GENETIC POPULATION STRUCTURE OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE PACIFIC NORTHWEST

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ABSTRACT

Variation at 25 polymorphic protein coding loci was examined for 86 populations of chinook salmon, *Oncorhynchus tshawytscha*, ranging from the Babine River in British Columbia to the Sacramento River in California. Substantial differences in allele frequencies identified patterns of genetic variability over the geographic range of the study. The following nine major genetically defined regions were formulated: 1) the Fraser River tributaries east of the Cascade Crest (no downstream drainages were sampled), 2) Georgia Strait, 3) Puget Sound, 4) a broad coastal region ranging from the west coast of Vancouver Island southward through northern California, 5) the Columbia River below The Dalles Dam, 6) the Columbia River above The Dalles Dam, 7) the Snake River, 8) the Klamath River, and 9) the Sacramento River. Populations sampled within a region tended to be genetically distinct from each other although they exhibited the general patterns of variability that defined the region. Within a region there was little distinction among populations returning to spawn at different times. The persistence of these geographic patterns in the face of natural opportunities for introgression, and sometimes massive transplantations, suggests that genetically adapted groups within regions have resisted large-scale introgression from other regions. Repopulation of deglaciated areas in the Fraser River, Georgia Strait, and Puget Sound apparently occurred from multiple sources; most likely sources included Columbia River populations and northern refuges rather than from the large coastal group of populations. Patterns of genetic distribution of chinook salmon differed from those of other anadromous salmonids studied within this region. A conservative policy for stock transfers was suggested based on distinct genetic differences observed both between and within regions.

Population studies of chinook salmon, *Oncorhynchus tshawytscha*, based on electrophoretically detected genetic variation have been carried out since the late 1960s. As data have accumulated, an increasingly clear picture of the breeding structure of this species has emerged. While early investigations based on only a few polymorphic loci identified differences among populations, they failed to identify any geographic trends (e.g., Utter et al. 1973; Kristiansson and McIntyre 1976). Differences within and among drainages became apparent as additional polymorphic loci were found and a more comprehensive sampling of populations was made (Utter et al. 1976, 1980; Gharrett et al. 1987).

This paper outlines the genetic structure of chinook salmon in the Pacific Northwest using allele frequency data collected for the purpose of estimating the stock composition of ocean caught chinook salmon (Milner et al. 1981[3]; 1983[4]; Miller et al. 1983; Utter et al. 1987). Our purpose is to examine these data in the light of other relevant biological and historical information 1) to understand genetic relationships among chinook salmon populations better and 2) to provide biologists with new insights to assist in the preservation and management of this important biological resource.

MATERIALS AND METHODS

Our data were obtained from samples of juvenile or adult fish collected at 86 locations ranging from British Columbia through California (Table 1, Fig. 1). These data include allele frequencies from 25 protein-coding loci with sample sizes between 38 and 200 individuals. Data were accumulated between 1980 and 1984 and were reported in part in Milner et al. (fn. 3, 4).

Electrophoretic procedures followed those de-

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[3]Milner, G. B., D. J. Teel, F. M. Utter, and C. L. Burley. 1981. Columbia River stock identification study: Validation of genetic method. Report to Bonneville Power Administration under contract DE-A179-80BP18488, 51 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

[4]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study. Report to Bonneville Power Administration under contract DE-A179-82BP28044M001, 95 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

