

Electrophoretic Evidence for a Genetic Admixture of Native and Nonnative Rainbow Trout in the Yakima River, Washington

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Abstract

Allele frequencies for wild rainbow trout *Salmo gairdneri* from the upper Yakima River and two tributary creeks were intermediate between those for introduced hatchery populations and those for inland populations native to other areas of the Columbia River basin. Previously published results had demonstrated a widespread geographic consistency in allele frequencies at two loci among both anadromous and nonanadromous populations in the Columbia River drainage east of the Cascade Mountains. The intermediate allele frequencies at these two loci for rainbow trout from the upper Yakima River, therefore, suggest that these populations represent genetic admixtures of native and nonnative stocks. Allele frequencies at several other loci plus field surveys of spawning fish further suggest that nonanadromous rainbow trout from domesticated hatchery strains, rather than hatchery-reared steelhead (anadromous *S. gairdneri*), have been responsible for the suspected introgression of nonnative genes into the Yakima River populations. We hypothesize that nonanadromous rainbow trout of hatchery origin may have survived and reproduced in relatively large numbers in the upper Yakima River because of major declines in the abundance of native steelhead and of two indigenous species of Pacific salmon *Oncorhynchus* sp.

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Rainbow trout *Salmo gairdneri* are native to western North America from northwestern Mexico to southwestern Alaska (MacCrimmon 1971). Throughout this range, the species is represented by both anadromous and nonanadromous populations. Anadromous fish are commonly called steelhead while nonanadromous fish are generally referred to as resident rainbow trout. The two types are indistinguishable by meristic (Needham and Gard 1959; Behnke 1972), karyotypic (Thorgaard 1983), and electrophoretic (Allendorf 1975; Utter et al. 1980) criteria, and are simply different life history forms of the same species. Whether a particular stream supports an anadromous or resident population appears to be the result of local adaptation to geographic location. Resident populations (native) are generally found hundreds of stream kilometres inland in the Columbia and Fraser river drainages, or above barrier falls in coastal drainages, whereas anadromous populations appear to be present wherever the species has access to the sea. Resident populations are, therefore, believed to be

polyphyletic in origin (Behnke 1972). Throughout this report, we use the names rainbow trout and *Salmo gairdneri* to refer to the species as a whole, or to specific fish whose life history attributes are unknown. We refer to anadromous fish as steelhead, because this is the common name of this form in the western United States, Canada, and Alaska. Nonanadromous (resident) fish or populations are specifically stated as such.

The native range of *S. gairdneri* includes a major portion of Washington state (MacCrimmon 1971). Most rivers draining into the Columbia River basin of eastern Washington, including the Yakima River, historically supported abundant runs of steelhead, but hydropower dams on the Columbia and Snake rivers have severely reduced or decimated these native populations (Allen 1977; Schwiebert 1977; Raymond 1979; Netboy 1980; Washington State Department of Game [WDG], unpublished data). During this period of decline, more than 3,400,000 nonanadromous rainbow trout and 830,000 juvenile steelhead were released into the Yakima River drainage from nonnative hatchery populations (WDG planting records, 1950-1980, Olympia, Washington). The historical abundance of nonanadromous rainbow trout in the

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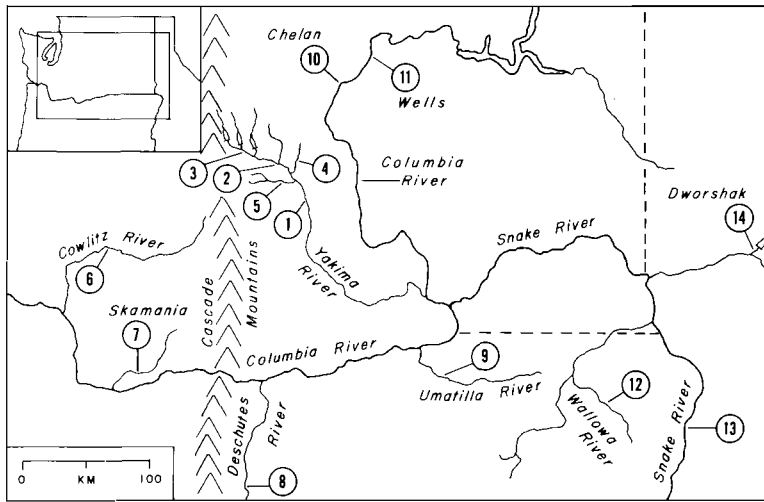


