GENETIC VARIATION IN CHINOOK, *ONCORHYNCHUS TSHAWYTSCHA*, AND COHO, *O. KISUTCH*, SALMON FROM THE NORTH COAST OF WASHINGTON

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ABSTRACT

We used starch-gel electrophoresis to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, in the major drainages of the north coast of Washington (the Quillayute, Hoh, Queets, and Quinault Rivers). Of 55 loci examined for electrophoretically detectable variation, 6 were polymorphic (frequency of the common allele was less than 0.95) in chinook salmon and 3 in coho salmon. Statistical tests of interdrainage and intradrainage variation for coho salmon were tenuous because most of the fish examined were from a single year class so that we could not account for variation among year classes. Nevertheless, these tests suggested that distinct stocks of coho salmon exist within drainages, and that variation was not significantly greater among drainages than within drainages. Interdrainage variation for wild chinook salmon was not significant. The data suggested that summer chinook salmon were electrophoretically different from fall chinook salmon, and the hatchery populations of chinook salmon were distinct from wild fish. A hatchery population developed primarily from north coast fish was electrophoretically more similar to wild chinook salmon than were the others.

Effective conservation and management of natural organisms require protection of the genetic resources (genes, gene combinations, gene pools) of these organisms (Altukhov 1981; Frankel 1983). Conservation of anadromous salmonids from the north coast of Washington (the area from the Quinault River to the Strait of Juan de Fuca) is receiving national attention because many of these fish spawn or rear in Olympic National Park, and the United States Congress has directed that the natural resources of National Parks be conserved. Olympic National Park is the only natural area administered by the National Park Service outside Alaska with substantial numbers of native anadromous salmonids. There is also international concern for conservation of natural (including genetic) resources in Olympic National Park, as indicated by inclusion of the park in the International Biosphere Reserve Program (Franklin 1977).

The present study was initiated to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, from the major drainages of the north coast: the Quillayute, Hoh, Queets, and Quinault Rivers (Fig. 1). Coho salmon from two other streams in northwestern Washington (the Snohomish River and Snow Creek) and chinook salmon from Elwha Hatchery and the Wynoochee River were also sampled to enhance our perspective for examining north coast fish. Chinook and coho salmon are native to the west coast of North America from California to Alaska (Scott and Crossman 1973) and are the only species of Pacific salmon that are abundant in each of the major north coast drainages. Starch-gel electrophoresis was used to genetically characterize the fish.

Our objectives were 1) to develop a baseline set of allele frequency data; 2) to determine whether allele frequencies varied among major drainages; 3) to determine the degree of genetic structuring in coho salmon within major drainages; 4) to determine whether summer chinook salmon are electrophoretically distinct from fall chinook salmon; and 5) to determine whether hatchery populations of chinook salmon are electrophoretically distinct from wild (i.e., naturally spawned) fish.

We could not examine genetic structuring in chinook salmon within major drainages because wild adults were sampled in the lower portions of the rivers and thus their destinations within the major drainages were unknown, and samples of

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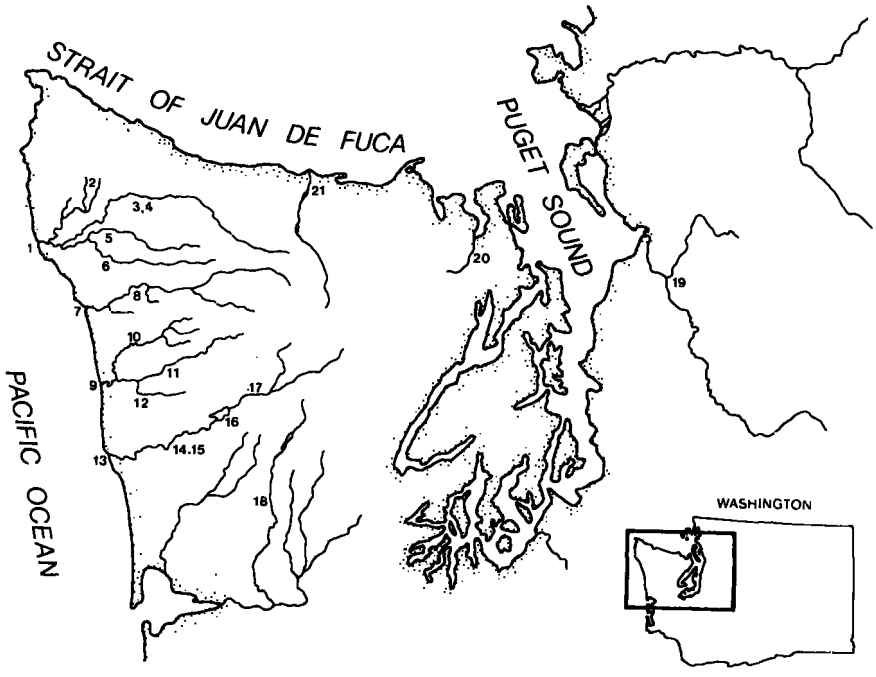


FIGURE 1.—Study area in northwestern Washington. This study focused on the four major stream systems of the north coast: the Quillayute (1), Hoh (7), Queets (9), and Quinault (13) drainages. Numbers identify sampling areas ("nets" indicates that adults were taken in the Indian gill net fisheries): (1) Quillayute River (nets); (2) Dickey River; (3) Soleduck River; (4) Soleduck Hatchery; (5) Calawah River; (6) Bogachiel River; (7) Hoh River (nets); (8) Hoh River; (9) Queets River (nets); (10) Clearwater River; (11) Upper Queets River, i.e., above the Salmon River; (12) Salmon River; (13) Quinault River (nets); (14) Lower Quinault River, i.e., below Lake Quinault; (15) Quinault National Fish Hatchery; (16) Quinault pens; (17) Upper Quinault River, i.e., above Lake Quinault; (18) Wynoochee River; (19) Snohomish River; (20) Snow Creek; (21) Elwha Hatchery.

wild juveniles contained unknown proportions of fish from genetically distinct runs.

MATERIALS AND METHODS

Three "runs" of chinook salmon and two runs of coho salmon occur in the study area. The runs are primarily distinguished by the time of year when the fish return to fresh water as adults. In general, spring chinook salmon return to fresh water from March to early June, summer chinook salmon from late June to August, and fall chinook salmon from mid-September to November. Similarly, summer coho salmon return to fresh water during August and early September, and fall coho salmon return from mid-October through November. Spring chinook salmon and summer coho salmon were not included in this study because returns to fresh water were low and few of these fish were available during our study. Adult salmon spawn in the autumn, and juveniles emerge from the gravel during the following winter or spring. Juvenile chinook salmon typically remain in the streams for several weeks to several months after emerging from the gravel, and enter the ocean during the summer or autumn; juvenile coho salmon remain in the streams for a year and enter the ocean during the spring.

Almost all summer coho salmon in the study area spawn in the Soleduck River (Quillayute River system) above Salmon Cascades (Houston 1983[3]). Our samples of fall-run juvenile coho salmon for the Soleduck River were taken from tributaries below Salmon Cascades to reduce the chance of including summer-run fish.

In addition to the fish rearing in streams,

[3]Houston, D. B. 1983. Andromous fish in Olympic National Park: a status report. Unpubl. rep. U.S. National Park Service, Port Angeles, WA.

salmon are raised in one federal, one state, and two tribal hatcheries along the north coast. Samples were taken from six hatchery populations (Table 1).

mouths of the rivers. At the hatcheries, samples of tissue were taken within 3 hours after the fish were killed for spawning. Adults from the fisheries were not available to us until they had been

Table 1.—Run times and stock origins for hatchery populations used in genetic characterization.

Species of salmon	Run	Hatchery	Stock origin[1]
Chinook	Fall	Quinault National Fish Hatchery (Quinault NFH)	Quinault River and transfers from Hoh and Queets Rivers, and University of Washington, Willapa, Nemah, Finch Creek, Deschutes, Green River, and Samish Hatcheries.
Chinook	Fall	Quinault Tribal Penned Rearing Facility (Quinault Pens)	Queets River and transfers from Quinault, Green River, Samish, and Deschutes Hatcheries.
Chinook	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.
Chinook	Spring-summer	Washington Department of Fisheries Soleduck Hatchery	Soleduck River and transfers from Dungeness, Cowlitz, and Umpqua Hatcheries.
Coho	Fall	Quinault NFH	Transfers from Quilcene, Purdy Creek, Moclips, Willapa, Soleduck, Simpson, Skagit, Green River, Hood Canal, and Cowlitz Hatcheries.
Coho	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.

[1]From Houston (see text footnote 3).

Sample Collection

Fish were collected during 1983 from the 21 areas identified in Figure 1 (some juvenile chinook salmon were also available from collections made in 1982). Juvenile fish at hatcheries were collected with dip nets at several locations along each raceway containing the fish to be studied. Juveniles in streams were collected by trapping, electrofishing, and seining. A few juvenile coho salmon (usually <15 in each age group) were taken from each of several sites throughout each drainage. Juvenile chinook salmon were taken from several sites in the lower portions of the rivers. Juveniles of both species were collected from areas where no hatchery fish were released or before hatchery fish were released; they were either kept alive or held on ice for up to 8 hours and then frozen at −10°C or −70°C until thawed for electrophoretic analysis.