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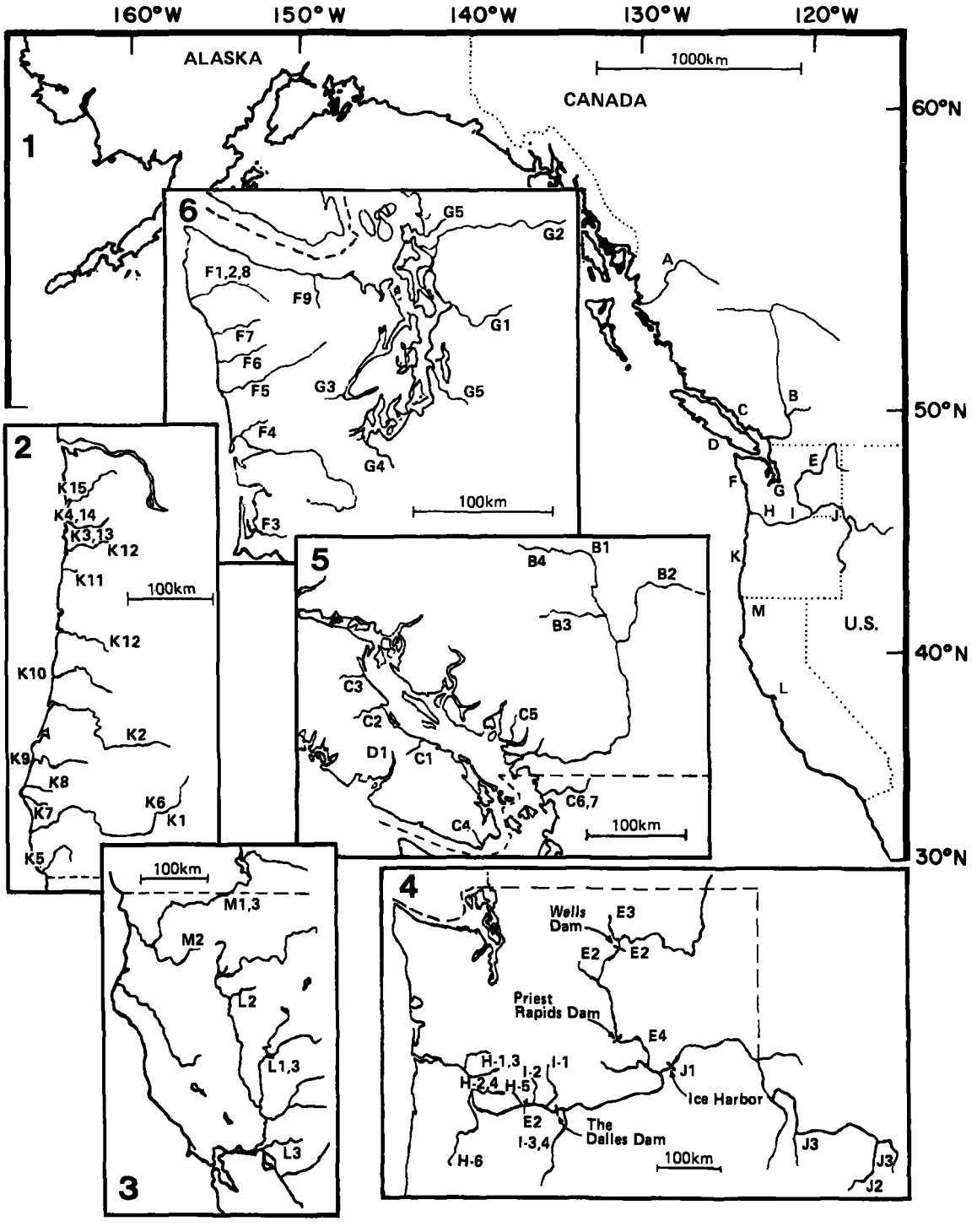

FIGURE 1.—Locations of sample collections based on map code of Table 1. 1. Total range of sampling identifying general locations or drainage systems. 2. Oregon (OR) coast. 3. California (CA). 4. Columbia River. 5. Georgia Strait, British Columbia (BC) coast, and Fraser River. 6. Washington (WA) coast and Puget Sound.

TABLE 1.—Chinook salmon collections made from British Columbia through California. Map codes refer to Figure 1. Samples representing a hatchery stock are marked by $. Locations followed by (a) represent adult samples; all other samples were from juvenile fish. Season of return identifies the time of entry by adults into freshwater. Pooled samples are indicated by hyphens.