FIGURE 1.—Sample sites for *Salmo gairdneri* populations compared electrophoretically in this study. (1) Yakima River, site 1; (2) Yakima River, site 2; (3) Yakima River, site 3; (4) Swauk Creek; (5) Taneum Creek; (6) Cowlitz River Hatchery; (7) Skamania Hatchery, Washougal River; (8) Warm Springs area and Round Butte Dam, Deschutes River; (9) Umatilla River; (10) Chelan Public Utility District Hatchery, upper Columbia River; (11) Wells Dam Hatchery, upper Columbia River; (12) Wallowa River; (13) Hell's Canyon Dam, Snake River; and (14) Dworshak Hatchery, Clearwater River. Allele frequencies for populations 6 through 14 were obtained from adult steelhead trapped during their upstream migration at the indicated locations or from juvenile offspring of these adults (Milner and Teel 1979). Two hatchery populations of nonanadromous rainbow trout were also sampled.

Yakima River drainage is unknown, but such resident populations are believed to have been relatively rare in western Washington and the Cascade Mountains prior to the artificial propagation and release of hatchery fish (Crawford 1979).

Native populations of rainbow trout in the northwestern United States and southwestern Canada form two geographic races that can be distinguished by divergent allele frequencies at two biochemical genetic loci (Huzyk and Tsuyuki 1974; Allendorf 1975; Allendorf and Utter 1979; Allendorf et al. 1980; Utter et al. 1980; Parkinson 1984; Wishard et al. 1984). These two races are represented by a coastal group inhabiting all major drainages west of the Cascade Mountains and an inland group inhabiting the Columbia and Fraser river drainages east of the Cascade Mountains. Most hatchery strains of nonanadromous rainbow trout were derived from a few common sources in northern California (Needham and Behnke 1962; MacCrimmon 1971; Kinunen and Moring 1978; Crawford 1979; Busack and Gall 1980), and these strains express allele frequencies consistent with those for the coastal group (Utter and Hodgins 1972; Allen-

dorf 1975; Busack et al. 1979; Milner et al. 1979; Guyomard 1981). The hatchery population of steelhead from which smolts have been released into the Yakima River was derived from fish native to the Washougal and Klickitat rivers on the lower Columbia River (Crawford 1979), and this population expresses allele frequencies consistent with those for the coastal group also (Utter et al. 1980).

In this paper, we compare electrophoretic profiles of wild rainbow trout inhabiting the upper Yakima River (upstream from Ellensburg, Washington) to profiles for two hatchery populations of nonanadromous rainbow trout, and to profiles for nine populations of steelhead representing the two geographic races in the Columbia River drainage. Our purpose was to determine whether wild rainbow trout presently inhabiting the upper Yakima River are native fish, the descendants of introduced hatchery fish, or a genetic admixture of the two groups. The Yakima River drains the east side of the Cascade Mountains and rainbow trout native to this area were expected to belong to the inland race, whereas introduced fish were derived from populations of the coastal race. Field surveys of spawning fish

TABLE 1.—Enzymes and loci examined in *Salmo gairdneri* from the Yakima–Columbia river system. Buffer systems I, II, and III were described by Ridgway *et al.* (1970), Markert and Faulhaber (1965), and Clayton and Tretiak (1972), respectively. Buffer system IV was the gel buffer from Clayton and Tretiak (1972) coupled with electrode buffer I from Shaw and Prasad (1970). Tissues M and L refer to muscle and liver, respectively.

Enzyme	Enzyme Commission number	Locus	Tissue	Buffer
Alcohol dehydrogenase	1.1.1.1	<i>ADH</i>	L	I
Aspartate aminotransferase	2.6.1.1	<i>AAT-1,2</i>	M	I
Creatine kinase	2.7.3.2	<i>CK-1</i>	M	I
		-2	M	I
Dipeptidase (substrate: glycyl-leucine)	3.4.13.11	<i>GLD</i>	M	II
Glucosephosphate isomerase	5.3.1.9	<i>GPI-1</i>	M	I
		-2	M	I
		-3	M, L	I
Glycerol-3-phosphate dehydrogenase	1.1.1.8	<i>G3PDH-1</i>	M	IV
		-2	M	IV
Isocitrate dehydrogenase	1.1.1.42	<i>IDH-1</i>	M	IV
		-2	M	IV
		-3,4	L	III
Lactate dehydrogenase	1.1.1.27	<i>LDH-1</i>	M	I
		-2	M	I
		-3	M	I
		-4	M, L	I
Malate dehydrogenase	1.1.1.37	<i>MDH-1,2</i>	L	III
		-3,4	M	IV
Mannosephosphate isomerase	5.3.1.8	<i>MPI</i>	M	II
Phosphoglucomutase	2.7.5.1	<i>PGM</i>	M	I
Phosphogluconate dehydrogenase	1.1.1.44	<i>PGD</i>	M, L	IV
Superoxide dismutase	1.15.1.1	<i>SOD</i>	L	I
Tripeptide aminopeptidase (substrate: leucyl-glycyl-glycine)	3.4.11.4	<i>LGG</i>	M	II

