	
LOWER TYGH	1984	56	.732	.268		62	1.000	
JORDAN	1984	116	.957	.043		106	1.000	
UPPER TYGH	1984	136	.956	.044		136	1.000	
LITTLE BADGER	1984	100	.570	.430		100	1.000	
THREEMILE	1984	92	.565	.435		100	1.000	
ROCK	1984	116	.940	.060		116	1.000	
GATE	1984	80	.700	.300		80	1.000	
BARLOW (SITE 1)	1984	78	.628	.359	.013	76	1.000	
(SITE 2)	1984	22	.318	.682		24	1.000	
ROUND BUTTE STRAIN	1984	184	.728	.272		200	1.000	
DESCHUTES STRAIN	1985	170	.612	.388		180	1.000	
CAPE COD STRAIN	1985	160	.988	.013		152	.526	.474
OAK SPRING STRAIN	1985	62	.968	.032		126	.738	.262
METOLIUS	1985	102	.696	.304		110	.800	.200

Table 9. Continued.

LOCATION	YEAR	ADA-2 N	ADA-2 100	ADA-2 93	ADH N	ADH -100	ADH -76	ADH -82
MAINSTEM	1984	148	1.000		148	1.000		
	1986	106	1.000		106	1.000		
BAKEOVEN (MOUTH)	1984	80	1.000		80	1.000		
	1985	60	1.000		60	.967	.033	
BAKEOVEN (DEEP CR.)	1984	120	1.000		120	.992		.008
	1985	136	1.000		136	1.000		
BUCK HOLLOW (LOWER)	1984	150	1.000		150	1.000		
	1985	98	1.000		98	1.000		
BUCK HOLLOW (MACKEN CNY)	1984	50	1.000		50	1.000		
	1985	96	1.000		96	1.000		
BIG LOG	1984	40	1.000		40	1.000		
	1985	100	1.000		100	1.000		
EAST FOLEY (BELOW)	1984	30	.967	.033	30	1.000		
EAST FOLEY (ABOVE)	1984	64	1.000		64	1.000		
	1985	88	.977	.023	88	1.000		
NENA (LOWER)	1984	40	1.000		40	1.000		
	1985	100	1.000		100	.980		.020
NENA (MIDDLE)	1984	42	1.000		42	1.000		
	1985	92	1.000		92	.967		.033
NENA (UPPER)	1984	86	.965	.035	86	1.000		
WAPINITIA	1984	32	1.000		32	1.000		
LOWER WHITE (SITE 1)	1984	58	1.000		58	.948	.052	
(SITE 2)	1984	26	1.000		26	1.000		
LOWER TYGH	1984	62	1.000		62	1.000		
JORDAN	1984	106	1.000		126	.976		.024
UPPER TYGH	1984	136	1.000		136	1.000		
LITTLE BADGER	1984	100	1.000		100	1.000		
THREEMILE	1984	100	1.000		100	1.000		
ROCK	1984	116	1.000		112	.964	.036	
GATE	1984	80	1.000		80	1.000		
BARLOW (SITE 1)	1984	76	1.000		92	1.000		
(SITE 2)	1984	24	1.000		24	1.000		
ROUND BUTTE STRAIN	1984	200	1.000		200	.990	.010	
DESCHUTES STRAIN	1985	180	1.000		180	1.000		
CAPE COD STRAIN	1985	160	1.000		160	.994	.006	
OAK SPRING STRAIN	1985	130	1.000		154	1.000		
METOLIUS	1985	138	1.000		138	1.000		

Table 9. Continued.

LOCATION	YEAR	CK-1 N	CK-1 100	CK-1 70	GPI-1 N	GPI-1 100	GPI-1 80	GPI-2 N	GPI-2 100	GPI-2 25
MAINSTEM	1984	148	1.000		148	1.000		148	1.000	
	1986	106	1.000		106	1.000		106	1.000	
BAKEOVEN (MOUTH)	1984	80	1.000		80	1.000		80	1.000	
	1985	60	1.000		60	1.000		60	1.000	
BAKEOVEN (DEEP CR.)	1984	120	1.000		120	1.000		120	1.000	
	1985	96	1.000		136	1.000		136	1.000	
BUCK HOLLOW (LOWER)	1984	150	1.000		150	1.000		150	1.000	
	1985	98	1.000		98	1.000		98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	50	1.000		50	1.000		50	1.000	
	1985	96	1.000		96	1.000		96	1.000	
BIG LOG	1984	40	1.000		40	1.000		40	1.000	
	1985	100	1.000		100	1.000		100	1.000	
EAST FOLEY (BELOW)	1984	30	1.000		30	1.000		30	1.000	
EAST FOLEY (ABOVE)	1984	64	1.000		64	1.000		64	1.000	
	1985	88	1.000		88	1.000		88	1.000	
NENA (LOWER)	1984	40	1.000		40	1.000		40	1.000	
	1985	100	1.000		100	1.000		100	1.000	
NENA (MIDDLE)	1984	42	1.000		42	1.000		42	1.000	
	1985	92	1.000		92	1.000		92	1.000	
NENA (UPPER)	1984	86	1.000		86	1.000		86	1.000	
WAPINITIA	1984	32	1.000		32	1.000		32	1.000	
LOWER WHITE (SITE 1)	1984	58	1.000		58	1.000		58	1.000	
(SITE 2)	1984	26	1.000		26	.962	.038	26	1.000	
LOWER TYGH	1984	62	1.000		62	1.000		62	1.000	
JORDAN	1984	126	1.000		126	1.000		126	1.000	
UPPER TYGH	1984	136	1.000		136	1.000		136	1.000	
LITTLE BADGER	1984	100	1.000		100	1.000		100	1.000	
THREEMILE	1984	100	1.000		100	1.000		100	.980	.020
ROCK	1984	116	1.000		116	1.000		116	1.000	
GATE	1984	80	1.000		80	1.000		80	1.000	
BARLOW (SITE 1)	1984	92	1.000		92	.989	.011	92	.870	.130
(SITE 2)	1984	24	1.000		24	1.000		24	.958	.042
ROUND BUTTE STRAIN	1984	186	.962	.038	200	1.000		200	1.000	
DESCHUTES STRAIN	1985	168	1.000		180	1.000		180	1.000	
CAPE COD STRAIN	1985	160	1.000		160	1.000		160	1.000	
OAK SPRING STRAIN	1985	60	1.000		154	1.000		154	1.000	
METOLIUS	1985	138	1.000		138	1.000		138	1.000	

Table 9. Continued.