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
A1	Babine (a)	Skeena R.	Inland	39	Summer
B1	Tete Jaune (a)	Fraser R.	Inland	38	Summer
B2	Clearwater (a)	Fraser R.	Inland	45	Summer
B3	Chilco	Fraser R.	Inland	49	Summer
B4	Stuart–Nechako (a)	Fraser R.	Inland	105	Summer
C1	$Big Qualicum	Georgia Strait	Coastal	85	Fall
C2	$Puntledge (a)	Georgia Strait	Coastal	100	Fall
C3	$Quinsam (a)	Georgia Strait	Coastal	97	Fall
C4	$San Juan	Georgia Strait	Coastal	50	Fall
C5	$Capilano	Georgia Strait	Coastal	99	Fall
C6	Nooksack, south fork	Georgia Strait	Coastal	50	Spring
C7	Nooksack, north fork	Georgia Strait	Coastal	50	Spring
D1	$Robertson Ck. (a)	British Columbia coast	Coastal	100	Fall
E1	$Wells Dam	Upper Columbia R.	Inland	50	Summer
E2	$Carson–$Leavenworth[1]	Upper Columbia R.	Inland	148	Spring
E3	$Winthrop	Upper Columbia R.	Inland	129	Spring
E4	$Priest Rapids	Upper Columbia R.	Inland	100	Fall
F1	$Soleduck	Washington coast	Coastal	100	Summer
F2	$Soleduck	Washington coast	Coastal	100	Spring
F3	$Naselle	Washington coast	Coastal	99	Fall
F4	$Humptulips	Washington coast	Coastal	50	Fall
F5	$Quinault	Washington coast	Coastal	100	Fall
F6	Queets	Washington coast	Coastal	120	Fall
F7	Hoh	Washington coast	Coastal	100	Fall
F8	$Soleduck	Washington coast	Coastal	50	Fall
F9	$Elwha	Washington coast	Coastal	100	Fall
G1	$Skykomish	Puget Sound	Coastal	100	Summer
G2	$Skagit	Puget Sound	Coastal	100	Summer
G3	$Hood Canal	Puget Sound	Coastal	98	Fall
G4	$Deschutes	Puget Sound	Coastal	150	Fall
G5	$Green R.–$Sammish	Puget Sound	Coastal	149	Fall
H1	$Cowlitz–$Kalama	Lower Columbia R.	Coastal	100	Spring
H2	$Lewis R.	Lower Columbia R.	Coastal	50	Spring
H3	$Cowlitz (a)–$Kalama	Lower Columbia R.	Coastal	149	Fall
H4	$Lewis R.	Lower Columbia R.	Coastal	50	Fall
H5	$Washougal R.	Lower Columbia R.	Coastal	50	Fall
H6	$Eagle Ck.–$McKenzie R.	Lower Columbia R. (Willamette)	Coastal	88	Spring
I1	$Klickitat R.	Mid-Columbia R.	Inland	50	Spring
I2	$Spring Ck.–$Big Ck.[2]	Mid-Columbia R.	Inland	150	Fall
I3	$Warm Springs–$Round Butte (a)	Mid-Columbia R.	Inland	109	Spring
I4	Deschutes (a)	Mid-Columbia R.	Inland	49	Fall
J1	Ice Harbor (a)	Snake R.	Inland	200	Fall
J2	McCall–Johnson Ck.	Snake R.	Inland	106	Summer
J3	$Rapid R.–Valley Ck.[3]	Snake R.	Inland	165	Spring
K1	$Cole R.–Hoot Owl Ck.	Oregon coast	Coastal	163	Spring
K2	$Rock Ck.	Oregon coast	Coastal	100	Spring
K3	$Cedar Ck.	Oregon coast	Coastal	99	Spring
K4	$Trask R.	Oregon coast	Coastal	100	Spring
K5	Chetco	Oregon coast	Coastal	100	Fall
K6	Lobster Ck.	Oregon coast	Coastal	50	Fall
K7	$Elk R.	Oregon coast	Coastal	100	Fall
K8	Sixes R. estuary	Oregon coast	Coastal	100	Fall
K9	Coquille R. estuary	Oregon coast	Coastal	115	Fall
K10	Siuslaw Bay	Oregon coast	Coastal	82	Fall
K11	$Salmon R.	Oregon coast	Coastal	99	Fall
K12	$Nestucca R.–$Alsea R.[4]	Oregon coast	Coastal	346	Fall
K13	$Cedar Ck.	Oregon coast	Coastal	100	Fall
K14	$Trask R.–Tillamook Bay	Oregon coast	Coastal	188	Fall
K15	Nehalem estuary	Oregon coast	Coastal	141	Fall

[1]Includes Little White Salmon.
[2]Includes Little White Salmon.
[3]Includes Sawtooth and Red River.
[4]Includes Siletz Estuary and $Fall Creek.

TABLE 1.—*Continued.*

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
L1	$Feather R.	Sacramento R.	Coastal	50	Spring
L2	$Coleman–$Nimbus	Sacramento R.	Coastal	300	Fall
L3	$Feather R.–$Mokelumne	Sacramento R.	Coastal	200	Fall
M1	$Trinity R.	Klamath R.	Inland	50	Spring
M2	$Iron Gate	Klamath R.	Inland	99	Fall
M3	$Trinity R.	Klamath R.	Inland	100	Fall

scribed in Aebersold et al. (1987). Buffer systems included the following: 1) a Tris-boric acid, EDTA system (pH 8.5) (Boyer et al. 1963); 2) an amine (3-aminopropyl morpholine) citrate system (pH 6.5) (Clayton and Tretiak 1972); and 3) a discontinuous Tris-citric acid (gel pH 8.15), lithium hydroxide, boric acid (electrode pH 8.0) system (Ridgway et al. 1970). Methods for visualizing enzyme activity followed Siciliano and Shaw (1976) and Harris and Hopkinson (1976). A system of nomenclature suggested by Allendorf and Utter (1979) was used to designate loci and alleles.