were also conducted to determine whether present populations of *S. gairdneri* in the upper Yakima River represent steelhead or nonanadromous rainbow trout. The results of our study suggest that populations of *S. gairdneri* currently inhabiting the upper Yakima River are nonanadromous and represent a genetic admixture of native and introduced stocks. The data further suggest that rainbow trout from nonanadromous hatchery strains are most likely responsible for this suspected genetic introgression.

Methods

Sampled Populations

Rainbow trout were collected by electroshocking from three mainstem sites and two tributary creeks (Swauk and Taneum) of the Yakima River during November 1979 (Fig. 1). The three mainstem sites were located (1) at Ellensburg, (2) immediately upstream from the confluence of the Teanaway River, and (3) at Nelson, approxi-

mately 5 km upstream from the confluence of the Cle Elum River. These locations are called sites 1, 2, and 3, respectively, throughout this report. Scale analyses revealed all but a few fish to be less than 2 years old (age 0+ or 1+), and all fish were the result of natural spawning (Johnston 1979). Fish of hatchery origin would have been easily detected by accelerated growth patterns on their scales, and by morphological deformations of the dorsal and caudal fins caused by being reared in concrete raceways. Fish retained for electrophoretic analysis were frozen in the field on dry ice.

Two hatchery populations of nonanadromous rainbow trout, both maintained by the Washington State Department of Game and representative of fish planted in the Yakima River during the past 30 years (Crawford 1979), were sampled for electrophoretic analysis (abbreviations and sample sizes in parentheses): (1) Goldendale rainbow trout (RBGD, $N = 49$) and (2) South Tacoma rainbow trout (RBST, $N = 30$). Allele

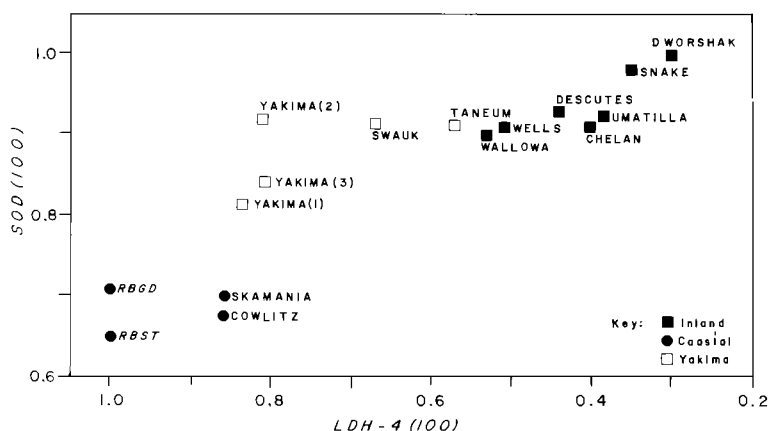


FIGURE 2.—Frequencies of the 100 allele at the lactate dehydrogenase LDH-4 and superoxide dismutase SOD loci for populations of Yakima-Columbia *Salmo gairdneri*. RBGD and RBST are hatchery strains of non-anadromous rainbow trout; other samples are identified by the sites in Fig. 1.

frequencies for nine populations of steelhead, representing fish native to the Columbia River drainage (Fig. 1), were obtained from Milner and Teel (1979) as reference data for the inland and coastal races of *S. gairdneri*. Allele frequencies for many of these populations have previously been summarized (Allendorf and Utter 1979; Utter et al. 1980) but not formally published. The Skamania Hatchery (site 7, Fig. 1) has been the source of steelhead smolts released into the Yakima River since the early 1960s.