LOCATION	YEAR	G3PDH-1 N	G3PDH-1 100	G3PDH-1 140	IDH-2 N	IDH-2 100	IDH-2 120
MAINSTEM	1984	142	.994	.056	0		
	1986	106	.943	.057	106	1.000	
BAKEOVEN (MOUTH)	1984	80	1.000		80	1.000	
	1985	60	.983	.017	60	1.000	
BAKEOVEN (DEEP CR.)	1984	120	1.000		120	1.000	
	1985	132	.985	.015	136	1.000	
BUCK HOLLOW (LOWER)	1984	150	.987	.013	150	1.000	
	1985	98	.990	.010	98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	50	.960	.040	50	1.000	
	1985	96	1.000		96	1.000	
BIG LOG	1984	40	1.000		40	1.000	
	1985	100	1.000		100	1.000	
EAST FOLEY (BELOW)	1984	30	1.000		30	1.000	
EAST FOLEY (ABOVE)	1984	64	1.000		64	1.000	
	1985	88	1.000		88	.989	.011
NENA (LOWER)	1984	40	1.000		40	1.000	
	1985	100	.990	.010	100	.990	.010
NENA (MIDDLE)	1984	42	.976	.024	42	1.000	
	1985	92	1.000		92	1.000	
NENA (UPPER)	1984	86	1.000		86	1.000	
WAPINITIA	1984	32	1.000		32	1.000	
LOWER WHITE (SITE 1)	1984	58	1.000		0		
(SITE 2)	1984	26	1.000		0		
LOWER TYGH	1984	62	.984	.016	0		
JORDAN	1984	126	.984	.016	0		
UPPER TYGH	1984	136	1.000		120	1.000	
LITTLE BADGER	1984	100	1.000		100	1.000	
THREEMILE	1984	100	.970	.030	40	1.000	
ROCK	1984	116	.974	.026	40	1.000	
GATE	1984	80	.988	.013	80	1.000	
BARLOW (SITE 1)	1984	92	1.000		0		
(SITE 2)	1984	24	1.000		0		
ROUND BUTTE STRAIN	1984	200	.995	.005	0		
DESCHUTES STRAIN	1985	180	.894	.106	180	1.000	
CAPE COD STRAIN	1985	160	.881	.119	160	.981	.019
OAK SPRING STRAIN	1985	152	.934	.066	154	1.000	
METOLIUS	1985	138	.978	.022	138	1.000	

Table 9. Continued.

LOCATION	YEAR	IDH-3,4 N	100	40	120	71	LDH-4 N	100	76	111
MAINSTEM	1984	292	.589	.178		.233	148	.493	.507	
	1986	156	.673	.147		.179	106	.547	.453	
BAKEOVEN (MOUTH)	1984	152	.691	.164		.145	80	.513	.488	
	1985	120	.733	.133		.133	60	.383	.617	
BAKEOVEN (DEEP CR.)	1984	224	.728	.089		.183	120	.367	.633	
	1985	272	.721	.147		.132	136	.382	.596	.022
BUCK HOLLOW (LOWER)	1984	228	.702	.114	.009	.175	150	.400	.600	
	1985	184	.717	.152	.005	.125	98	.316	.673	.010
BUCK HOLLOW (MACKEN CNY)	1984	76	.684	.145		.171	50	.360	.640	
	1985	192	.703	.172		.125	90	.433	.567	
BIG LOG	1984	80	.700	.163		.138	38	.342	.658	
	1985	188	.734	.112	.016	.138	100	.320	.680	
EAST FOLEY (BELOW)	1984	60	.550	.217	.017	.217	30	.333	.667	
EAST FOLEY (ABOVE)	1984	128	.633	.133	.008	.227	64	.297	.703	
	1985	160	.781	.100		.119	88	.352	.648	
NENA (LOWER)	1984	68	.735	.088		.176	40	.550	.450	
	1985	144	.688	.167		.146	100	.390	.610	
NENA (MIDDLE)	1984	84	.702	.131		.167	42	.405	.595	
	1985	176	.648	.153	.023	.176	92	.359	.641	
NENA (UPPER)	1984	172	.657	.157	.017	.169	86	.372	.628	
WAPINITIA	1984	44	.659	.136		.205	32	.219	.781	
LOWER WHITE (SITE 1)	1984	96	.729	.115		.156	58	.862	.138	
(SITE 2)	1984	52	.692	.096		.212	26	.885	.115	
LOWER TYGH	1984	116	.690	.103		.207	62	1.000		
JORDAN	1984	224	.728	.125		.147	126	1.000		
UPPER TYGH	1984	212	.750	.005		.245	136	1.000		
LITTLE BADGER	1984	200	.715			.285	100	1.000		
THREEMILE	1984	200	.715	.075	.005	.205	100	.980	.020	
ROCK	1984	204	.770	.103	.049	.078	116	.983	.017	
GATE	1984	108	.722	.102		.176	80	1.000		
BARLOW (SITE 1)	1984	136	.794			.206	92	1.000		
(SITE 2)	1984	40	.725	.025	.025	.225	24	1.000		
ROUND BUTTE STRAIN	1984	388	.680	.152		.168	200	.445	.555	
DESCHUTES STRAIN	1985	280	.668	.086		.246	180	.667	.333	
CAPE COD STRAIN	1985	320	.647	.206	.022	.125	160	1.000		
OAK SPRING STRAIN	1985	200	.735	.080	.045	.140	154	1.000		
METOLIUS	1985	220	.682	.159		.159	138	.790	.210	

Table 9. Continued.

LOCATION	YEAR	LDH-5 N	LDH-5 100	LDH-5 97	MDH-1,2 N	MDH-1,2 100	MDH-1,2 140	MDH-1,2 40
MAINSTEM	1984	148	1.000		296	1.000		
	1986	106	1.000		212	1.000		
BAKEOVEN (MOUTH)	1984	80	1.000		160	1.000		
	1985	60	1.000		120	1.000		
BAKEOVEN (DEEP CR.)	1984	120	1.000		240	1.000		
	1985	136	1.000		272	.996	.004	
BUCK HOLLOW (LOWER)	1984	150	1.000		300	.997	.003	
	1985	98	1.000		192	.932	.047	.021
BUCK HOLLOW (MACKEN CNY)	1984	50	1.000		100	.990	.010	
	1985	96	1.000		196	.954		.046
BIG LOG	1984	40	1.000		80	1.000		
	1985	100	1.000		200	.995	.005	
EAST FOLEY (BELOW)	1984	30	1.000		60	1.000		
EAST FOLEY (ABOVE)	1984	64	1.000		128	1.000		
	1985	88	1.000		176	.989	.011	
NENA (LOWER)	1984	40	1.000		80	1.000		
	1985	100	1.000		200	1.000		
NENA (MIDDLE)	1984	42	1.000		184	1.000		
	1985	92	1.000		84	1.000		
NENA (UPPER)	1984	86	1.000		172	1.000		
WAPINITIA	1984	32	1.000		64	.984	.016	
LOWER WHITE (SITE 1)	1984	58	1.000		116	1.000		
(SITE 2)	1984	26	1.000		52	1.000		
LOWER TYGH	1984	62	1.000		124	1.000		
JORDAN	1984	126	1.000		252	1.000		
UPPER TYGH	1984	136	1.000		272	1.000		
LITTLE BADGER	1984	100	1.000		200	.940	.060	
THREEMILE	1984	100	1.000		200	1.000		
ROCK	1984	116	1.000		232	1.000		
GATE	1984	80	.988	.013	160	1.000		
BARLOW (SITE 1)	1984	92	1.000		184	1.000		
(SITE 2)	1984	24	1.000		48	1.000		
ROUND BUTTE STRAIN	1984	200	1.000		400	1.000		
DESCHUTES STRAIN	1985	180	1.000		360	1.000		
CAPE COD STRAIN	1985	160	.994	.006	320	1.000		
OAK SPRING STRAIN	1985	130	1.000		308	1.000		
METOLIUS	1985	138	1.000		276	1.000		

Table 9. Continued.