The 25 polymorphic loci (Table 2) were selected from a larger set of loci known to be variable in chinook salmon. Variable loci were excluded when data were unavailable for one or more of the sampling locations listed in Table 1. Much of the descriptive data for the loci and alleles were previously reported (Utter et al. 1980; Milner et al. fn. 4). Two previously unreported polymorphic enzymes in chinook salmon, Gr and Gpi-1(H), were used for population studies and are described in the appendix.

Allele frequencies were calculated directly from phenotypic classes for 14 nonduplicated loci. Tests for departures of genotypes from the expected binomial distribution (Hardy-Weinberg equilibrium) were made using a G statistic (Sokal and Rohlf 1969) with degrees of freedom equaling the number of expected genotypes minus the number of alleles. The isoloci Aat-1,2; Idh-3,4; Mdh-1,2; Mdh-3,4; and Pgm-1,2 (see Allendorf and Thorgaard 1984) were excluded from such tests because every individual was scored on the basis of four allelic doses from two loci. Combined allele frequencies of both loci were calculated directly from phenotypic expressions and were assumed to be the same at both loci for statistical calculations. The data for the Gpi-2 locus and the *Gpi-1(H)* allele were also excluded from Hardy-Weinberg calculations because common homozygotes and heterozygotes could not be reliably distinguished, and allele frequency estimates were

TABLE 2.—Background information on chinook salmon tissue samples for protein coding loci.

Protein name and enzyme number	Locus	Tissue[1]	Buffer system	Reference[2]
Aconitate hydratase (4.2.1.3)	Ah	L	2	1
Adenosine deaminase (3.5.4.4)	Ada-1	E,H,M	1	1
Aspartate aminotransferase (2.6.1.1)	Aat-1,2	H,M	1	1
	Aat-3	E	1	1
Dipeptidase (3.4.13.11)	Dpep-1	E,H,M	1,3	1
	Dpep-2	E	1,3	1
Glucose-6-phosphate isomerase (5.3.1.9)	Gpi-1	M	3	2
	Gpi-2	M	3	1
	Gpi-3	M	3	1
Glutathione reductase (16.4.2)	Gr	E,M	1,3	2
Isocitrate dehydrogenase (1.1.1.42)	Idh-3,4	E,L,H,M	2	1
Lactate dehydrogenase (1.1.1.27)	Ldh-4	E,L,M	1	1
	Ldh-5	E	1	1
Malate dehydrogenase (1.1.1.37)	Mdh-1,2	L,H,M	2	1
	Mdh-3,4	E,H,M	2	1
Mannose-6-phosphate isomerase (5.3.1.8)	Mpi	E,L.H.M	1	1
Phosphoglucomutase (2.7.5.1)	Pgm-1,2	E,L,H,M	2	1
Phosphoglycerate kinase (2.7.2.3)	Pgk-2	E,L,M	2	1
Superoxide dismutase (1.15.1.1)	Sod	L	1	1
Tripeptide aminopeptidase (3.4.11.4)	*Tapep-1*	E,H,M	3	1

[1]L = liver, E = eye, H = heart, M = muscle.
[2]1 = Milner et al. 1983, 2 = variation described in this study.

based on the frequency of homozygotes for the respective variant alleles. Expected heterozygosities were calculated for polymorphic loci. Pairwise comparisons were made for all loci between all populations by a contingency table analysis using a G statistic. Two or more sample collections lacking significant allele frequency differences for any polymorphic locus were considered a single population. All subsequent analyses were performed on the resulting 65 individual and pooled populations. A critical value of 1% was used (for both the Hardy-Weinberg and the pairwise population comparisons) to reduce the erroneous rejection of the null hypothesis when using multiple tests. Nei's (1975) measure of genetic distance (D) was used to compare pairwise levels of genetic divergence between individual or pooled populations. A dendrogram based on a matrix of these comparisons was constructed by the unweighted pair group method (UPGM) (Sneath and Sokal 1973). Principal component analysis of the allele frequency data followed procedures outlined in Sneath and Sokal (1973). A nested gene diversity analysis followed procedures described by Nei (1973) and Chakraborty (1980) and was performed through the NEGST computer program described by Chakraborty et al. (1982).