Electrophoresis

The methods of horizontal starch gel electrophoresis used by us and Milner and Teel (1979) both followed the procedures described by May et al. (1979). Enzymes, loci, and alleles (Table 1) were designated according to the nomenclature system proposed by Allendorf and Utter (1979). Each locus is given a three-letter, italicized abbreviation of the enzyme for which it codes, followed by a hyphenated numeral when multiple loci code for the same enzyme (e.g., *LDH-3*, *LDH-4*). The most frequent allele at a locus is given the number 100, and variant alleles are assigned values according to their relative anodic mobilities (e.g., 90, 125, etc.). Duplicated loci (*AAT-1,2*; *IDH-3,4*; *MDH-1,2*; *MDH-3,4*) were treated as two disomic loci with identical allele frequencies because allelic variation could not be attributed to a specific locus (see Allendorf et al. 1975; May et al. 1979). Staining methods followed standard procedures and have been de-

scribed elsewhere (e.g., Shaw and Prasad 1970; Harris and Hopkinson 1976).

Statistics

Genotypes for rainbow trout from the Yakima River system were tested for goodness of fit to Hardy-Weinberg proportions with the likelihood-ratio test or *G*-statistic (Sokal and Rohlf 1969). Gametic (linkage) disequilibria between loci were estimated by Burrows' composite measure and tested for significance with the statistic Nr^2 , where *N* is the number of individuals (sample size) and *r* is the estimated correlation between alleles, corrected for deviations from Hardy-Weinberg proportions (Weir 1979). Nei's (1972) index of genetic similarity was calculated between all population pairs and the resulting relationships were graphically represented in two dimensions by projecting the populations onto the first two principal coordinate axes (Gower 1966; Everitt 1978).

Spawning Surveys

Field surveys of spawning rainbow trout were conducted during April 1980 in the following tributaries to the upper Yakima River: Badger Creek, Big Creek, Little Creek, Manashtash Creek, Naneum Creek, Reeser Creek, Shea Creek, Swauk Creek, Taneum Creek, Umtanem Creek, Wilson Creek, and Whipple Wasteway (Johnston 1980). Adult fish were captured by electroshocking, anesthetized with tricaine, and then examined visually for sex and maturity. The fork length of

TABLE 2.—*Allele frequencies for rainbow trout from the Yakima River, two hatchery strains of nonanadromous rainbow trout, and steelhead from the Columbia River drainage. The steelhead data are from Milner and Teel (1979), and are reproduced here with permission. The reference populations of steelhead are partitioned into coastal and inland races. Loci not listed were monomorphic for the 100 allele in all samples. S1, S2, and S3 refer to sample sites 1, 2, and 3, respectively.*

Locus	Allele, sample size	Yakima River					Hatchery rainbow		Coastal steelhead	
		S1	S2	S3	Swauk	Taneum	RBGD	RBST	Cowlitz	Skamania
AAT-1,2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	85								<0.01	
	N	70	85	66	38	50	49	30	179	693
ADH	−100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	−200									
	N	70	85	79	38	50	49	30	171	96
G3PDH-1	−100	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.98	0.86
	100			0.02					0.02	0.14
	N	70	85	78	38	50	49	30	215	995
GLD	110	0.06	0.06	0.01	0.12	0.14		0.05	0.10	0.02
	100	0.94	0.94	0.99	0.88	0.86	1.00	0.95	0.90	0.97
	90									0.01
GPI-3	N	70	85	69	38	50	49	30	40	956
	110									
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.92
IDH-2	90								0.01	0.08
	N	70	85	79	38	50	49	30	139	954
IDH-3,4	120	0.17	0.29	0.17	0.04	0.08	0.36	0.25		
	100	0.83	0.71	0.83	0.96	0.92	0.64	0.75		
	N	66	85	52	38	50	48	30	0	0
IDH-3,4	124	0.03		0.02	0.02			0.04	0.04	0.02
	100	0.82	0.85	0.85	0.75	0.82	0.90	0.64	0.67	0.64
	72	0.04	0.02	0.01	0.03	0.03	0.03	0.03	0.13	0.17
	44	0.11	0.13	0.13	0.20	0.15	0.08	0.27	0.17	0.17
	38	0.01						0.02		
	N	69	82	63	38	50	49	30	78	95
LDH-4	100	0.84	0.81	0.81	0.67	0.57	1.00	1.00	0.86	0.86
	74	0.16	0.19	0.19	0.33	0.43			0.14	0.14
	N	70	83	79	38	50	49	30	213	978
LGG	138	0.04								
	100	0.96	1.00	1.00	1.00	1.00	1.00	1.00		1.00
	N	70	85	69	38	50	49	30	0	500
MDH-1,2	132				0.02					
	100	0.96	0.99	0.99	0.97	0.98	1.00	1.00	1.00	1.00
	37	0.04	0.01	0.01	0.01	0.02				
MDH-3,4	N	70	85	77	38	50	49	30	218	310
	110	0.01								
	100	0.89	0.96	0.91	0.97	0.94	0.81	0.96	0.92	0.91
	85	0.09	0.03	0.09	0.03	0.06	0.19	0.04	0.01	0.01
	78	0.01	0.02	0.01					0.08	0.08
	N	69	85	79	38	50	49	30	218	958
MPI	100	0.96	0.98	0.98	0.97	0.95	1.00	1.00	1.00	1.00
	95	0.04	0.02	0.02	0.03	0.05				
	N	70	85	79	38	50	49	30	119	351
PGM	100	0.97	0.92	0.91	0.97	0.94	0.99	0.73	1.00	1.00
	85	0.03	0.08	0.09	0.03	0.06	0.01	0.27		
	N	66	85	79	38	50	49	30	212	604
SOD	142	0.14	0.07	0.13	0.04	0.06	0.29	0.35	0.32	0.30
	100	0.81	0.92	0.84	0.91	0.91	0.71	0.65	0.68	0.70
	43	0.04	0.01	0.03	0.05	0.03				
	N	70	85	79	38	50	49	30	217	961