LOCATION	YEAR	MDH-3,4 N	100	83	110	70	ME-3 N	100	93
MAINSTEM	1984	284	.989	.007	.004		148	1.000	
	1986	212	.995	.005			106	1.000	
BAKEOVEN (MOUTH)	1984	160	.944		.013	.044	80	1.000	
	1985	120	.975			.025	60	1.000	
BAKEOVEN (DEEP CR.)	1984	240	.892	.008		.100	120	1.000	
	1985	272	.945	.015		.040	136	1.000	
BUCK HOLLOW (LOWER)	1984	300	.970		.007	.023	150	1.000	
	1985	196	.954			.046	98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	100	.980			.020	50	1.000	
	1985	192	.990			.010	96	1.000	
BIG LOG	1984	80	.975			.025	40	1.000	
	1985	200	.940	.040		.020	100	1.000	
EAST FOLEY (BELOW)	1984	60	.983	.017			30	1.000	
EAST FOLEY (ABOVE)	1984	128	.969			.031	64	1.000	
	1985	176	.994	.006			88	1.000	
NENA (LOWER)	1984	80	.925			.075	40	1.000	
	1985	200	.980			.020	100	1.000	
NENA (MIDDLE)	1984	84	.940			.060	42	1.000	
	1985	184	.929			.071	92	1.000	
NENA (UPPER)	1984	172	.994			.006	86	1.000	
WAPINITIA	1984	64	.984			.016	32	1.000	
LOWER WHITE (SITE 1)	1984	116	.871	.060	.043	.026	58	.983	.017
(SITE 2)	1984	52	.808	.038	.135	.019	26	1.000	
LOWER TYGH	1984	124	.911	.032	.056		62	.984	.016
JORDAN	1984	252	.917	.060	.016	.008	126	.921	.079
UPPER TYGH	1984	272	1.000				136	1.000	
LITTLE BADGER	1984	200	1.000				100	1.000	
THREEMILE	1984	200	0.985	.015			100	1.000	
ROCK	1984	232	.927	.052		.022	116	.974	.026
GATE	1984	160	.975	.025			80	1.000	
BARLOW (SITE 1)	1984	184	.973			.027	92	1.000	
(SITE 2)	1984	48	.979			.021	24	.958	.042
ROUND BUTTE STRAIN	1984	392	.954	.043	.003		200	1.000	
DESCHUTES STRAIN	1985	344	.988	.012			180	.967	.033
CAPE COD STRAIN	1985	320	.759	.241			160	1.000	
OAK SPRING STRAIN	1985	308	.903	.097			154	.831	.169
METOLIUS	1985	276	.971	.022		.007	138	1.000	

Table 9. Continued.

LOCATION	YEAR	ME-4 N	ME-4 100	ME-4 85	DPEP N	DPEP 100	DPEP 110	DPEP 85	
MAINSTEM	1984	148	1.000		148	.939	.061		
	1986	106	1.000		106	.915	.028		.057
BAKEOVEN (MOUTH)	1984	80	1.000		80	.913	.088		
	1985	60	1.000		60	.883	.100	.017	
BAKEOVEN (DEEP CR.)	1984	120	1.000		114	.886	.105		.009
	1985	136	1.000		136	.934	.059	.007	
BUCK HOLLOW (LOWER)	1984	150	1.000		150	.920	.047		.033
	1985	98	1.000		98	.939	.041		.020
BUCK HOLLOW (MACKEN CNY)	1984	50	1.000		50	.960			.040
	1985	96	1.000		96	.896	.031		.073
BIG LOG	1984	40	1.000		40	.875	.075	.050	
	1985	100	1.000		100	.860	.090	.050	
EAST FOLEY (BELOW)	1984	30	1.000		30	1.000			
EAST FOLEY (ABOVE)	1984	64	1.000		64	.938	.063		
	1985	88	1.000		88	.886	.102	.011	
NENA (LOWER)	1984	40	1.000		40	.950	.025		.025
	1985	100	1.000		100	.970	.030		
NENA (MIDDLE)	1984	42	1.000		42	.952	.048		
	1985	92	1.000		92	.935	.065		
NENA (UPPER)	1984	86	1.000		86	.802	.105		.093
WAPINITIA	1984	32	1.000		32	.971			.029
LOWER WHITE (SITE 1)	1984	58	.983	.017	58	1.000			
(SITE 2)	1984	26	1.000		26	1.000			
LOWER TYGH	1984	62	.984	.016	62	.952	.048		
JORDAN	1984	126	.968	.032	126	1.000			
UPPER TYGH	1984	136	1.000		136	1.000			
LITTLE BADGER	1984	100	1.000		100	1.000			
THREEMILE	1984	100	1.000		100	.970	.030		
ROCK	1984	116	.983	.017	116	.991	.009		
GATE	1984	80	1.000		80	.938	.063		
BARLOW (SITE 1)	1984	92	1.000		92	1.000			
(SITE 2)	1984	24	.958	.042	24	1.000			
ROUND BUTTE STRAIN	1984	200	1.000		200	.933	.067		
DESCHUTES STRAIN	1985	180	.967	.033	160	.944	.006		
CAPE COD STRAIN	1985	160	1.000		160	.994	.006		
OAK SPRING STRAIN	1985	154	.831	.169	154	.987			.013
METOLIUS	1985	138	1.000		138	.831	.029		.140

Table 9. Continued.

LOCATION	YEAR	PGM-1 N	PGM-1 -100	PGM-1 -85	PGM-1 -115	PGM-2 N	PGM-2 -100	PGM-2 -140
MAINSTEM	1984	148	1.000			148	1.000	
	1986	106	.991		.009	106	1.000	
BAKEOVEN (MOUTH)	1984	80	.975	.013	.013	80	1.000	
	1985	60	1.000			60	1.000	
BAKEOVEN (DEEP CR.)	1984	120	.967	.025	.008	120	1.000	
	1985	136	.993		.007	136	1.000	
BUCK HOLLOW (LOWER)	1984	150	1.000			150	1.000	
	1985	98	1.000			98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	50	1.000			50	1.000	
	1985	96	.979	.021		96	1.000	
BIG LOG	1984	40	1.000			40	1.000	
	1985	100	1.000			100	1.000	
EAST FOLEY (BELOW)	1984	30	1.000			30	1.000	
EAST FOLEY (ABOVE)	1984	64	1.000			64	1.000	
	1985	88	1.000			88	1.000	
NENA (LOWER)	1984	38	1.000			40	1.000	
	1985	100	1.000			100	1.000	
NENA (MIDDLE)	1984	44	.955	.045		42	1.000	
	1985	92	1.000			92	1.000	
NENA (UPPER)	1984	86	1.000			86	1.000	
WAPINITIA	1984	32	1.000			32	1.000	
LOWER WHITE (SITE 1)	1984	58	.983	.017		58	.966	.034
(SITE 2)	1984	26	1.000			26	.962	.038
LOWER TYGH	1984	62	1.000			62	1.000	
JORDAN	1984	126	1.000			126	1.000	
UPPER TYGH	1984	136	1.000			136	1.000	
LITTLE BADGER	1984	100	1.000			100	.980	.020
THREEMILE	1984	100	1.000			100	.990	.010
ROCK	1984	116	1.000			116	.888	.112
GATE	1984	80	1.000			80	1.000	
BARLOW (SITE 1)	1984	92	1.000			92	1.000	
(SITE 2)	1984	24	1.000			24	.958	.042
ROUND BUTTE STRAIN	1984	156	.987	.013		200	1.000	
DESCHUTES STRAIN	1985	180	1.000			180	1.000	
CAPE COD STRAIN	1985	160	1.000			156	.994	.006
OAK SPRING STRAIN	1985	154	1.000			154	.812	.188
METOLIUS	1985	120	1.000			134	.948	.052

Table 9. Continued.