Samples of tissue from eye, liver, white muscle, and heart were taken from adult fish spawned at hatcheries or caught in gill net fisheries at the delivered to wholesale fish buyers. Some fish were delivered more than a day after the fish were killed; although most were kept on ice or refrigerated during this interval, some isozyme activity was lost. Tissue samples from all adults were placed on ice within 30 minutes after excision and were frozen at −10°C or −70°C within 6 h.

Electrophoresis

We used horizontal starch-gel electrophoresis (Utter et al. 1974; May et. al. 1979) to assay fish tissues. Eye, heart, liver, and muscle tissues were removed from partly thawed juveniles just before electrophoretic analysis. We identified alleles at loci encoding specific enzymes, using the staining methods of Harris and Hopkinson (1976) and Allendorf et al. (1977). The nomenclature used to describe the gene loci and the allele variants followed Allendorf and Utter (1979).

Of the 40 enzymes examined, 30 had sufficient activity and resolution to be used in this study

(Table 2). Initially all 30 enzymes were examined in all fish; in later samples, however, we omitted the loci in chinook salmon that had been determined to be monomorphic in previous studies or in our initial screening.

TABLE 2.—Enzymes and loci examined in chinook and coho salmon. Enzyme commission numbers are in parentheses. Tissue E refers to eye, H to heart, L to liver, and M to white muscle. Buffer system 1 was described by Ridgway et al. (1970), 2 by Clayton and Tretiak (1972), and 3 by Markert and Faulhaber (1965) and Kobayashi et al. (1984).

Enzyme	Chinook salmon			Coho salmon		
	Loci	Tissue	Buffer	Loci	Tissue	Buffer
β-N-Acetyl-galactosaminidase (3.2.1.23)	[1]*bGala-2*	L	2	[1]*bGala-1*	L	2
				bGala-2	L	2
N-Acetyl-B-glucosaminidase (3.2.1.30)	[1]*bGa-1*	L	1	[1]*bGa-1*	L	1
Acid phosphatase (3.1.3.2)	[1]*Acp-1*	L	2	[1]*Acp-1*	L	2
	[1]*Acp-2*	L	2	[1]*Acp-2*	L	2
Aconitate hydratase (4.2.1.3)	[1]*Ah-1*	H	2	[1]*Ah-1*	H	2
	[1]*Ah-2*	H	2	[1]*Ah-2*	H	2
	Ah-3	L	2	*Ah-3*	L	2
Adenosine deaminase (3.5.4.4)	—	—	—	[1]*Ada-1*	M	1,3
				Ada-2	M,E	1,3
Adenylate kinase (2.7.4.3)	[1]*Ak-1*	M	2	[1]*Ak-1*	M	2
Alanine aminotransferase (2.6.1.2)	[1]*Alat-1*	M	1	[1]*Alat-2*	M	1
Alcohol dehydrogenase (1.1.1.1)	*Adh-1*	L	2	[1]*Adh-1*	L	2
Aspartate aminotransferase (2.6.1.1)	[1]*Aat-1*	L	2	[1]*Aat-1,2*	L	2
	[1]*Aat-3,4*	M	2	*Aat-3,4*	M	2
	[1]*Aat-5*	E	2	[1]*Aat-5*	E	2
Creatine kinase (2.7.3.2)	[1]*Ck-1*	M	1	*Ck-1*	M	1
	[1]*Ck-2*	M	1	[1]*Ck-2*	M	1
	[1]*Ck-3*	M	1	[1]*Ck-3*	M	1
Diaphorase-NADH (1.6.*.*)	[1]*Dia-1*	L	1	[1]*Dia-1*	L	1
Diaphorase-NADPH (1.6.*.*)	[1]*DiaP-1*	L	1	[1]*DiaP-1*	L	1
Fructose bisphosphate aldolase (4.1.2.3)	[1]*Fbald-1*	E	2	[1]*Fbald-1*	E	2
	[1]*Fbald-2*	E	2	[1]*Fbald-2*	E	2
Fumarate hydratase (4.2.1.2)	[1]Fh-1	M	1	[1]*Fh-1*	M	1
Glucose-6-phosphate isomerase (5.3.1.9)	[1]*Gpi-1*	M	1	*Gpi-1*	M	1
	Gpi-2	M	1	*Gpi-2*	M	1
	Gpi-3	M	1	*Gpi-3*	M	1
β-Glucuronidase (3.2.1.31)	[1]*bGus-1*	L	1	[1]*bGus-1*	L	1
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	[1]*Gapdh-3*	E	2	[1]*Gapdh-3*	E	2
	[1]*Gapdh-4*	E	2	[1]*Gapdh-4*	E	2
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	[1]*G3pdh-1*	M	2	*G3pdh-1*	M	2
	[1]*G3pdh-2*	M	2	[1]*G3pdh-2*	M	2
	[1]*G3pdh-3,4*	H	2			
L-Iditol dehydrogenase (1.1.1.14)	*Iddh-1,2*	L	1	—	—	—
Isocitrate dehydrogenase (1.1.1.42)	[1]*Idh-1*	M	2	[1]*Idh-1*	M,H	2
	Idh-2	M	2	[1]*Idh-2*	M,H	2
	Idh-3,4	M,L	2	*Idh-3,4*	L,H	2
L-Lactate dehydrogenase (1.1.1.27)	[1]*Ldh-1*	M	1	[1]*Ldh-1*	M	1
	[1]*Ldh-2*	M	1	[1]*Ldh-2*	M	1
	[1]*Ldh-3*	E	1	*Ldh-3*	E	1
	[1]*Ldh-4*	L	1	*Ldh-4*	L	1
	[1]*Ldh-5*	E	1	[1]*Ldh-5*	E	1
Lactoylglutathione lyase (4.4.1.5)	[1]*Lgl-1*	E,M	1	*Lgl-1*	E,M	1
Malate dehydrogenase (1.1.1.37)	*Mdh-1,2*	L	2	*Mdh-1,2*	L	2
	Mdh-3,4	M	2	*Mdh-3,4*	M	2
Malate dehydrogenase (NADP+) (1.1.1.40)	[1]*MdhP-1*	M	2	*MdhP-1*	M	2
	[1]*MdhP-2*	M	2	[1]*MdhP-2*	M	2
	[1]*MdhP-3*	L	2	[1]*MdhP-3*	L	2
Mannose-6-phosphate isomerase (5.3.1.8)	*Mpi-1*	E	2	*Mpi-1*	E	2
α-Mannosidase (3.2.1.24)	[1]*aMan-1*	L	1	[1]*aMan-1*	L	1
Phosphoglucomutase (5.4.2.2)	*Pgm-1*	M	1	[1]*Pgm-1*	M	2
				Pgm-2	M	2
Phosphogluconate dehydrogenase (1.1.1.44)	*Pgdh-1*	M	2	*Pgdh-1*	M	2
Phosphoglycerate kinase (2.7.2.3)	[1]*Pgk-1*	M	2	[1]*Pgk-1*	M	2
	Pgk-2	M	2	[1]*Pgk-2*	M	2
Superdioxide dismutase (1.15.1.1)	*Sod-1*	L,H	1	[1]*Sod-1*	L	1,2
	[1]*Sod-2*	L	2			

[1]No isozyme variation observed.

Data Analysis

Goodness-of-Fit Tests

We used the chi-square test to examine genotype frequencies for deviation from the (Hardy-Weinberg) proportions expected with random mating. Cells with an expected number <5 were combined with the next larger cell. The significance level for each test was modified to account for the increase in type I error when multiple tests of the same hypothesis are made (Cooper 1968). Tests were considered significant if the chi-square statistic exceeded the critical value for chi-square associated with a probability of $0.05/n$, where n was the number of loci tested within a sample. In this way the overall probability of rejecting H_0 by chance alone was approximately $1 - (1 - 0.05/n)^n \cong 0.05$ for each sample. Genotypes for *Idh-3,4*, *Mdh-1,2*, and *Mdh-3,4* were not tested because these systems consisted of pairs of loci with identical electrophoretic mobility, and genotypes at each locus could not be determined.

The likelihood ratio test (G-test; Sokal and Rohlf 1981) was used to test equality in allele frequencies between year classes. Here also, cells with an expected number <5 were combined with the next largest cell. The G-statistics, summed over all loci, were considered significant if they exceeded the critical value for chi-square associated with a probability of $0.05/s$, where s was the number of samples tested. Samples from streams and samples from hatcheries were tested as separate groups. The correction for multiple comparisons was made because each of the three H_0—no interbrood variation by drainage, by streams within drainages, or by hatchery—was independently tested for several drainages, streams, or hatcheries, respectively.