TABLE 2.—*Extended.*

Locus	Allele, sample size	Inland steelhead						
		Chelan	Deschutes	Dworshak	Snake	Umatilla	Wallowa	Wells
<i>AAT-1,2</i>	100	1.00	1.00	0.99	1.00	0.99		1.00
	85			0.01		0.01		<0.01
	N	149	78	111	40	48	0	80
<i>ADH</i>	−100	1.00	0.99	1.00	1.00	0.97	1.00	1.00
	−200		0.01		<0.01	0.03		
	N	123	168	274	140	48	31	80
<i>G3PDH-1</i>	−100	0.98	1.00	1.00	1.00	1.00	0.99	0.98
	100	0.02					0.01	0.02
	N	234	165	303	140	21	36	129
<i>GLD</i>	110	0.09	0.06	0.52	0.16	0.09	0.07	0.08
	100	0.91	0.91	0.48	0.84	0.90	0.93	0.92
	90		0.04		0.01	0.01		
<i>GPI-3</i>	N	90	72	241	100	48	36	84
	110	0.02						0.01
	100	0.96	1.00	1.00	1.00	1.00	1.00	0.97
<i>IDH-2</i>	90	0.01						0.03
	N	173	128	250	100	48	36	90
<i>IDH-3,4</i>	120							
	100							
	N	0	0	0	0	0	0	0
<i>LDH-4</i>	124		0.03			0.01		
	100	0.62	0.63	1.00	0.59	0.57		0.68
	72	0.13	0.16		0.27	0.24		0.13
<i>LGG</i>	44	0.25	0.18		0.14	0.17		0.19
	38							
	N	107	63	50	38	20	0	32
<i>MDH-1,2</i>	100	0.40	0.44	0.30	0.35	0.39	0.53	0.51
	74	0.60	0.56	0.70	0.65	0.61	0.47	0.49
	N	251	161	325	139	48	35	148
<i>MDH-3,4</i>	138							0.02
	100	1.00		1.00	1.00		1.00	0.98
	N	50	0	39	100	0	36	49
<i>MPI</i>	132			0.01				0.01
	100	1.00	1.00	0.99	1.00	1.00	1.00	0.99
	37							
<i>PGM</i>	N	167	168	330	140	21	33	66
	110	0.02	0.01	0.01		0.01	0.01	0.01
	100	0.95	0.96	0.99	1.00	0.97	0.98	0.96
<i>SOD</i>	85					0.01		
	78	0.03	0.03	0.01		0.01	0.01	0.03
	N	244	165	291	140	48	35	130
<i>WPI</i>	100	1.00	0.98	1.00	1.00	0.82	1.00	1.00
	95		0.02			0.18		
	N	154	124	164	100	48	36	130
<i>WPI</i>	100	1.00	1.00	0.99	1.00	1.00	0.99	1.00
	85			0.01			0.01	
	N	213	168	328	140	48	36	130
<i>WPI</i>	142	0.07	0.06		0.02	0.03	0.04	0.07
	100	0.91	0.93	1.00	0.98	0.92	0.90	0.91
	43	0.02	0.01			0.05	0.06	0.02
	N	245	168	281	140	48	36	158

TABLE 3.—Estimates of gametic disequilibrium between LDH-4 and SOD for rainbow trout from five locations in the Yakima River drainage. $D + D_B$ is Burrows' composite measure of gametic disequilibrium, r is the estimated correlation between alleles corrected for deviations from Hardy-Weinberg proportions, and χ^2 is the chi-square statistic ($= Nr^2$) with 1 df for testing $H_0: D + D_B = 0$ (Weir 1979). S1, S2, and S3 refer to sample sites 1, 2, and 3, respectively, of the Yakima River. Asterisk denotes * $P < 0.05$.