LOCATION	YEAR	SOD N	SOD 100	SOD 152	SOD 48	LGG N	LGG 100	LGG 74
MAINSTEM	1984	148	.932	.034	.034	148	1.000	
	1986	106	.915	.047	.038	106	1.000	
BAKEOVEN (MOUTH)	1984	80	.913	.038	.050	80	1.000	
	1985	60	.917	.033	.050	52	1.000	
BAKEOVEN (DEEP CR.)	1984	120	.892	.083	.025	120	.992	.008
	1985	136	.912	.044	.044	136	.971	.029
BUCK HOLLOW (LOWER)	1984	150	.927	.033	.040	150	1.000	
	1985	98	.867	.031	.102	98	1.000	
BUCK HOLLOW (MACKEN CNY)	1984	50	.920		.080	50	1.000	
	1985	96	.917	.021	.063	96	1.000	
BIG LOG	1984	40	.950	.050		40	1.000	
	1985	100	.990		.010	100	1.000	
EAST FOLEY (BELOW)	1984	30	.967		.033	30	1.000	
EAST FOLEY (ABOVE)	1984	64	.953	.031	.016	64	1.000	
	1985	88	.943	.011	.045	88	1.000	
NENA (LOWER)	1984	40	.950	.050		40	1.000	
	1985	100	.940	.050	.010	100	1.000	
NENA (MIDDLE)	1984	42	.905	.095		42	1.000	
	1985	92	.913	.087		92	1.000	
NENA (UPPER)	1984	86	.977		.023	86	1.000	
WAPINITIA	1984	32	.906	.094		32	1.000	
LOWER WHITE (SITE 1)	1984	58	.897	.103		58	1.000	
(SITE 2)	1984	26	.885	.115		26	1.000	
LOWER TYGH	1984	62	.887	.113		62	1.000	
JORDAN	1984	126	.849	.151		136	.985	.015
UPPER TYGH	1984	136	1.000			124	.960	.040
LITTLE BADGER	1984	100	1.000			100	.990	.010
THREEMILE	1984	100	.970	.030		100	1.000	
ROCK	1984	116	.698	.302		116	1.000	
GATE	1984	80	.975	.025		80	.988	.013
BARLOW (SITE 1)	1984	92	.989	.011		92	.989	.011
(SITE 2)	1984	24	1.000			24	.958	.042
ROUND BUTTE STRAIN	1984	200	.910	.055	.035	200	.990	.010
DESCHUTES STRAIN	1985	180	.906	.094		164	.994	.006
CAPE COD STRAIN	1985	160	.888	.113		160	1.000	
OAK SPRING STRAIN	1985	146	.541	.459		154	1.000	
METOLIUS	1985	134	.913	.087		138	1.000	

APPENDIX B

Evidence of Biochemical and Morphological Differentiation of a Wild Rainbow Trout (Salmo gairdneri) Population Due to Interbreeding of Native and Nonnative Trout.

INTRODUCTION

Rainbow trout (Salmo gairdneri), a genetically diverse species native to western North America, have been introduced and reintroduced extensively throughout their native range and much of the world (MacCrimmon 1971, 1972). Based on comparisons of morphological data from rainbow trout collected at the beginning of the century and recently, Behnke (1979) has concluded that in many parts of the range, unique phenotypes of native rainbow trout in isolated or partially isolated populations have been altered or lost because of interbreeding with introduced, nonnative rainbow trout. Campton and Johnston (1985) have suggested that the decline of anadromous salmonids in the Columbia River may be favoring introgression between nonanadromous rainbow trout of hatchery origin and native rainbow trout in many of the tributaries of the Columbia River. For fishery managers and others challenged with identifying and maintaining genetic diversity in wild populations (Larkin 1972) such changes in genetic structure of wild populations are of great concern.

The extent of such loss is difficult to measure. Phenotypic variation may also be caused by different environmental effects. Recent application of electrophoretic techniques to infer gene flow

based on biochemical genetic markers have not resolved the question. Allelic frequencies that suggest rainbow trout of mixed ancestry occur in populations of Montana's Kootenai River (Allendorf et al. 1980), Washington's Yakima River (Campton and Johnston 1985), and California's Eagle Lake (Busack et al. 1980). Wishard et al. (1984), however, found no evidence of hybridization between nonnative and native rainbow trout in tributaries of the Owyhee and Snake Rivers, Idaho.

Complementary analyses of more than one type of genetically controlled character were used in the study of Eagle Lake rainbow trout (Busack et al. 1980) but have not been used in similar studies within the Columbia River drainage. Although Wishard et al. (1984) note the similarity of their interpretations based on biochemical data to unpublished analyses based on meristic data, they give no details. In this report, I present complementary biochemical and meristic evidence of mixed ancestry for a wild population of rainbow trout in the headwaters of Metolius River, Oregon, a tributary of the Deschutes River that is now blocked to anadromous fishes by hydroelectric dams. Wild rainbow trout, which are protected by catch-and-release regulations in this area, may represent native phenotypes or a combination of phenotypes caused by the introgression of native and hatchery rainbow trout. Hatchery rainbow trout, which may be kept by anglers, have been stocked in the Metolius River since at least 1934 (Oregon Department of Fish and Wildlife Stocking Records 1934-1984). I also document the usefulness of biochemical variation at a locus that has not been used in previous studies of mixed ancestry but that

may be useful as a diagonistic allele in future studies in populations east of the Cascade Mountains in the Columbia River basin.

METHODS

Collection of Samples

Oregon Department of Fish and Wildlife biologists collected 89 wild rainbow trout from the headwaters of the Metolius River in 1985. Hatchery rainbow trout may be identified by clipped fins; rainbow trout with whole fins were assumed to be wild: the progeny of rainbow trout spawning in the Metolius River. Twenty rainbow trout were randomly selected, preserved in 10% formalin, and stored in 40% isopropanol for meristic analysis. The remaining rainbow trout were frozen immediately on dry ice and stored for up to three weeks at -10C for electrophoretic analysis.

Collection of Data

Meristic data were the number of scales in the lateral series and were collected following the methods of Hubbs and Lagler (1957). Biochemical data were obtained by electrophoresis. Prior to electrophoresis, eyes, liver, and a portion of white muscle were extracted from each fish and placed in culture tubes. Tissue samples were homogenized with two drops of distilled water and centrifuged. Procedures for electrophoresis followed the methodology of Utter et al. (1974) and May (1975, 1979). Three buffer systems were used: (1) RW - a tris,citric acid gel buffer at pH 8.5, lithium hydroxide,boric acid tray buffer at pH 8.5 (Ridgway et al. 1970); (2) MF - a

tris, boric acid, EDTA gel and tray buffer at pH 8.5 (Markert and Faulhaber 1965); and (3) AC - an amine citrate gel and tray buffer at pH 6.5 or 7.0 (Clayton and Tretiak 1972). Staining for enzyme activity followed methods outlined by Harris and Hopkinson (1976) and Allendorf et al. (1977). Table 1 of the main thesis lists the names, abbreviations, and numbers of loci expressed for the enzyme stains used. Nomenclature follows the system suggested by Allendorf and Utter (1979).

Analysis

The statisical analysis of biochemical variation is based on isozyme frequencies for alternative enzymes. Alternative forms of these enzymes, coded by different deoxynucleic acid sequences that comprise synonymous genes occuring at the same locus, are treated as alleles (Allendorf and Utter 1979). I tested the hypothesis that the Metolius River collection was drawn from a single, randomly mating unit by examining the observed distribution of genotypes at each locus for departures from the distribution expected under assumptions of Hardy-Weinberg equilibrium using a log likelihood ratio test (Sokal and Rohlf 1981). Tests were limited to those samples with expected values greater than one. Duplicated loci, IDH-3,4 and MDH, were not tested because variation could not be assigned to individual loci and expected values could not be generated. I calculated average heterozygosity by the average under Hardy-Weinberg expectations of all loci.