Analysis of Variance

We used analysis of variance (ANOVA) to test interdrainage differences, differences between hatchery and wild chinook salmon, and differences between summer and fall runs of chinook salmon. Data for coho salmon were not tested by ANOVA because data were available for only one year class from most locations, and estimates of interbrood variation in allele frequencies would have come from only two sample locations. The data used were from the loci scored for fish from each major north coast drainage and with frequencies <0.95 for the common (100) allele. The values used in the analysis were the arcsin of the square root of the frequency of the common allele at each locus. Differences were tested by contrasts (Table 3) or by partitioning the sum of squares within a one-way ANOVA for each locus (Snedecor and Cochran 1967; SPSS, Inc. 1983). Groups included in this analysis were as follows (adults would have spawned in 1983):

Cell	*Group*	*Run*	*Replicate*
1	Quillayute River	Mixed	1981 brood
			1982 brood
2	Hoh River	Mixed	1981 brood
			1982 brood
3	Queets River	Mixed	1981 brood
			1982 brood
4	Quinault River	Mixed	1981 brood
			1982 brood
5	Wynoochee River	Mixed	1982 brood
6	Quinault Pens	Fall	1982 brood
7	Quinault NFH	Fall	1981 brood
			1982 brood
8	Soleduck Hatchery	Fall	1981 brood
			1982 brood
9	Hoh River	Fall	Adults
10	Queets River	Fall	Adults
11	Soleduck Hatchery	Spring-summer	(data from Milner et al. 1983[1])
			1982 brood
			Adults
12	Hoh River	Summer	Adults
13	Queets River	Summer	Adults

[1]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. Rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

Juveniles from the different runs of chinook salmon were morphologically indistinguishable and our estimates of error variance were probably inflated because they were based on samples (of juveniles) that vary from year to year in the proportion of fish from each race. As a result, the (discriminatory) power for detecting differences between groups was impaired. In view of this reduced discriminatory power, differences with $0.05 \leq P < 0.1$ were noted in the text; statistical significance, however, was reserved for differences with $P < 0.05$.

Adult fall and summer chinook salmon from the Quillayute River and adult fall chinook salmon from the Quinault River were not included in the ANOVA because adults returning to these streams include large numbers of hatchery fish (Houston fn. 3). Adult summer chinook

TABLE 3.—Chinook salmon—coefficients for contrasts (Snedecor and Cochran 1967) within the analysis of variance. Cell numbers refer to groups identified in text. Within each contrast, the mean allele frequencies for groups with positive coefficients were compared with the mean frequencies for groups with negative coefficients.

Contrast	Cell												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Interdrainage variation													
1 Fall-run adults	0	0	0	0	0	0	0	0	−1	1	0	0	0
2 Summer-run adults	0	0	0	0	0	0	0	0	0	0	0	−1	1
Hatchery vs. wild													
3 Summer run	0	0	0	0	0	0	0	0	0	0	−2	1	1
Fall run:													
4 Quinault Pens	0	0	0	0	0	−2	0	0	1	1	0	0	0
5 Quinault NFH	0	0	0	0	0	0	−2	0	1	1	0	0	0
6 Soleduck Hatchery	0	0	0	0	0	0	0	−2	1	1	0	0	0
Summer vs. fall													
7 Adults	0	0	0	0	0	0	0	0	−1	−1	0	1	1

salmon from the Quinault River were not included because many hatchery fall chinook salmon return to the Quinault River with the summer-run salmon (during August, when most of our sampling was done) and our samples probably included a high proportion of fall-run hatchery fish (Larry Gilbertson[4]).

Gene Diversity Analysis

We used a modification of Chakraborty's (1980) gene diversity analysis to examine the hierarchical structure of genic diversity among the samples of wild coho salmon from the north coast. This analysis partitions total gene diversity (H_t, heterozygosity of allele frequencies over locations) into interdrainage and intradrainage components (Nei 1973). We considered three levels of population subdivision (Fig. 2)—broods (b), streams within drainages (w), and drainages (d)—so that $H_t = H_s + D_{bw} + D_{wd} + D_{dt}$, where H_s is the average heterozygosity within samples, D_{bw} is the gene diversity between broods, D_{wd} is the diversity within drainages, and D_{dt} is the diversity among drainages. Relative gene diversities (G_{ij}) are the proportions of H_t associated with a particular hierarchical level; for example, $G_{wd} = D_{wd}/H_t$.

[4] Larry Gilbertson, Quinault Tribal biologist, Quinault Indian Nation, P.O. Box 189, Taholah, WA 98587, pers. commun. August 1983.

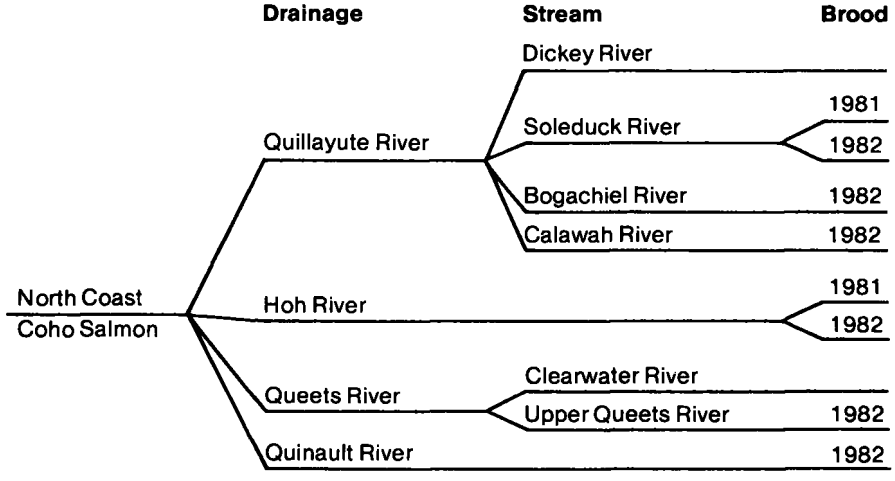


FIGURE 2.—Coho salmon—hierarchical subdivisions used in the gene diversity analysis for wild fish from the north coast of Washington (see test). Where brood is not identified, fish were from both the 1981 and 1982 broods.

The modification to Chakraborty's (1980) analysis consisted of giving equal weight to subgroups within a cell, rather than weighting them according to the number of samples within each subgroup. Our sampling design did not include all possible or desirable subgroups; the design was a compromise that allowed us to evaluate the different levels of subdivision and still remain within our budget. We felt that equal weighting was necessary because the number of subgroups within a cell usually did not reflect the "true" number of subgroups that may have existed for that cell. Donald Campton (University of Florida, Gainesville) provided a computer program, coded in Fortran 77, that included the required modification to Chakraborty's equations.

Cluster Analysis

The unweighted pair group method of cluster analysis (UPGM analysis; Sneath and Sokal 1973) and (nonmetric) multidimensional scaling (Gordon 1981; Kruskal and Wish 1977) were used to illustrate genetic similarities among samples. These two cluster analyses were applied to values of Nei's (1972) genetic distance calculated for each pair of samples. Data from the separate broods were pooled with equal weight for these analyses.

RESULTS

Chinook Salmon

Although fish from two locations showed significant deviation from Hardy-Weinberg proportions ($P < 0.05/n_i$ where n_i was the number of loci tested for location i)—juveniles of the 1982 brood from the Bogachiel River were deficient in heterozygotes at the *Pgk-2* locus and juveniles of the 1982 brood from the Hoh River had an excess of heterozygotes at the *Gpi-2* locus—these deviations are probably spurious, given the large number (20) of samples tested.

Interbrood variation in allele frequencies was significant ($P < 0.01$) for wild fish and for hatchery fish (Table 4). Six loci, or pairs of loci, showed sufficient variation and were scored for enough fish ($n > 25$) to be used in the ANOVA (Fig. 3, App. Table 1). Variation between drainages was not significant, although summer-run fish may differ between drainages ($P = 0.07$, Table 4). Hatchery fish were different from wild fish (contrasts 3 to 6 in Table 5).

The UPGM cluster analysis showed that the hatchery populations were distinct from wild juveniles and from all but one (Quinault River) sample of adults (Fig. 4). Of the hatchery populations, fall-run fish from Soleduck Hatchery were

TABLE 4.—Chinook salmon—likelihood ratio analysis of interbrood variation at 10 codominant loci. Significant levels were evaluated for totals only. G = likelihood ratio statistic.