Site	$D + D_B$	r	χ^2
Yakima River, S1	-0.004	-0.026	0.05
S2	-0.009	-0.081	0.55
S3	0.035	0.269	5.70*
Swauk Creek	-0.008	-0.048	0.09
Taneum Creek	-0.028	-0.206	2.12

each fish was measured and scales were taken for age determinations. Hatchery fish were identified by morphological deformations of the caudal and dorsal fins, and confirmed by scale analysis. All fish were released alive back into their respective tributaries.

Results

The reference populations of inland and coastal steelhead (data from Milner and Teel 1979) formed two distinct, geographic groups at the LDH-4 and SOD loci (Fig. 2). These two loci are the ones that had previously been shown to distinguish the inland and coastal races of *S. gairdneri* (Allendorf and Utter 1979; Utter et al. 1980). The two hatchery populations of non-anadromous rainbow trout, RBGD and RBST, grouped (as expected) with the two coastal populations of steelhead at the two diagnostic loci. In contrast, allele frequencies for the five samples of rainbow trout from the Yakima River drainage were intermediate between those for the inland and coastal groups (Fig. 2; Table 2). Allele frequencies for rainbow trout from the two tributary creeks (Swauk and Taneum) were more similar to those for the inland group than were allele frequencies for the three samples from the mainstem Yakima River.

Genotypes for fish from the five sample sites in the Yakima River system conformed to Hardy-Weinberg proportions ($P > 0.05$) at all loci, with one exception: fish from site 2 (Fig. 1) had a deficit of heterozygotes at the IDH-2 locus ($G = 12.8$; $P < 0.001$). The reason for this one sig-

nificant result is unknown. However, we do not consider it evidence for nonrandom mating because of the number of intralocus comparisons (32) that were made.

Estimates of gametic disequilibrium between LDH-4 and SOD were not significant ($P > 0.05$) for fish from four of the five sample sites in the Yakima River system (Table 3). A noninterbreeding mixture of rainbow trout from both the coastal and inland races, or a recent interbreeding of fish from the two races, would be expected to produce a negative correlation between alleles at these two loci. Although four of the five estimates were less than zero, they were all nonsignificant. However, our sample sizes were too small to detect low to moderate levels of disequilibrium (Brown 1975). The one significant result represented a positive correlation between alleles at the two loci, but its significance probability was within the range expected by chance for one of five comparisons (Cooper 1968).

Projections of the populations onto the first two principal coordinates axes, based on Nei's (1972) index of genetic similarity, again separated the Yakima River samples from the other inland populations (Fig. 3). In contrast to Fig. 2, which depicts similarities based on only two loci, Fig. 3 shows a relatively close similarity between the Goldendale hatchery population (RBGD) and the three samples from the main stem Yakima River. In addition, the Dworshak population was projected as an outlier, reflecting its divergent allele frequencies at GLD and IDH-3,4 (Table 2). This population of steelhead was derived from fish native to the North Fork of the Clearwater River in northern Idaho, and its distinctive allele frequencies have been described previously (Milner 1977).

Forty-nine fish were captured in tributaries of the Yakima River during the April 1980 spawning surveys, and none of these appeared to be steelhead (Johnston 1980). The fork lengths of the mature fish ranged from 130 to 486 mm and averaged 269 and 313 mm for males and females, respectively. In contrast, the lengths of mature steelhead in Washington typically range from about 600 to 900 mm (excluding precocious males). The ages of the mature females ranged from 2 to 4 years (mean = 2.9 years) while males ranged in age from 1 to 5 years (mean = 2.5 years). Four fish were of hatchery origin, including a spawned-out female.