Testing the hypothesis that differentiation of the Metolius River population could be due to genetic mixing of native and nonnative

hatchery trout is difficult because the allelic frequencies and meristic characteristics of the original native populations are not known. Strong inferences are possible based on two lines of investigation. First, I examined native populations in the Deschutes River, the Metolius River population, and hatchery populations for biochemical and meristic taxonomic differences. Where native and nonnative populations belong to different taxonomic groups, the biochemical genetic and meristic differences between the two groups are suitable taxonomic characters for discriminating between native and nonnative populations. If gene flow from hatchery introductions is significant, the wild population with mixed ancestry should be intermediate for these allelic frequencies and meristic traits. Known differences between two major taxonomic groups of rainbow trout in western North America are useful. A coastal group of course-scaled rainbow trout is characterized by very little variation at the LDH-4 locus and to a lesser degree by greater variation at the SOD locus than the inland group. This inland group of fine-scaled rainbow trout is characterized by high levels of variation at the LDH-4 locus and relatively little variation at the SOD locus (Huzyk and Tsuyuki 1974, Allendorf and Utter 1979, Milner et al. 1980, Schreck et al. 1986). Second, I examined Metolius River rainbow trout for the presence of alleles that might be common in the hatchery strains but are absent in other wild populations in the drainage to infer genetic influence of specific hatchery strains.

In the absence of biochemical and morphological data for the

original native rainbow trout in the Metolius River, I estimated the divergence of the present population from a hypothetical native population. I tested for allelic heterogeneity between the Metolius wild rainbow trout population and the mean frequencies for wild rainbow trout populations in the Deschutes drainage. Wild rainbow trout populations include resident rainbow trout from the Deschutes River, rainbow trout above barriers in Nena Creek and East Foley Creek, and rainbow trout from nonisolated populations in Bakeoven, Buck Hollow, Wapinitia, Nena, East Foley, and Big Log creeks (Appendix A). Stocking records and biochemical genetic examination of these populations in the main text of this thesis indicate that these populations are probably representative of native rainbow trout in the Deschutes River. I tested for differences in mean scale counts between the Metolius River population and rainbow trout in the Deschutes River (Schreck et al. 1986) using Student's t-test and compared the mean for the Metolius River population to means for 24 populations from east and west of the Cascades Mountains in the Columbia River drainage (Schreck et al. 1986) and Cape Cod and Oak Springs hatchery strains (Table 7 in the main text of this thesis), which are not native to the Deschutes drainage.

The genetic similarity of the Metolius River rainbow trout to other wild populations and hatchery populations was examined by cluster analysis of biochemical genetic data. A phenogram was derived by the unweighted pair-group method using arithmetic averages (UPGMA) algorithm (Sneath and Sokal 1973) and was based on a matrix of Nei's genetic distance values (Nei 1972, 1978). Allelic frequencies for

the two nonnative hatchery strains and the Deschutes hatchery strain of rainbow trout were included in the analysis (Appendix A). The Deschutes strain is derived from resident rainbow trout native to the Deschutes River (Kinunen and Moring 1978).

RESULTS

Hardy-Weinberg Equilibrium and Average Heterozygosity

Genotypic distribution failed to conform to that expected under Hardy-Weinberg equilibrium at two loci. Fewer heterozygotes than expected occurred at the ADA-1 locus and the DPEP locus indicating assortative mating, loss of heterozygotes from the population through selection or emigration, or inbreeding at these loci. Average heterozygosity in the Metolius wild rainbow trout population is 0.079 and is consistent with my estimates for other wild populations in the Deschutes River basin (Table 3 in the main text of this thesis) and for rainbow trout in general (Allendorf and Utter 1979). The absence of a low level of genetic variation, which should occur in a small, isolated population subject to inbreeding and random genetic drift, indicates that inbreeding is not a likely cause of the departures from Hardy-Weinberg equilibrium.

Allelic Heterogeneity and Biochemical Genetic Similarity

Allelic frequencies for the Metolius River population are similar to the mean for the native populations with several exceptions. The frequency of the LDH-4(76) allele is significantly lower ($P < 0.001$). The ADA-1(92) allele is common in the Metolius River population and

extremely rare in other wild populations ($P < 0.001$). Variation at DPEP and PGM-2 is greater in the Metolius River population than in the hypothetical original population ($P < 0.05$).

Based on an examination of the distribution of LDH-4(76) and SOD alleles, native Deschutes River populations clearly belong to the inland group and lack the alternative allele for ADA-1 (Figure 8). The Deschutes hatchery strain also belongs to the inland group but has less of the alternative allele for LDH-4. Cape Cod and Oak Springs strains clearly belong to the coastal group and have significant levels of the alternative allele for ADA-1. The Metolius River population has allelic frequencies intermediate between these two groups.

All populations of Deschutes River origin, including the Metolius River and the Deschutes hatchery strain, are more similar to each other than they are to the two introduced hatchery populations (Figure 9). However, the Metolius River population is genetically most similar to the Deschutes hatchery strain. Both of these populations are clearly differentiated from the wild, native populations, which form a more homogenous group.

Number of Scales in the Lateral Series

The Metolius River rainbow trout have a mean of 138.9 and a standard deviation of 5.62 scales in the lateral series. This is significantly lower ($t = 5.22$, $df = 38$, $P < .001$) than the 149.4 mean for native populations in the Deschutes River. It is intermediate between a sharp cline of low numbers of scales typical of coastal populations, which are west of the Cascade Mountains, and the higher

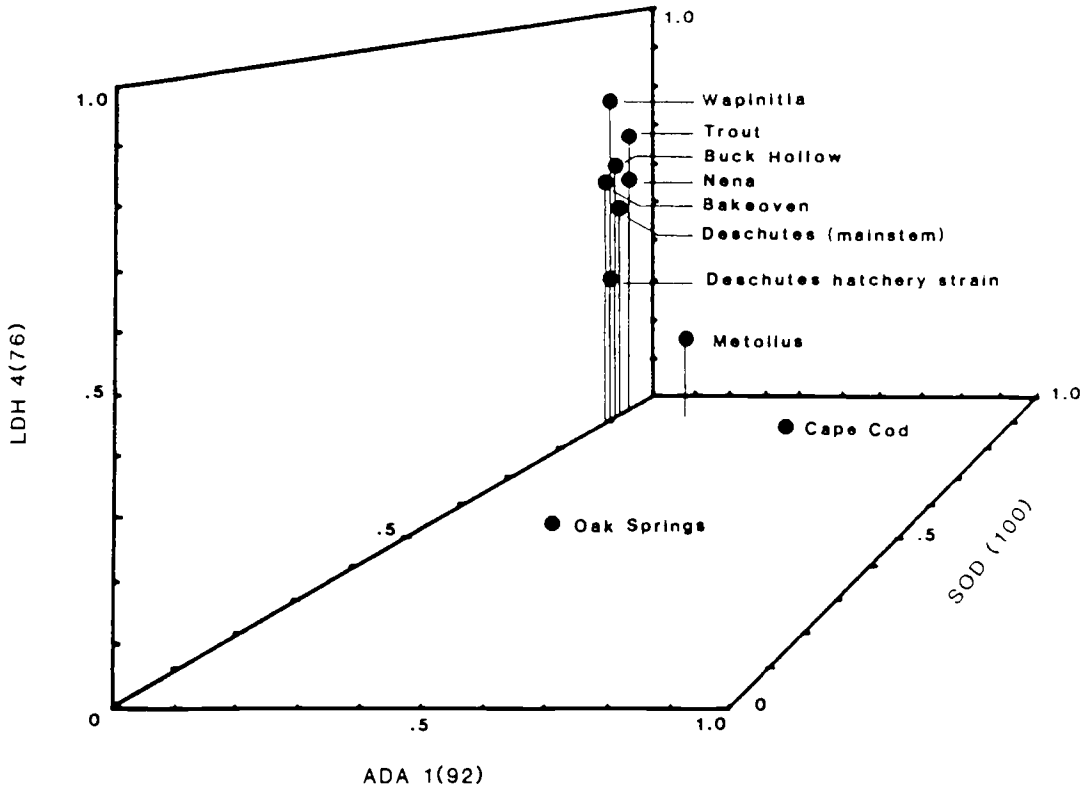

Figure 8. Distribution of wild and hatchery rainbow trout populations by allelic frequencies at three diagonistic loci. Sites within tributaries are combined to simplify viewing.