	Ah-3		*Gpi-2*		*Idh-3,4*		*Mdh-3,4*		*Mpi-1*		*Pgm-1*		*Pgk-2*		*Sod-1*		Total	
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	df	G	df	G
Interbrood variation for drainages																		
Quillayute River	1	1.36	—	—	1	15.61	1	6.26	1	0.25	1	0.00	1	3.90	1	3.63	7	31.01**
Hoh River	2	2.66	—	—	1	10.21	—	—	1	1.78	1	3.22	1	0.09	1	0.21	7	18.16*
Queets River	1	0.00	—	—	1	0.05	—	—	1	2.73	1	0.19	1	1.12	1	0.32	6	4.41
Group total																	20	53.58†
Interbrood variation for streams (within drainages)																		
Soleduck River	1	4.77	—	—	—	—	—	—	1	1.83	1	0.65	1	4.79	1	3.85	5	15.89*
Bogachiel River	1	0.20	—	—	—	—	1	5.81	1	0.33	1	0.44	1	0.55	1	0.81	6	8.14
Hoh River	2	2.66	—	—	1	10.20	—	—	1	1.78	1	3.22	1	0.08	1	0.21	7	18.16*
Queets River above Salmon River	1	0.42	—	—	1	2.58	—	—	1	3.64	1	16.55	1	2.22	1	0.34	6	25.76**
Clearwater River	1	0.43	—	—	1	2.73	—	—	1	0.57	1	6.57	1	0.07	1	0.02	6	10.39
Group total																	30	78.34†
Interbrood variation for hatcheries																		
Soleduck Hatchery																		
Spring/summer	2	1.98	1	0.29	2	6.46	—	—	2	9.56	—	—	2	4.45	2	12.58	11	35.31**
Fall	1	2.26	—	—	—	—	—	—	1	0.89	—	—	—	—	1	0.31	3	3.46
Quinault NFH (Fall)	1	1.63	—	—	1	5.99	—	—	1	9.53	1	2.21	1	11.41	1	1.29	6	32.06**
Elwha Hatchery	—	—	1	9.58	—	—	—	—	1	2.28	—	—	1	7.15	1	0.30	4	19.34**
Group total																	24	90.17†

*$P < 0.05/n$; **$P < 0.01/n$; where n = 3 for interbrood variation within drainages, n = 5 for variation within streams, and n = 4 for variation within hatcheries. These are corrections for multiple comparisons (Cooper 1968).
†$P < 0.01$.

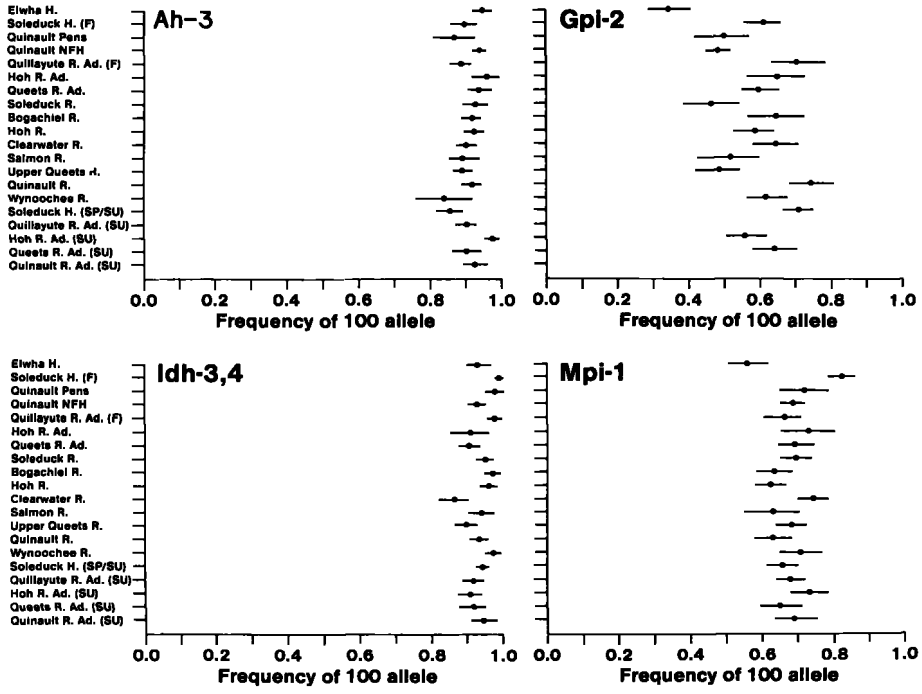


FIGURE 3a.—Chinook salmon—common-allele frequencies (q) for four protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

TABLE 5.—Chinook salmon—results from multivariate (MANOVA) and univariate analyses of the variance among frequencies (q) of the 100 allele at each of six loci or pairs of loci. Actual values in the analyses were transformed frequencies: arcsin $\sqrt{q}$. Hypothesis numbers correspond to those in the text table for contrasts under Materials and Methods. F = F statistics, df = degrees of freedom for the F statistics.

Hypothesis	*P* value from MANOVA		Tests at individual loci					
			Ah-3	*Idh-3,4*	*Mpi-1*	*Pgm-1*	*Pgk-2*	*Sod-1*
Interdrainage variation								
1 Fall run adults	0.54	F	0.15	0.00	0.14	0.52	0.27	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
2 Summer run adults	0.07	F	5.39	0.00	0.51	0.00	1.00	0.14
		df	1,7	1,7	1,7	1,7	1,7	1,7
Juveniles	—	F	0.43	1.45	0.54	0.38	0.85	0.31
		df	3,6	3,7	3,7	3,7	3,7	3,6
Hatchery vs. wild								
3 Summer run	0.34	F	11.46	0.54	0.44	22.15*	0.28	5.67
		df	1,7	1,7	1,7	1,7	1,7	1,7
Fall run								
4 Quinault Pens	0.03*	F	4.93	1.50	0.00	0.06	4.40	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
5 Quinault NFH	0.06	F	0.18	0.33	0.09	0.53	8.91	7.45
		df	1,7	1,7	1,7	1,7	1,7	1,7
6 Soleduck Hatchery	0.03*	F	6.06	4.37	2.79	11.44	0.00	2.84
		df	1,7	1,7	1,7	1,7	1,7	1,7
Summer vs. fall								
7 Adults	0.06	F	0.00	0.05	0.10	1.32	1.71	0.67
		df	1,7	1,7	1,7	1,7	1,7	1,7

*$P < 0.05$ for MANOVA, or $P < 0.05/6$ for univariate tests.

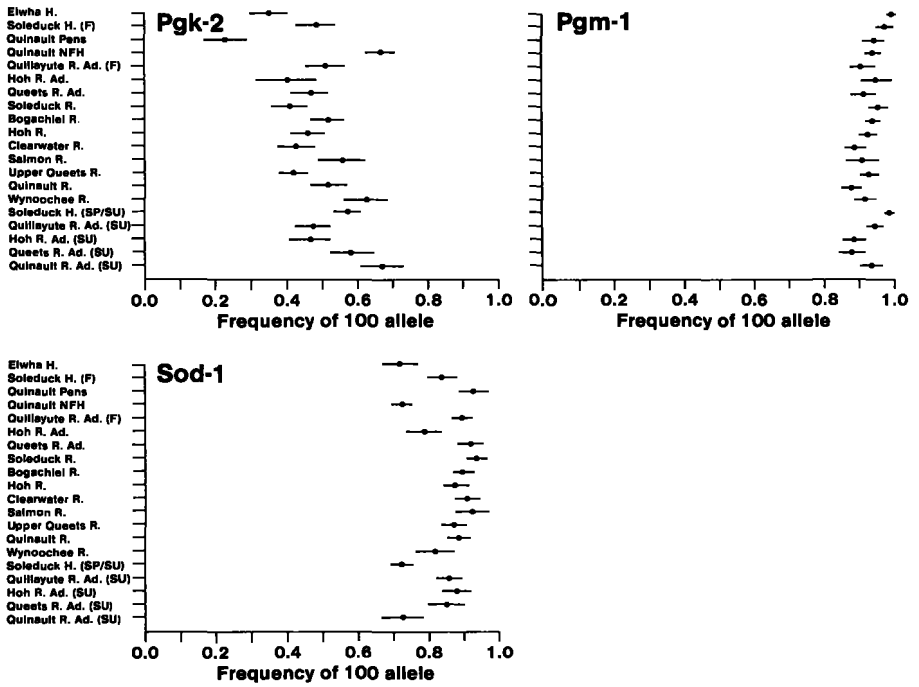
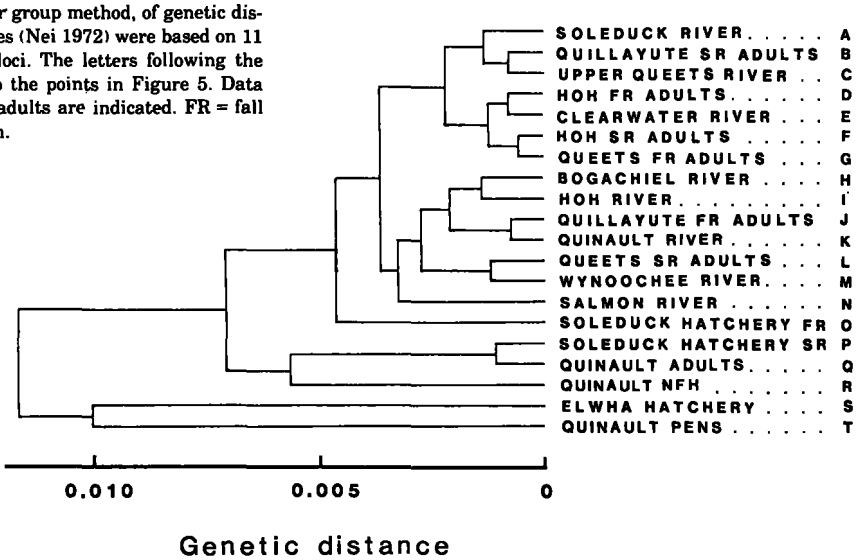


FIGURE 3b.—Chinook salmon—common-allele frequencies (q) for three protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

FIGURE 4.—Chinook salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances (Nei 1972) were based on 11 protein-coding loci or pairs of loci. The letters following the names of samples correspond to the points in Figure 5. Data were from juvenile fish unless adults are indicated. FR = fall run; SR = spring or summer run.



most similar to wild fish. Summer-run adults and fall-run adults from the Quillayute River both clustered with the wild fish, suggesting that a large proportion of the fish in these samples were wild fish. Multidimensional scaling gave similar results and more clearly illustrated that hatchery populations were distinct not only from the wild fish but also from each other (Fig. 5).