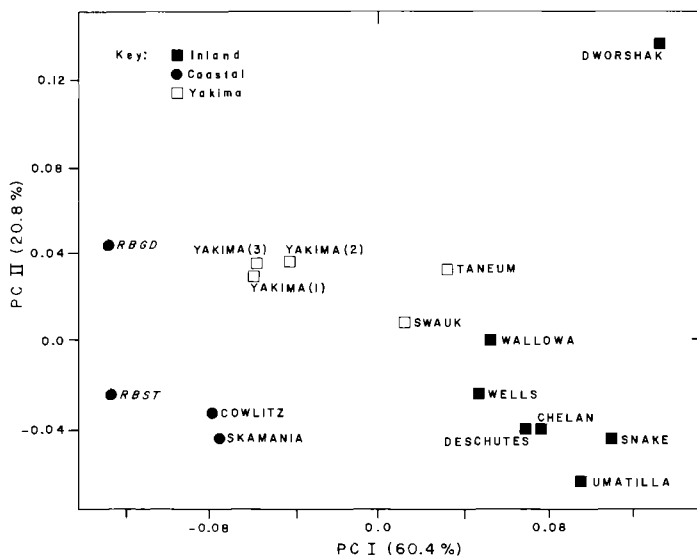


FIGURE 3.—Principal coordinates (PC) analysis (Gower 1966; Everitt 1978) of *Salmo gairdneri* populations in the Yakima–Columbia system based on Nei's (1972) index of genetic similarity. The populations have been projected onto the first two principal coordinates axes, which accounted for over 81% of the total variation among genetic similarity values (PC I: 60.4%; PC II: 20.8%). RBGD and RBST are hatchery strains of nonanadromous rainbow trout; other samples are identified by the sites in Fig. 1.

Discussion

Previous studies have demonstrated a widespread and consistent geographic pattern in the frequencies of alleles at the *LDH-4* and *SOD* loci for inland and coastal populations of rainbow trout (Huzyk and Tsuyuki 1974; Allendorf 1975; Milner and Teel 1979; Utter et al. 1980; Parkinson 1984; Wishard et al. 1984). These allele frequencies are independent of whether the populations are resident or anadromous, and appear to be determined strictly by geographic origin. For example, allele frequencies at *LDH-4* and *SOD* for resident populations in southwest Idaho (Wishard et al. 1984), anadromous populations in the Columbia River basin (Allendorf 1975; Allendorf and Utter 1979; Milner and Teel 1979), and distinct populations of resident and anadromous fish in the upper Fraser River drainage (Huzyk and Tsuyuki 1974; Parkinson 1984) are, in general, very similar (see range of values in Fig. 2). Allele frequencies for these inland populations contrast sharply with those for anadromous populations in the lower Columbia River (below The Dalles Dam), the lower Fraser River (below Hell's Gate), and drainages along the Washington and British Columbia coasts

(Huzyk and Tsuyuki 1974; Allendorf 1975; Parkinson 1984). This major subdivision between inland and coastal populations of rainbow trout presumably reflects an evolutionary divergence dating back to the last glacial era. The inland group is postulated (Allendorf and Utter 1979) to have descended from fish migrating into a large freshwater impoundment resulting from the glacial diversion of the upper Fraser and Columbia rivers (McKee 1972). The coastal group presumably descended from anadromous populations that survived outside this glacial mass. These interpretations are supported by the geographic distributions of other fishes in the Columbia and Fraser rivers where Celilo Falls (now inundated by the reservoir behind The Dalles Dam) and Hell's Gate, respectively, historically demarcated the inland or coastal distributions of many species in the two river systems (Scott and Crossman 1973). These two areas thus represent major transition zones in the native ichthyofauna of the Pacific Northwest.

The intermediate allele frequencies observed for rainbow trout from the Yakima River system (Fig. 2; Table 2) suggest that these fish either represent native populations that do not conform to the allele frequency patterns of other inland

populations in the Columbia, Snake, and Fraser river drainages or have a mixed ancestry derived from both native and introduced fish. Neither of these hypotheses can be falsified with the data presented in this report. However, we believe the available data do suggest that the second hypothesis is more likely. First, we know that steelhead and nonanadromous rainbow trout from nonnative hatchery populations have been continuously stocked in the Yakima River since the early 1940s (Crawford 1979; Campton 1980). Second, allele frequencies at the *LDH-4* and *SOD* loci differed *simultaneously* between fish from the mainstem river and fish from the two tributary creeks (Fig. 2). These differences are consistent with the mixed-ancestry hypothesis and were repeated at the *GLD* and *IDH-2* loci (Table 2). As a result, fish from the two tributary creeks actually appeared to be genetically more similar to some of the inland populations of steelhead (e.g., Wallowa and Wells) than to fish collected from the mainstem Yakima River (Figs. 2 and 3). One would expect populations indigenous to the Yakima River drainage to be genetically more similar to one another than to populations outside the drainage because the *a priori* assumption is that native populations would most likely be the descendants of a single ancestral invasion following the last period of glaciation. The consistent allele frequencies at *LDH-4* and *SOD* for other inland populations of *S. gairdneri* throughout the Columbia River drainage (e.g., Utter et al. 1980; Wishard et al. 1984), coupled with their sharp divergences from those for coastal populations, argue against a multiple invasion hypothesis. One would also expect native populations in the Yakima River drainage to have maintained some high level of genetic identity through geographic proximity and gene flow. The data, therefore, support the mixed-ancestry hypothesis and suggest that nonnative fish have genetically contributed to populations in Swauk and Taneum creeks to a lesser extent than to fish residing in the mainstem Yakima River (Fig. 2). The absence of any nonrandom allelic associations at *LDH-4* and *SOD*, either within or between loci, further suggests that native and introduced fish have randomly interbred where they came in contact to form present populations. That is, we detected no evidence for the maintenance of two separate gene pools representing native and introduced fish in the Yakima River drainage. These populations appear to represent sim-