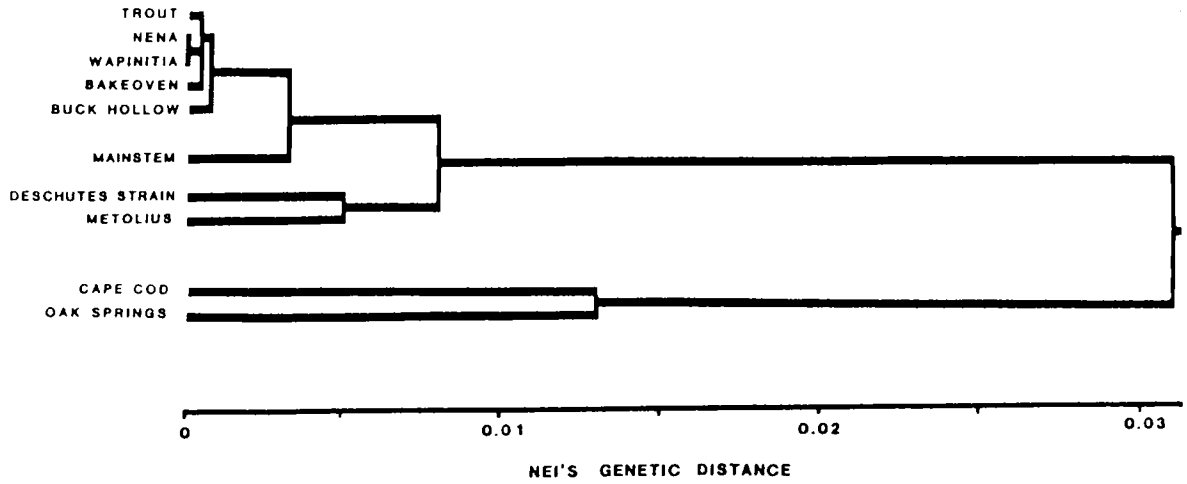

Figure 9. Phenogram of biochemical genetic similarity of hatchery and wild rainbow trout in the Deschutes River basin.

numbers of scales typical of inland populations, which are east of the Cascade Mountains (Figure 10). Scale numbers for nonnative hatchery strains of rainbow trout are typical of coastal populations.

DISCUSSION

The genetic differentiation of the Metolius River rainbow trout population may be the result of gene flow, random effects of small population size, selection, or mutation. Although random genetic drift and natural selection may have caused genetic differentiation of this population prior to the introduction of nonnative strains of rainbow trout, I believe that interbreeding of nonnative and native rainbow trout explains much of the meristic and biochemical differentiation of Metolius River rainbow trout documented in this study. Similar observations for biochemical Mendelian traits and a meristic, polygenic trait indicate that the evolutionary forces responsible for this differentiation of the Metolius River population have acted simultaneously and in a similar direction on a large portion of the genome rather than at single traits or loci. Biochemically and meristically the native populations of rainbow trout in these tributarties are typical of inland rainbow trout. The nonnative hatchery strains that I examined are typical of coastal rainbow trout populations. This is consistent with results from investigations of other hatchery strains. The common origin in coastal streams and especially the McCloud River for many established strains of hatchery rainbow trout is well documented (Needham and Behnke 1962, MacCrimmon 1971, Busack and Gall 1980). Cape Cod and Oak

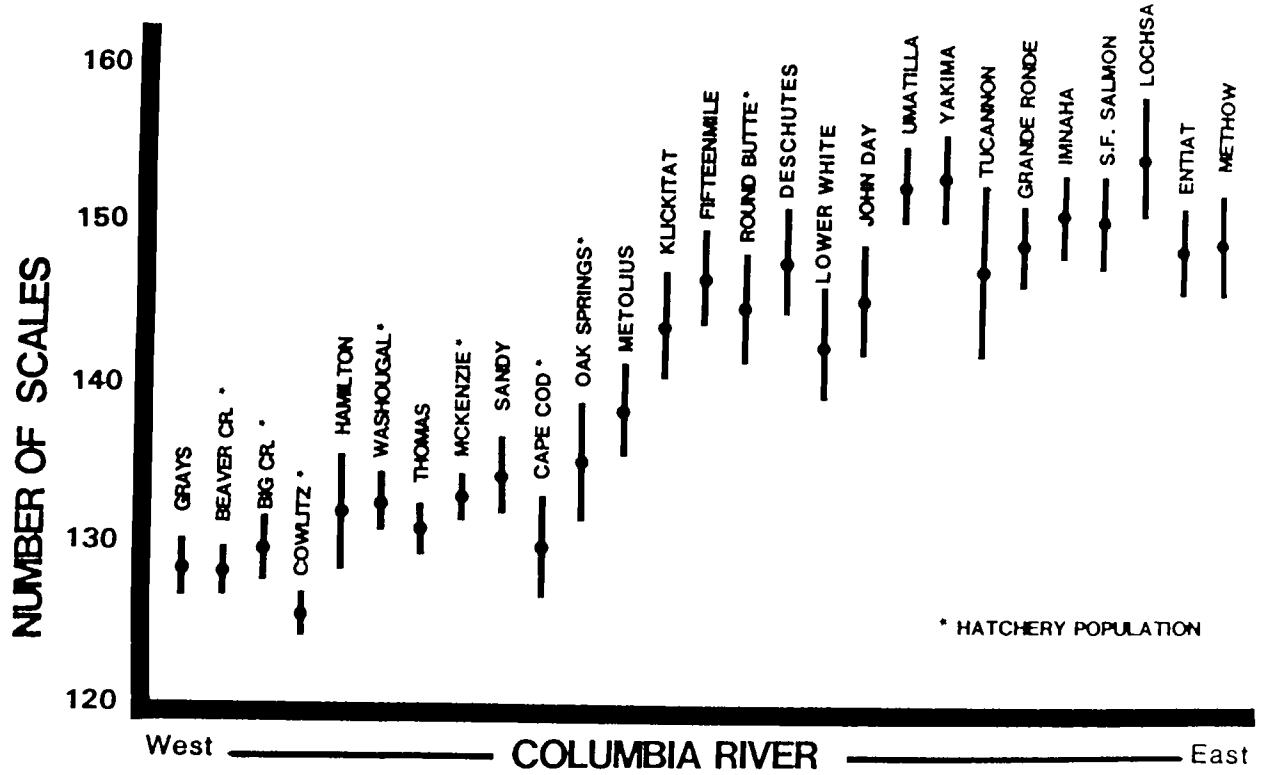

Figure 10. Means and 95% confidence intervals for number of scales in the lateral series for wild and hatchery rainbow trout in the Columbia River drainage.

Springs strains may share a common origin in "Utah trout", which are most likely derived from McCloud River rainbow trout (Kinunen and Moring 1978, Dollar and Katz 1964), and thus may be presumed to represent other nonnative hatchery strains that have been stocked in the river. The rainbow trout in the Metolius River, a tributary into which nonnative rainbow trout have been introduced, are intermediate between these two groups. This pattern of differentiation at these characters is more easily explained by introgression between nonnative and native forms of rainbow trout than by random genetic drift or natural selection.