Coho Salmon

Coho salmon showed genic variability at 21 loci or pairs of loci; however, the frequency of the common allele was <0.95 for most samples at only 2 loci: *bGala-2* and *Idh-3,4* (Fig. 6, App. Table 2). Allendorf and Utter (1979) found a similar lack of variation, reporting that coho salmon display the least amount of electrophoretic variation of the five Pacific salmon species in North America.

Hierarchical analysis of genic diversity (heterozygosity) showed that the interbrood level accounted for 2% (= 0.09/(0.09 + 0.85 + 3.97; Table 6) of the genic diversity observed among samples of coho salmon; the within-drainage level accounted for 17% and the interdrainage level for 81%. Variation at *Pnp-1* had a substantial influence on the average locus values. Unfortunately, data for *Pnp-1* were missing for several of the samples because the methodology for this enzyme was not stabilized until we were well into our study. With *Pnp-1* excluded from the analysis, the interbrood level accounted for 5% of the genic diversity observed among samples, the within-drainage level accounted for 39%, and the interdrainage level accounted for 56%.

Variation in allele frequencies among streams within the Quillayute and Queets drainages was statistically significant (tested at *bGala-2*, *Idh-3,4*, and *Pnp-1*; $G = 11.27$ with 5 degrees of freedom; $P < 0.05$); however, interpretation of this result is complicated because data were not available to adequately account for variation among year classes. Variation among drainages was not significantly greater than variation within drainages ($P > 0.10$, hierarchical likelihood ratio

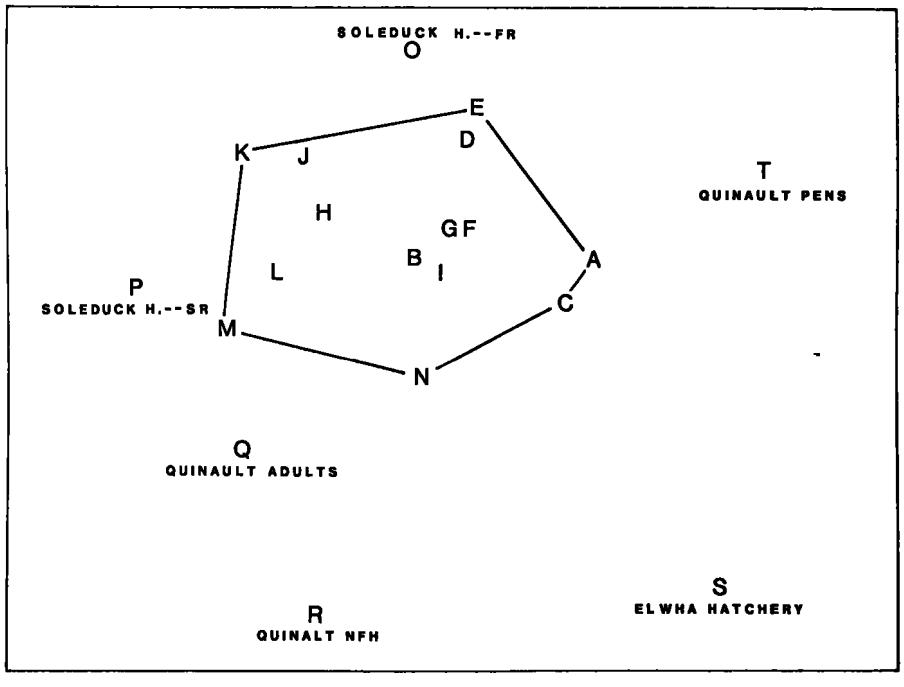


FIGURE 5.—Chinook salmon—two-dimensional representation (from multidimensional scaling) of genetic distances among samples collected for this study. The letters correspond to the groups identified in Figure 4. The polygon encloses the samples of wild fish (A through N). The aim of multidimensional scaling is to represent each group by a point in two-dimensional space so that the relative distances among points represent the relative (genetic) distances between groups.

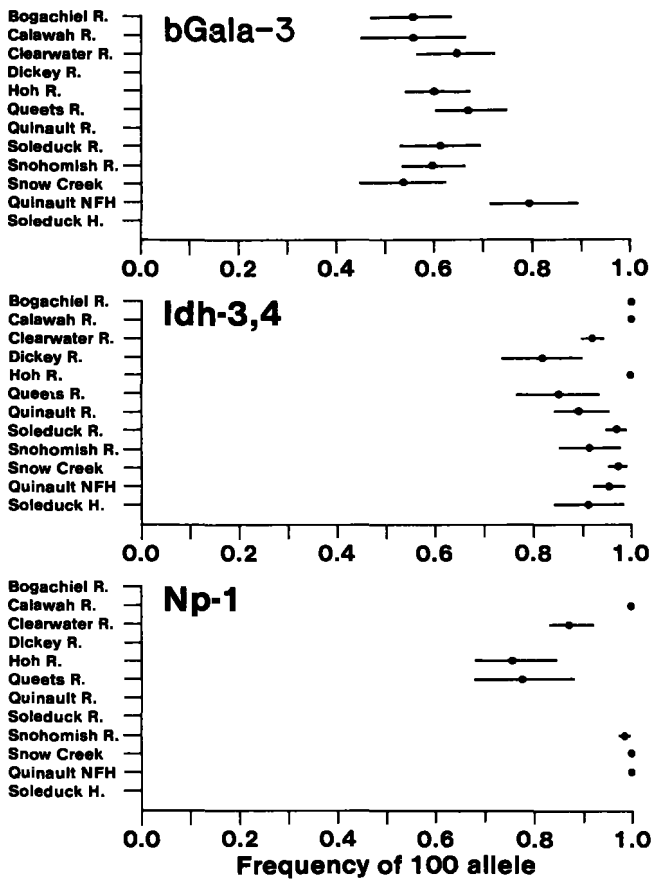


FIGURE 6.—Coho salmon—common-allele frequencies (q) for several protein-coding loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not shown and were not used in analysis.

TABLE 6.—Coho salmon—hierarchical analysis of electrophoretically detectable gene diversity for coho salmon from the Quillayute, Hoh, Queets, Quinault and Wynoochee Rivers. Analysis was based on 58 loci, including 36 that were monomorphic. The hierarchical design is shown in Figure 3.

		Relative gene diversity (%)			
Locus	Total gene diversity (H_T)	Within samples	Among broods	Within drainages	Among drainages
Average	0.021	95.09	0.09	0.85	3.97
Average excluding *Pnp-1*	0.016	97.64	0.12	0.93	1.31

analysis; Grant et al. 1980; Smouse and Ward 1978).

Samples without data for *bGala-1* or *Idh-3,4*, the most variable loci, were omitted from the UPGM cluster analysis (Fig. 7) and multidimensional scaling (Fig. 8). Both analyses showed that fish from Quinault NFH were distinct from wild fish; much of this distinctiveness occurred at the *bGala-2* locus (Fig. 6). Fish from Snow Creek and the Snohomish River clustered among the wild fish from the north coast. The results were similar when *Pnp-1* was excluded from the analysis, except that fish from the upper Queets River were no longer distinct from the other wild fish.

DISCUSSION

Wild Populations

Variation in allele frequencies among drainages for chinook salmon was not statistically significant. The inability to detect differences among drainages could have resulted from 1) low statistical power (probability of rejecting H_0 if it is false) because we had too few broods or because variation in racial composition of juveniles in different years inflated the estimates of error variance, 2) our exclusive reliance on data for genes that can be sampled by electrophoresis, or 3) a lack of true genetic difference among groups. We

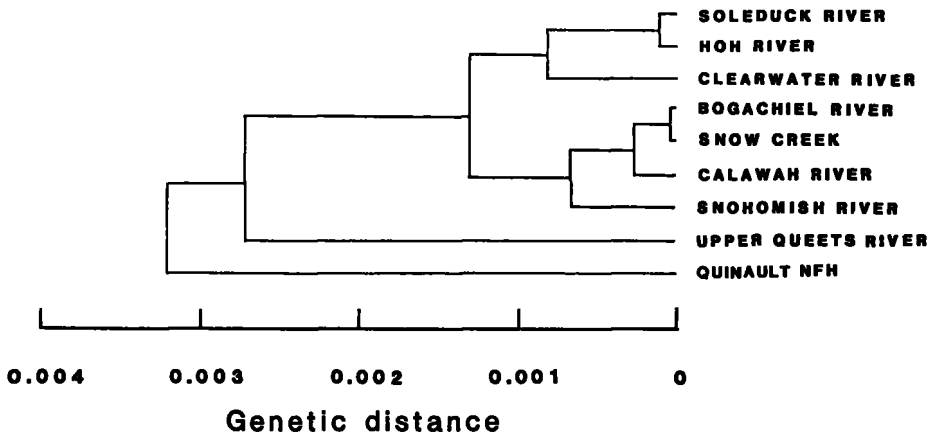


FIGURE 7.—Coho salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances were based on 24 protein-coding loci or pairs of loci.