ple genetic admixtures of native and nonnative stocks.

Close inspection of Table 2 provides further insight concerning the introgression of nonnative genes into the Yakima River populations. The frequencies of the *G3PDH-1* (100) and *GPI-3* (92) alleles among the sampled and reference populations suggest that steelhead from the Skamania Hatchery have contributed little or no genetic material to the Yakima River populations. On the other hand, the relatively high frequencies of the *MDH-3,4* (85) and *PGM* (85) alleles in the RBGD and RBST populations, respectively, and their scarcity in the inland steelhead populations, suggest that these alleles occur at their observed frequencies in the Yakima River populations because of introgression from the nonanadromous hatchery strains. Field surveys of adult fish support these interpretations; only nonanadromous rainbow trout were observed in the upper Yakima River during the spawning surveys of April 1980. As previously mentioned, one of these fish was a spawned-out female of hatchery origin.

The Yakima River historically supported abundant runs of steelhead but these runs may now be extinct, or nearly so, in the upper portions of the watershed. A U.S. Bureau of Reclamation dam, the Roza Diversion Dam, currently blocks the Yakima River approximately 35 km downstream from Ellensburg. The dam is 20.4 m high and was built in 1939. A fish ladder is present, but it becomes frozen over during winter and goes dry during the summer and very few fish, if any, are believed to bypass the dam (Lewis Lund, Regional Fish Biologist, Washington Department of Game, personal communication). This dam and others below it on the Columbia River may, therefore, have selected against steelhead in the Yakima River in favor of nonanadromous rainbow trout.

The results of our study contrast with those of Wishard et al. (1984) who found no evidence of genetic introgression from hatchery fish among populations of rainbow trout in southwestern Idaho, despite documented plantings in the area. The harsh thermal conditions of streams in southwestern Idaho are believed to have prevented nonnative rainbow trout from surviving or reproducing, especially in competition with native fish, which appear to be adaptively tolerant of the local conditions (Robert J. Behnke, Colorado State University, personal communi-

cation). In contrast, nonnative rainbow trout introduced into the Kootenai River in western Montana appear to have randomly interbred with native fish wherever the two groups have encountered one another (Allendorf et al. 1980). These results are identical to ours and suggest that native and nonnative rainbow trout will randomly interbreed to panmixia wherever the local habitat conditions are favorable to the introduced fish. The decline in abundance of steelhead, chinook salmon *Oncorhynchus tshawytscha*, and coho salmon *O. kisutch* in the upper Yakima River (Schwiebert 1977) may have allowed nonanadromous rainbow trout of hatchery origin to survive and reproduce in relatively large numbers because of reduced competition from the native salmonid fishes. Such genetic introgression may be occurring on a widescale basis in the Columbia River drainage but has heretofore gone undetected because of the general lack of sampling in the upper reaches of major tributaries where resident populations are most likely to become established.

Biochemical genetic markers have been used to detect natural hybridization between species of *Salmo* (Busack and Gall 1981; Leary et al. 1984; Campton and Utter 1985), to evaluate the success of fish stocking programs (Schweigert et al. 1977; Murphy et al. 1983), and to determine the genetic origins of rainbow trout populations that may have a mixed ancestry (Allendorf et al. 1980; Busack et al. 1980; Wishard et al. 1984; this paper). We believe the techniques used in this paper to identify the genetic origins of rainbow trout in the upper Yakima River can be applied to other extant populations of *S. gairdneri* in the Columbia River basin, especially those native populations that should be protected under the U.S. Endangered Species Act of 1973 (Utter 1981).

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