The high frequency of ADA-1(92) allele in the Metolius River population and the two nonnative hatchery strains when compared to other wild populations in the Deschutes River is especially convincing evidence of the gene flow from nonnative hatchery rainbow trout. In other wild populations in the Deschutes River, I found an ADA-1(92) allele in a single fish in Big Log Creek and in a single fish in East Foley Creek, both tributaries to Trout Creek, out of nearly 1400 fish examined. Given the relatively recent divergence of the Metolius River population from other Deschutes River populations based on lesser differences at loci that are not diagonistic of inland and coastal taxa and the lack of evidence of stochastic effects of small population size operating in the population, it is highly unlikely the population would have accumulated this level of variation by mutation or by random genetic drift. In the absence of other data, natural selection must also be considered a possible evolutionary force that has acted on this locus. However, under such conditions, similar

selection pressures on other wild populations in nearby streams, which might receive migrants from the Metolius River, should favor the allele in those populations as well. This apparently has not happened.

Stronger inferences should be possible when more loci and morphological data are included in the analyses than when inferrences are based on differences at two biochemical loci. The use of variation at the ADA-1 locus to infer gene flow from several popular strains of hatchery rainbow trout, which is important in my study, may have applications beyond the Deschutes River. The ADA-1(92) allele, which is common in the Cape Cod and Oak Springs rainbow trout strains, may be rare in the entire Columbia River basin. Schreck et al. (1986) examined wild steelhead populations in all major tributaries of the Columbia River but do not give data for ADA-1. Their unpublished data indicate that the allele occurred in only the Wenatchee River, but data were not available for a number of major tributaries. Because brood stock for Cape Cod and Oak Springs strains are maintained at different hatcheries in Oregon and apparently have not been mixed (Kinunen and Moring 1978), the presence of the ADA-1(92) allele in both strains may indicate a common origin that occurred prior to their use in the Oregon hatchery system. Consequently, the ADA-1(92) allele may also be common to other hatchery strains. If so, or if the source of the allele in wild populations can be determined, it may be useful as a diagonistic allele for future studies of populations with mixtures of native and nonnative rainbow trout in a larger

geographical area.

When the ADA-1(92) allele is considered a genetic marker of hatchery rainbow trout, the deviation of the Metolius River population from Hardy-Weinberg equilibrium at the ADA-1 locus is intriguing. If the deviation is caused by assortative mating, then hatchery rainbow trout may be preferentially mating with other hatchery rainbow trout and wild trout may be preferentially mating with other wild trout. Behavioral differences, such as differences in spawning times, might account for such assortative mating patterns. Knowledge of the genetic basis for such behavioral differences and the potential ecological and genetic segregation of the two forms in the wild could be extremely valuable in managing fisheries to conserve native populations while providing the opportunities for anglers to keep rainbow trout. Alternatively, the deviation from Hardy-Weinberg equilibrium may reflect the loss of heterozygotes from the population by selection or migration. The possibility that such losses are associated with changes in the fitness of the wild population because of interbreeding of nonnative and native rainbow trout is clearly a concern that needs further investigation.

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APPENDIX C

Reexamination of the Use of Otolith Nuclear Dimensions in the Identification of Juvenile Anadromous and Nonanadromous Rainbow Trout (Salmo gairdneri)

INTRODUCTION

Otoliths are a potential source of taxanomic characters for identifying stocks of fish. Differences in dimensions of the otolith nucleus provided a basis for separating winter and summer races of steelhead (anadromous rainbow trout), as well as resident and steelhead life history forms (McKern et al. 1974, Rybock et al. 1975). Recently, however, Neilson et al. (1985) studied the development of sagittal otoliths in resident rainbow and steelhead trout (Salmo gairdneri) from south-central British Columbia and were unable to find morphometric differences. The difference in mean length of the otolith nuclei between the rainbow trout that Rybock et al. (1975) studied and those that Neilson et al. (1985) studied suggests population differences or differences in defining the nuclear boundary. These disparate results limit the usefulness of otolith nuclear dimensions in racial identification of juvenile rainbow trout until the source of these differences is better understood. To determine whether juvenile steelhead and resident rainbow trout could be distinguished by differences in otolith nuclear dimensions, I measured the nucleus of the sagitta from steelhead and resident rainbow trout from the same Deschutes River locations used by Rybock

et al. (1975) using definitions proposed by Rybock et al. (1975) and Neilson et al. (1985) and compared them with published values and each other.

METHODS

Resident rainbow trout and steelhead were collected from three locations in the Deschutes River. Spawning rainbow trout with fork lengths between 280 and 450 mm were collected from the mainstem near the mouth of Nena Creek in 1985 and were assumed to be resident rainbow trout. Juvenile progeny of steelhead were collected from Round Butte Hatchery in 1984. Wild juvenile rainbow trout (fork lengths less than 200 mm) of unknown parental origin were collected from Bakeoven Creek, an important spawning tributary for steelhead, in 1984 and 1985.

Sagittae were removed from the rainbow trout and stored in 90% ethanol for up to 2 months. Prior to viewing, one otolith from each pair was mounted concave face up with epoxy on a glass slide. The reverse face of the slide was blackened with indelible ink. The otolith was ground by hand with 600 grit wet sandpaper and periodically inspected under a light microscope at 100X until the microstructures of the nucleus, as described by Neilson et al. (1985), were visible. The otolith was rinsed with 5% HCL for several seconds to remove scratches and enhance resolution.

To reduce bias, each slide was coded with a random number and ordered sequentially for viewing. Otoliths were viewed with a Zeiss dissecting microscope at 125X. A camera lucida attachment allowed use

of a computer digitizer to measure three dimensions of the otolith. Length and width of the central nucleus were measured using the nuclear boundary defined by Neilson et al. (1985). In addition, the distance along the longest axis through an area defined by the first metamorphic check encompassing all primordia was measured to replicate the measurements of Rybock et al. (1975).

I tested for significant differences in each otolith nuclear dimension among groups in my study using analysis of variance. Where adequate data were available, I tested for significant differences between groups in my study and similar groups in Rybock et al. (1975) and Neilson et al. (1985) for mean otolith nuclear dimensions. To evaluate the potentially confounding effects of incubation temperature on the comparisons of otolith dimensions between my samples and those of Rybock et al. (1975), I tested the hypothesis that water temperatures during 1967-1969 were greater than those during 1982-1983 using a paired t-test of average daily water temperatures recorded on the first and fifteenth day of each month during 1967-1969 and 1982-1983 from January 1 to August 1. I plotted the mean daily water temperature recorded by the U.S. Geological Survey at in the Deschutes River in 1967-1969 and 1982-1983 during the months that rainbow trout and steelhead eggs incubate (Water Resources Data for Oregon, 1967, 1968, 1969, 1982, 1983). These dates represent the incubation periods for most of the resident rainbow trout and steelhead sampled by Rybock et al. (1975) and by me. Incubation temperature for steelhead at Round Butte Hatchery is from hatchery records. I estimated spawning and incubation periods for resident rainbow trout and steelhead based

on Oregon Department of Fish and Wildlife reports (Fessler 1972) and personal observation.

RESULTS

For all dimensions, I failed to reject the hypothesis that rainbow trout collected from different populations for my study have otoliths nuclei of the same size (Table 10). I concluded that these dimensions could not be used to discriminate between the resident and steelhead life history forms of rainbow trout sampled for my study.

Table 10. Means, standard errors, and sample size for three otolith dimensions in resident rainbow trout and steelhead from three Deschutes River populations.