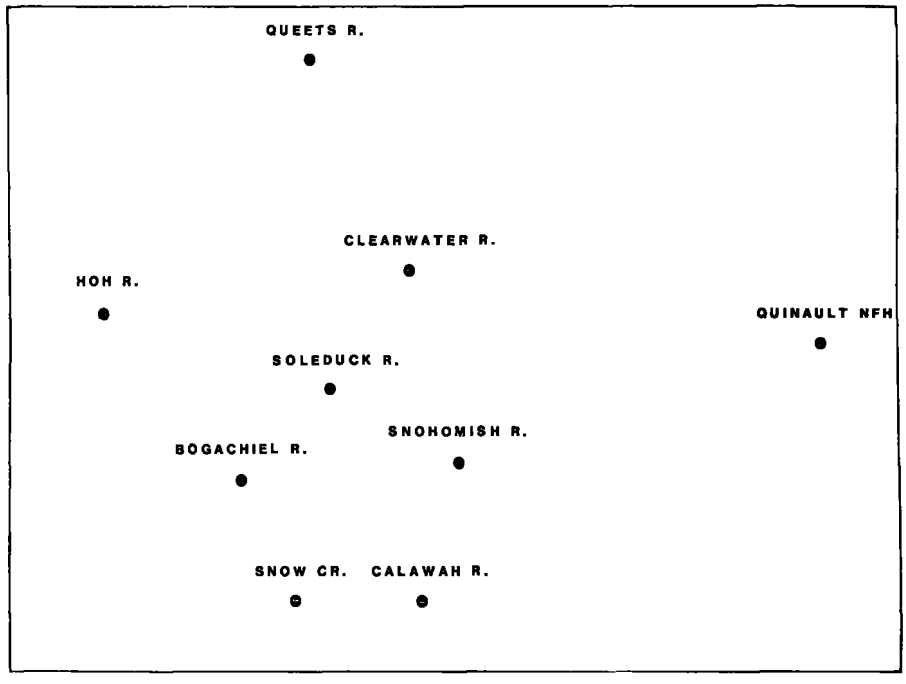


FIGURE 8.—Coho salmon—two-dimensional representation (from nonmetric multidimensional scaling) of genetic distances among samples collected for this study. Only samples scored for *bGala-2* and *Idh-3,4* were included in the analysis.

emphasize that the lack of differentiation in frequencies of electrophoretically detectable alleles does not preclude the existence of important genetic differences or status as separate stocks (genetic populations). The high degree of "homing" by both chinook salmon (see, e.g., Rich and Holmes 1928) and coho salmon (see, e.g., Shapavalov and Taft 1954) to the streams from which they originate suggests that salmon from different drainages should be considered as separate

stocks unless strong evidence exists to the contrary.

Our data suggested that summer chinook salmon were distinct from fall chinook salmon ($P = 0.06$, Table 5). Electrophoretic differences between distinct runs or life history types of chinook salmon were also found within the Nanaimo River system (Carl and Healey 1984) and within the Columbia River system (Kristiansson and McIntyre 1976). Summer-run fish from different streams along the north coast were not sufficiently similar to form a cluster separate from the fall-run fish (Figs. 4, 5), and the differences among populations of summer-run fish may be as great as the differences between summer- and fall-run fish. Unfortunately the small number of populations precluded rigorous comparison of these differences.

The (significant) variation in allele frequencies between year classes of juvenile chinook salmon may have been exaggerated by variation between years in the proportion of fish from the three different runs. This possibility illustrates the need for sampling adult chinook salmon (only adults can be distinguished according to run) in river systems where juveniles from different runs occur together. Of course, the utility of sampling adults to genetically describe wild populations is compromised if adult hatchery and wild fish occur together and cannot be reliably separated.

The gene diversity analysis for coho salmon showed that diversity within drainages was eight to nine times the diversity among broods, with or without *Pnp-1* included in the analysis, and suggested that separate breeding units exist within drainages as well as between drainages. Separate breeding units within drainages were also suggested by the likelihood ratio analysis.

Hatchery Fish Versus Wild Fish

Analysis of variance for hatchery and wild chinook salmon, and the cluster analyses for both chinook and coho salmon showed that the hatchery populations of the north coast were genetically distinct from the populations of wild fish. Indeed, coho salmon from Snow Creek or from the Snohomish River were more similar to wild coho salmon from the north coast than were coho salmon from Quinault National Fish Hatchery (Fig. 7).

The differences between hatchery and wild fish were to be expected because the hatchery populations were developed with fish from locations in addition to the local stream or exclusive of the local stream. Among chinook salmon, fall-run fish at Soleduck Hatchery were the most similar to wild fish (Fig. 5), probably because the Soleduck Hatchery population was the only hatchery population developed primarily with local fish (Houston fn. 3). Fall coho salmon at Soleduck Hatchery were also primarily developed with local fish but were not included in the analysis because of missing data. We would expect these coho salmon to be more similar to wild fish than were the coho salmon from Quinault National Fish Hatchery—and that expectation held for allele frequencies at *Ada-2* and *Ldh-4*, and was not countered by evidence from any other loci (App. Table A2).

It is reasonable to assume that interbreeding with fall chinook salmon (or fall coho salmon) from Soleduck Hatchery will cause less reduction of fitness and less genetic change for wild fish than will interbreeding with the other (less similar) hatchery fish (Helle 1981; Reisenbichler 1984). The observed differences between fall chinook salmon at Soleduck Hatchery and wild fish probably exist because few wild fish are included in the hatchery brood stock. Data for steelhead, *Salmo gairdneri*, (Reisenbichler and Phelps 1985[5]) illustrate that the continued use of wild fish in the hatchery brood stock and avoidance of selective breeding are necessary to maintain a hatchery population that is genetically similar to wild fish. Where hatchery populations can be managed separately from wild populations and where few hatchery fish stray onto natural spawning areas, perhaps there is little reason to ensure that hatchery fish are genetically similar to wild fish. However, where substantial numbers of hatchery fish successfully spawn in streams and where genetic resources are to be conserved, hatchery fish should be as genetically similar as possible to the wild fish (e.g., Helle 1981).

ACKNOWLEDGMENTS

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[5]Reisenbichler, R. R., and S. R. Phelps. 1985. Genetic structure of steelhead, *Salmo gairdneri*, from the north coast of Washington State. Unpubl. rep. National Fishery Research Center, Seattle, WA.

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APPENDIX TABLE 1.—Allele frequencies for chinook salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample names correspond to locations shown in Figure 1.

			Ah-3				*Adh-1*		*Gpi-2*			
Location and sample	Brood	*N*	100	85	118	108	−100	−50	100	67	−15	150
Quillayute River												
1 Fall-run adults	[1](1983)	99	0.892	0.097	0.011	—	0.990	0.010	0.714*	0.276*	0.010	—
1 Summer-run adults	[1](1983)	120	0.906	0.094	—	—	0.996	0.004	—	—	—	—
3 Soleduck River	1981	70	0.884	0.101	0.014	—	0.971	0.029	—	—	—	—
	1982	40	0.971	0.029	—	—	—	—	0.462	0.488	0.010	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982		0.840	0.130	—	0.030	0.990	0.010	—	—	—	—
	1982	40	—	—	—	—	—	—	0.662	0.288	0.012	0.038
Spring/summery run	[2]pre-1982		0.850	0.150	—	—	0.980	0.020	—	—	—	—
	1982	50	0.830	0.170	—	—	1.000	—	0.700	0.300	—	—
	[1](1983)	77	0.889	0.111	—	—	1.000	—	0.761	0.239	—	—
6 Bogachiel River	1981	70	0.926	0.066	0.008	—	0.985	0.015	—	—	—	—
	1982	40	0.894	0.091	—	0.015	—	—	0.650	0.338	—	0.012
Hoh River												
7 Fall-run adults	[1](1983)	37	0.957	0.043	—	—	0.973	0.027	0.650	0.350	—	—
7 Summer-run adults	[1](1983)	86	0.983	0.017	—	—	0.960	0.040	0.574	0.426	—	—
8 Juveniles	1981	70	0.900	0.064	0.036	—	0.991	0.009	—	—	—	—
	1982	76	0.950	0.029	0.021	—	—	—	0.592	0.388	0.020	—
Queets River												
9 Fall-run adults	[1](1983)	94	0.944	0.044	0.012	—	0.978	0.022	0.595	0.399	0.006	—
9 Summer-run adults	[1](1983)	60	0.907	0.074	0.019	—	0.969	0.031	0.652	0.348	—	—
10 Clearwater River	1981	70	0.891	0.094	0.014	—	0.957	0.043	—	—	—	—
	1982	48	0.917	0.052	0.031	—	0.980	0.020	0.650	0.350	—	—
12 Salmon River	1982	48	0.880	0.109	0.011	—	0.943	0.057	0.531	0.469	—	—
11 Upper Queets River	1981	70	0.906	0.087	0.007	—	0.957	0.043	—	—	—	—
	1982	54	0.880	0.070	0.050	—	—	—	0.491	0.500	0.009	—
Quinault River												
13 Adults	[1](1983)	64	0.927	0.073	—	—	0.976	0.024	—	—	—	—
14 Lower Quinault River	1982	55	—	—	—	—	—	—	0.750	0.236	0.014	—
17 Upper Quinault River	1982	53	0.904	0.096	—	—	—	—	—	—	—	—
15 Quinault NFH	[2]pre-1982	99	0.920	0.080	—	—	0.980	0.020	—	—	—	—
	1982	50	0.958	0.042	—	—	1.000	—	0.411	0.589	—	—
16 Quinault Pens	1982	50	0.870	0.054	0.076	—	1.000	—	0.500	0.500	—	—
Others												
18 Wynoochee River	1982	66	—	—	—	—	—	—	0.635	0.365	—	—
21 Elwha Spawning Channel	1981	39	—	—	—	—	—	—	0.500	0.500	—	—
	1982	40	0.962	0.038	—	—	1.000	—	0.237	0.745	—	—

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Iddh-1,2*		*Idh-3,4*				*Mdh-1,2*		*Mdh-3,4*		
		100	36	100	120	87	60	100	120	100	115	67
Quillayute River												
1 Fall-run adults	[1](1983)	—	—	0.976	0.024	—	—	1.000	—	0.980	0.020	—
1 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.971	0.025	0.004
3 Soleduck River	1981	—	—	0.911	0.057	0.032	—	0.987	0.013	0.993	0.007	—
	1982	—	—	1.000	—	—	—	1.000	—	0.975	0.025	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982	—	—	0.990	0.010	—	—	1.000	—	0.990	0.010	—
	1982	—	—	1.000	—	—	—	1.000	—	0.938	0.062	—
Spring/summer run	[2]pre-1982	—	—	0.955	0.035	0.010	—	1.000	—	0.975	0.015	0.010
	1982	—	—	0.985	0.010	0.005	—	1.000	—	0.985	0.015	—
	[1](1983)	—	—	0.915	0.078	0.003	0.004	1.000	—	0.987	0.006	0.007
6 Bogachiel River	1981	—	—	0.946	0.054	—	—	1.000	—	0.975	0.025	—
	1982	—	—	1.000	—	—	—	1.000	—	0.888	0.112	—
Hoh River												
7 Fall-run adults	[1](1983)	—	—	0.910	0.090	—	—	1.000	—	0.959	0.041	—
7 Summer-run adults	[1](1983)	—	—	0.922	0.078	—	—	1.000	—	0.973	0.027	—
8 Juveniles	1981	—	—	0.929	0.071	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.996	0.004	—	—	1.000	—	0.990	0.010	—
Queets River												
9 Fall-run adults	[1](1983)	—	—	0.915	0.085	—	—	1.000	—	0.979	0.021	—
9 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.992	0.008	—
10 Clearwater River	1981	—	—	0.903	0.060	0.037	—	1.000	—	0.961	0.039	—
	1982	0.897	0.103	0.825	0.175	—	—	1.000	—	0.970	0.025	0.005
12 Salmon River	1982	—	—	0.938	0.062	—	—	0.990	0.010	0.974	0.026	—
11 Upper Queets River	1981	—	—	0.873	0.127	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.936	0.064	—	—	1.000	—	0.995	0.005	—
Quinault River												
13 Adults	[1](1983)	—	—	0.952	0.048	—	—	1.000	—	0.988	—	0.012
14 Lower Quinault River	1982	—	—	0.943	0.057	—	—	1.000	—	0.991	0.009	—
17 Upper Quinault River	1982	—	—	0.931	0.069	—	—	1.000	—	0.990	0.010	—
15 Quinault NFH	[2]pre-1982	—	—	0.900	0.090	0.010	—	1.000	—	0.990	0.010	—
	1982	—	—	0.974	0.026	—	—	1.000	—	1.000	—	—
16 Quinault Pens	1982	—	—	0.978	0.022	—	—	1.000	—	0.995	0.005	—
Others												
18 Wynoochee River	1982	—	—	0.980	0.020	—	—	1.000	—	0.996	0.004	—
21 Elwha Spawning Channel	1981	—	—	0.894	0.106	—	—	1.000	—	0.929	—	0.071
	1982	0.938	0.062	0.950	0.050	—	—	1.000	—	1.000	—	—

[1]Offspring from these adults would have belonged to the 1983 year class.

[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Mpi-1*			*Pgm-1*			*Pgdh-1*		*Pgk-2*	
		100	116	90	100	129	150	100	90	100	81
Quillayute River											
1 Fall-run adults	[1](1983)	0.672	0.328	—	0.909	0.091	—	1.000	—	0.512	0.488
1 Summer-run adults	[1](1983)	0.688	0.312	—	0.951	0.049	—	1.000	—	0.475	0.525
3 Soleduck River	1981	0.743	0.257	—	0.936	0.064	—	1.000	—	0.486	0.514
	1982	0.650	0.350	—	0.962	0.038	—	1.000	—	0.325	0.675
4 Soleduck Hatchery											
Fall run	[2]pre-1982	0.810	0.190	—	1.000	—	—	1.000	—	0.370	0.630
	1982	0.862	0.138	—	0.988	0.012	—	1.000	—	—	—
Spring/summer run	[2]pre-1982	0.620	0.370	0.010	1.000	—	—	1.000	—	0.490	0.510
	1982	0.580	0.410	0.010	0.990	0.010	—	1.000	—	0.610	0.390
	[1](1983)	0.753	0.247	—	0.980	0.020	—	1.000	—	0.617	0.383
6 Bogachiel River	1981	0.621	0.379	—	0.949	0.022	0.029	1.000	—	0.543	0.457
	1982	0.663	0.337	—	0.925	0.075	—	1.000	—	0.487	0.513
Hoh River											
7 Fall-run adults	[1](1983)	0.743	0.257	—	0.946	0.054	—	1.000	—	0.405	0.595
7 Summer-run adults	[1](1983)	0.738	0.262	—	0.886	0.114	—	1.000	—	0.473	0.527
8 Juveniles	1981	0.593	0.407	—	0.900	0.086	0.014	1.000	—	0.470	0.530
	1982	0.669	0.331	—	0.954	0.039	0.007	1.000	—	0.454	0.546
Queets River											
9 Fall-run adults	[1](1983)	0.704	0.296	—	0.914	0.086	—	1.000	—	0.467	0.533
9 Summer-run adults	[1](1983)	0.661	0.339	—	0.882	0.118	—	1.000	—	0.591	0.409
10 Clearwater River	1981	0.732	0.268	—	0.943	0.050	0.007	1.000	—	0.421	0.579
	1982	0.775	0.225	—	0.843	0.147	0.010	1.000	—	0.438	0.562
12 Salmon River	1982	0.638	0.362	—	0.906	0.052	0.042	1.000	—	0.562	0.438
11 Upper Queets River	1981	0.636	0.364	—	0.864	0.079	0.057	1.000	—	0.369	0.631
	1982	0.750	0.250	—	0.991	0.009	—	1.000	—	0.463	0.537
Quinault River											
13 Adults	[1](1983)	0.746	0.254	—	0.984	0.016	—	0.992	0.008	0.597	0.403
14 Lower Quinault River	1982	0.632	0.368	—	0.864	0.136	—	1.000	—	0.539	0.461
17 Upper Quinault River	1982	0.654	0.346	—	0.896	0.104	—	1.000	—	0.500	0.500
15 Quinault NFH	[2]pre-1982	0.610	0.390	—	0.930	0.050	0.020	—	—	0.580	0.420
	1982	0.786	0.214	—	0.970	0.030	—	0.980	0.020	0.776	0.224
16 Quinault Pens	1982	0.730	0.270	—	0.940	0.040	0.020	1.000	—	0.235	0.765
Others											
18 Wynoochee River	1982	0.723	0.269	0.008	0.917	0.083	—	1.000	—	0.632	0.368
21 Elwha Spawning Channel	1981	0.500	0.482	0.018	0.987	—	0.013	1.000	—	0.468	0.532
	1982	0.632	0.368	—	1.000	—	—	1.000	—	0.250	0.750