Populations Compared	Sample Size	Nuclear Dimension: Nucleus Length	Nucleus Width	Check Length
Resident Rainbow Trout	44	0.173 (0.006)	0.070 (0.003)	0.323 (0.012)
Hatchery Steelhead	30	0.190 (0.006)	0.070 (0.002)	0.349 (0.009)
Suspected Wild Steelhead	32	0.178 (0.006)	0.069 (0.002)	0.312 (0.007)

Water temperatures during 1967-1969 were slightly greater than those during 1982-1983 ($t = 2.03$, $df = 14$, $P = 0.03$). Mean difference between the two periods was 0.8C. Spawning and incubation times for resident rainbow trout and steelhead vary (Figure 11). Steelhead

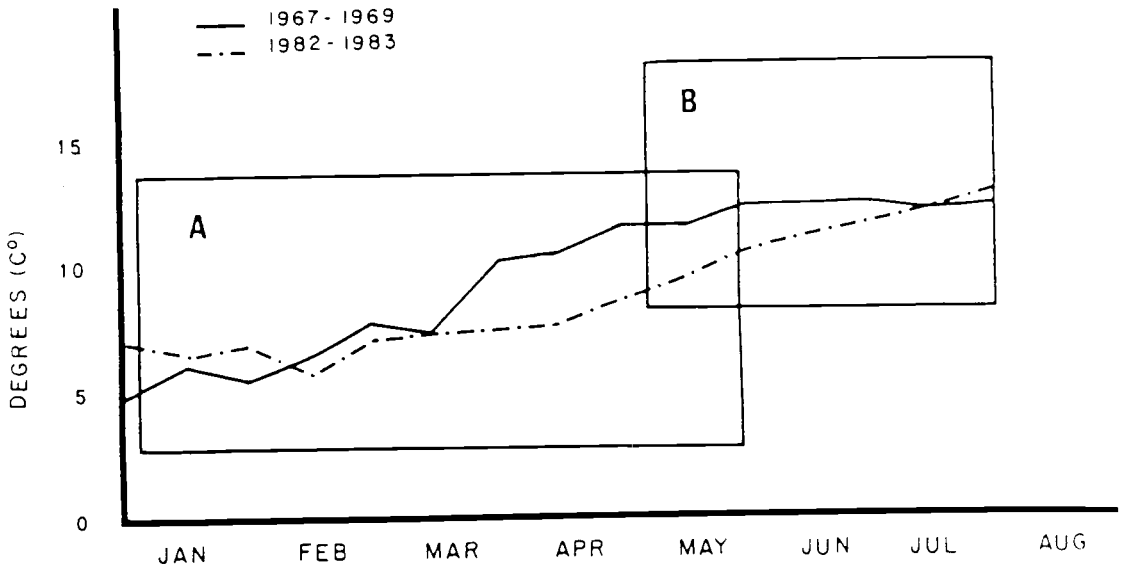

Figure 11. Water temperatures in the mainstem of the Deschutes River. Box A contains water temperatures during steelhead spawning and incubation; Box B contains water temperatures during resident rainbow trout spawning and incubation.

spawn in eastern tributaries (Bakeoven Creek) from January through March; steelhead spawn in western tributaries from March through April; resident rainbow trout spawn in the mainstem from May through mid July (Fessler 1972). Mean water temperature during the period of steelhead egg incubation was 8.4C for 1967-1969 and 7.6C for 1982-1983. Mean water temperature during the period resident rainbow trout eggs are incubating in the mainstem of the river was 12.6C for 1967-1969 and 11.9C for 1982-1983. Incubation temperature for steelhead at Round Butte Hatchery is a constant 10C.

Sizes of otolith nuclei from resident and steelhead rainbow trout in my study were indistinguishable from those from British Columbia. No significant difference in mean otolith nuclear length exists between suspected wild steelhead from Bakeoven Creek or Round Butte Hatchery steelhead incubated at 10C and the British Columbia steelhead incubated at 9.5C or 15C. Mean otolith nuclear length for Deschutes River resident rainbow trout is also not significantly different from those in British Columbia incubated at 9.5C or 15C. Testing the hypothesis that means from this study are not different from those of Rybock et al. (1975) was not possible because Rybock et al. (1975) did not provide variances. However, mean otolith nuclear length and width for my study were 29% and 55% less for resident rainbow trout and 49% to 70% less for steelhead than those of Rybock et al. (1975).

DISCUSSION

Comparisons of nuclear size between studies of different populations or races within a drainage must consider the environmental

and genetic variables affecting nuclear size as well as differences in methodology between investigators. Rybock et al. (1975) hypothesized that otolith nuclear size was associated with egg size and that females of the larger steelhead produced larger eggs. Changes in genetic or environmental variables that effect a change in egg or body size might explain differences in size of the otolith nucleus, but I found no evidence that significant changes in size distribution of Deschutes resident rainbow trout and steelhead have occurred.

Neilson et al. (1985) demonstrated that nuclear length increases significantly with increase in incubation temperature from 6.5C to 9.5C but not from 9.5C to 15C. It is unlikely, however, that such differences completely explain the greater estimates of mean otolith nuclear length and width in the earlier study by Rybock et al. (1975). Water temperatures during 1982-1983 were an average of 0.8C lower than those in 1967-1969. Rybock et al. (1975) calculated a mean nuclear length of 0.354 mm and a mean nuclear width of 0.230 mm for steelhead; they calculated a mean nuclear length of 0.243 mm and a mean nuclear width of 0.154 mm for resident rainbow trout in the Deschutes River. My estimates are 29% to 70% less than those of Rybock et al. (1975) for less than 1C differences. Under controlled conditions in British Columbia, mean nuclear length for resident rainbow trout at 6.5C was 18% less for resident rainbow trout and 21% less for steelhead than those incubated at 9.5C - a three degree difference (Neilson et al. 1985).

The similar results of my study and that of Neilson et al. (1985)

following similar methods might be expected for different populations under similar genetic and environmental control. The disparate results of this study and that of Rybock et al. (1975) for the same populations after minimal genetic and environmental change partially reflects the use of different definitions for the nucleus. I defined the nuclear boundary as the first growth ring surrounding all the fused primordia. Rybock et al. (1975) defined the nucleus as the hyaline area in the center of the otolith that is bounded by a metamorphic check formed at hatching; they resolved the check by rendering the otolith with HCL. I also measured the length of the first metamorphic check surrounding the nucleus. The close similarity between my estimate for Round Butte hatchery steelhead (0.349mm) and the mean for steelhead calculated by Rybock et al. (1975) (0.354mm) suggested similar metamorphic checks. It is unclear, however, why values for resident rainbow trout for this dimension and the results of tests to discriminate races are different between the two studies. Rybock (1973) noted that the nuclear check could not be distinguished in 29% of the otoliths and that the use of HCL may have caused the frequent confusion between groups of daily growth rings and the metamorphic check. Grinding and polishing otoliths greatly reduces this source of error. Neilson et al. (1985) also discouraged use of metamorphic checks as boundaries because the causal links between checks and developmental events have not yet been established.

Comparisons of otolith nuclear dimensions between resident rainbow trout and steelhead incubated at similar temperatures would establish whether significant differences exist for these measurements

between the two races from the Deschutes River. Use of a common definition of nuclear boundaries would allow better comparisons between studies. However, given results of this attempt to replicate the original study and the failure to discriminate races using both nuclear definitions proposed by Neilson et al. (1985) and Rybock et al. (1975), the usefulness of such measurements in identifying sympatric juvenile progeny of resident rainbow trout and steelhead reared in the wild may be limited.

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