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Sod-1* −100	*Sod-1* −225	*Sod-1* 400
Quillayute River				
1 Fall-run adults	[1](1983)	0.904	0.096	—
1 Summer-run adults	[1](1983)	0.860	0.140	—
3 Soleduck River	1981	0.903	0.097	—
	1982	0.975	0.025	—
4 Soleduck Hatchery				
Fall run	[2]pre-1982	0.800	0.200	—
	1982	0.833	0.167	—
Spring/summer run	[2]pre-1982	0.620	0.380	—
	1982	0.840	0.160	—
	[1](1983)	0.724	0.276	—
6 Bogachiel River	1981	0.885	0.115	—
	1982	0.926	0.074	—
Hoh River				
7 Fall-run adults	[1](1983)	0.892	0.108	—
7 Summer-run adults	[1](1983)	0.879	0.121	—
8 Juveniles	1981	0.886	0.114	—
	1982	0.868	0.132	—
Queets River				
9 Fall-run adults	[1](1983)	0.919	0.081	—
9 Summer-run adults	[1](1983)	0.852	0.148	—
10 Clearwater River	1981	0.913	0.080	0.007
	1982	0.907	0.093	—
12 Salmon River	1982	0.927	0.073	—
11 Upper Queets River	1981	0.886	0.107	0.007
	1982	0.861	0.139	—
Quinault River				
13 Adults	[1](1983)	0.703	0.297	—
14 Lower Quinault River	1982	0.949	0.051	—
17 Upper Quinault River	1982	0.824	0.176	—
15 Quinault NFH	[2]pre-1982	0.780	0.210	0.010
	1982	0.720	0.200	0.080
16 Quinault Pens	1982	0.929	0.071	—
Others				
18 Wynoochee River	1982	0.821	0.179	—
21 Elwha Spawning Channel	1981	0.741	0.259	—
	1982	0.697	0.303	—

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 2.—Allele frequencies for coho salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample name correspond to locations shown in Figure 1.

			bGala-2		*Ah-3*				*Ada-2*			*Aat-3,4*	
	Brood	*N*	100	128	100	91	115	130	100	110	91	100	87
Quillayute River													
2 Dickey River	1981	52	—	—	0.990	—	—	0.010	0.990	0.010	—	1.000	—
3 Soleduck River	1981	37	0.660	0.340	0.973	0.027	—	—	0.933	0.967	—	1.000	—
	1982	48	0.583	0.417	1.000	—	—	—	1.000	—	—	1.000	—
4 Soleduck Hatchery	1981	40	—	—	0.988	0.012	—	—	1.000	—	—	1.000	—
5 Calawah River	1982	40	0.551	0.449	0.925	0.050	0.025	—	0.988	0.013	—	1.000	—
6 Bogachiel River	1982	74	0.546	0.454	1.000	—	—	—	1.000	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	48	0.061	0.399	1.000	—	—	—	0.990	0.010	—	1.000	—
Pin Creeks	1982	44	—	—	0.989	0.011	—	—	1.000	—	—	1.000	—
8 Other tributaries	1982	45	0.616	0.384	1.000	—	—	—	1.000	—	—	1.000	—
Queets River													
10 Clearwater River	1981	210	0.637*	0.363	0.979	0.021	—	—	0.995	0.005	—	1.000	—
11 Upper Queets River	1981	76	0.674	0.326	1.000	—	—	—	0.993	0.007	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	60	—	—	—	—	—	—	1.000	—	—	0.923	0.077
15 Quinault NFH	1981	40	—	—	1.000	—	—	—	0.961	0.039	—	1.000	—
	1982	40	0.814	0.186	0.988	0.012	—	—	0.988	—	0.012	1.000	—
Others													
19 Snohomish River	1981, 1982	106	0.595	0.405	0.986	0.009	0.005	—	1.000	—	—	1.000	—
20 Snow Creek	1981	60	0.542	0.458	1.000	—	—	—	—	—	—	1.000	—

		Ck-1		*Gpi-1*		*Gpi-2*			*Gpi-3*		*G3pdh-1*	
	Brood	100	127	100	250	100	157	67	100	90	−100	−15
Quillayute River												
2 Dickey River	1981	1.000	—	1.000	—	0.990	0.010	—	1.000	—	0.990	0.010
3 Soleduck River	1981	1.000	—	1.000	—	0.986	0.014	—	1.000	—	1.000	—
	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.969	0.031
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	0.987	0.013
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Hoh River												
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	1.000	—	0.989	0.011	—	1.000	—	1.000	—
Queets River												
10 Clearwater River	1981	1.000	—	0.998	0.002	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	1.000	—	0.993	0.007	0.993	—	0.007	1.000	—	0.987	0.013
Quinalt River												
13 Lower Quinault River	1982	1.000	—	1.000	—	0.991	0.009	—	1.000	—	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.959	0.041
	1982	1.000	—	1.000	—	0.950	0.050	—	0.975	0.025	1.000	—
Others												
19 Snohomish River	1981, 1982	0.995	0.005	1.000	—	0.981	—	0.019	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.992	0.008

APPENDIX TABLE 2.—*Continued.*

		Idh-3,4					*Ldh-3*			*Ldh-4*		*Lgl-1*	
	Brood	100	130	70	123	157	100	45	140	100	110	100	80
Quillayute River													
2 Dickey River	1981	0.825	0.169	0.006	—	—	0.971	0.029	—	1.000	—	1.000	—
3 Soleduck River	1981	0.973	—	0.007	0.020	—	0.986	—	0.014	1.000	—	1.000	—
	1982	—	—	—	—	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	0.964	0.036	—	—	—	1.000	—	—	1.000	—	1.000	—
5 Calawah River	1982	1.000	—	—	—	—	1.000	—	—	1.000	—	0.963	0.037
6 Bogachiel River	1982	0.996	—	0.004	—	—	0.993	—	0.007	1.000	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	0.995	—	0.005	—	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	0.978	—	0.022	—	—	0.988	0.012	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	—	—	0.989	0.011	—	1.000	—	1.000	—
Queets River													
10 Clearwater River	1981	0.924	0.073	0.001	0.002	—	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	0.858*	0.132*	—	0.006*	0.004*	1.000	—	—	0.994	0.006	1.000	—
Quinalt River													
13 Lower Quinault River	1982	0.905	0.095	—	—	—	1.000	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	0.917	0.077	—	—	0.006	1.000	—	—	1.000	—	1.000	—
	1982	1.000	—	—	—	—	0.988	0.012	—	0.975	0.025	1.000	—
Others													
19 Snohomish River	1981, 1982	0.920	0.070	0.007	—	0.003	1.000	—	—	0.972	0.028	1.000	—
20 Snow Creek	1981	0.985	0.015	—	—	—	1.000	—	—	1.000	—	1.000	—

		Mdh-1,2			*Mdh-3,4*					*Mdh-5*		*MdhP-1*	
	Brood	100	37	210	100	123	110	89	140	100	107	100	130
Quillayute River													
2 Dickey River	1981	1.000	—	—	0.991	0.009	—	—	—	0.971	0.029	1.000	—
3 Soleduck River	1981	1.000	—	—	0.967	0.020	—	—	0.013	—	—	1.000	—
	1982	1.000	—	—	1.000	—	—	—	—	—	—	—	—
4 Soleduck Hatchery	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—
5 Calawah River	1982	1.000	—	—	0.988	0.012	—	—	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	—	0.993	0.007	—	—	—	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	1.000	—	—	0.985	0.005	0.010	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	—	0.955	0.040	—	0.006	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	0.956	0.044	—	—	—	—	—	1.000	—
Queets River													
10 Clearwater River	1981	1.000	—	—	0.985	0.010	—	0.005	—	0.960	0.040	0.990	0.010
11 Upper Queets River	1981	0.994	0.003	0.003	0.997	0.003	—	—	—	1.000*	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	1.000	—	—	1.000	—	—	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	1.000	—	—	1.000	—	—	—	—	0.950	0.050	1.000	—
	1982	1.000	—	—	0.994	0.006	—	—	—	—	—	1.000	—
Others													
19 Snohomish River	1981, 1982	0.997	0.003	—	0.998	0.002	—	—	—	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—

APPENDIX TABLE 2.—*Continued.*

	Brood	*Mpi-1*		*Pgm-2*		*Pgdh-1*		*Pnp-1*	
		100	123	−100	−55	100	92	100	155
Quillayute River									
2 Dickey River	1981	1.000	—	0.990	0.010	1.000	—	—	—
3 Soleduck River	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	—	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	—
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	—
Hoh River									
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	0.673	0.327
8 Other tributaries	1982	1.000	—	1.000	—	1.000	—	—	—
Queets River									
10 Clearwater River	1981	0.995	0.005	1.000	—	1.000	—	0.877*	0.123*
11 Upper Queets River	1981	1.000	—	1.000	—	1.000	—	0.780*	0.220*
Quinault River									
13 Lower Quinault River	1982	1.000	—	1.000	—	0.974	0.026	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	1.000	—
Others									
19 Snohomish River	1981, 1982	1.000	—	1.000	—	1.000	—	0.995	0.005
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	1.000	—