RESULTS AND DISCUSSION

Tests for Hardy-Weinberg Equilibrium

Tests for significant deviations from Hardy-Weinberg proportions were made on each of the 86 data sets for 14 loci including Ah, Ada-1, Aat-3, Dpep-1, Dpep-2, Gpi-1 (excluding the subsequently described *Gpi-1(H)* allele affecting heterodimer formation), Gpi-3, Gr, Ldh-4, Ldh-5, Mpi, Pgk-2, Sod-1, and Tapep-1. Six deviations were observed (Table 3). These deviations probably were random errors expected from the 1,204 independent calculations at the 1% level of significance. The direction of the deviations indicates both excesses and deficits of heterozygotes in both instances where the same locus is involved (Mpi and Sod-1). Two of the populations having significant deviations, Eagle Creek and Stuart, were combined for subsequent analysis with other populations having Hardy-Weinberg proportions; combinations were based on overall nonsignificant differences of allele frequencies. The high significance of the Stuart sample for Sod-1 is inflated through an expected value less than unity for the homozygous genotype of the (*−260*) allele.

TABLE 3.—Populations and loci with significant (α = 0.01) departures from expected Hardy-Weinberg proportions.

Population (map code)	Locus	Level of significance	Excess*/deficit- of heterozygotes
Queets (F6)	Dpep-1	0.005	+
Humptulips (F4)	Mpi	0.01	−
Washougal (H5)	Mpi	0.005	+
Lobster Creek (K6)	Pgk-2	0.005	+
Eagle Creek (H6)	Sod-1	0.005	+
Stuart (B4)	Sod-1	0.0001	−

Description of Allelic Distribution

The allele frequencies observed for all 25 polymorphic loci over the geographic range of this study (Appendix) indicate considerable heterogeneity among loci with regard to levels of variation and geographic distribution. This variation is summarized from three perspectives—heterozygosity, frequency range for common allele, and index of gene diversity (G_{st}) (Table 4). Heterozygosity measures within-population variation. Those loci having higher heterozygosities have greater potential for divergence of allele frequencies among populations. Mean heterozygosity over all loci was 0.102, and five loci (Ah, Mpi, Pgk-2, Sod-1, Tapep-1) exceeded 0.200.

The range of allele frequencies and the index of gene diversity reflect the actual divergences observed among populations. The range is a simple identification of allele frequency extremes. The index of gene diversity is a quantitative measure of genotype deviations of the overall data set from those expected in a single panmictic population. Seven of the eight most heterozygous loci (Pgk-2, Mpi, Sod-1, Ah, Tapep-1, Gpi-2, Dpep-1) were among the eight loci having either the greatest range in frequency or the highest index of gene diversity, indicating considerable genetic differences among the populations samples. Typically, adjacent populations tended to have allele frequencies more similar to one another than to those from other areas (see Appendix). Notable examples include the following: 1) restriction of Gpi-2 variation largely to coastal populations from Vancouver Island through Oregon, 2) the highest frequency of the *Gpi-1(H)* allele in populations from the Sacramento River, 3) Aat-3 variation that is largely restricted to populations from Georgia Strait and western Vancouver Island, 4) low frequencies of variant alleles for most loci in all Klamath River populations and in spring and summer run populations from the Snake River, and 5) high frequencies of Tapep-1 variants in Puget Sound populations.

Two procedures for graphic analysis (a dendrogram [Fig. 2] based on pairwise genetic distance

TABLE 4.—Outline of frequency range for common alleles, heterozygosity, and diversity for 25 polymorphic loci of chinook salmon sampled from British Columbia through California. Single entries for isoloci assume identical allele frequencies for individual loci. Locations and areas are based on map codes of Table 1 and Figure 1. Only areas are identified when one or more populations of an area have a maximum value of 1.000. Both locations and areas are identified for maximum values less than 1.000.

Locus	Frequency range for common allele (location and area)		Heterozygosity	Diversity (Gst)
	Minimum	Maximum		
Ah	0.366 (C3)	1.000 (I,J,M)	0.232	0.091
Ada-1	0.865 (G1)	1.000 (C–F,H,I,K–M)	0.044	0.045
Aat-1,2	0.888 (G3)	1.000 (A–C,E,F,H–J,L,M)	0.030	0.035
Aat-3	0.735 (C2)	1.000 (B,E–M)	0.030	0.143
Dpep-1	0.652 (K3,K9)	1.000 (B,D,E,J,M)	0.164	0.116
Dpep-2	0.939 (B3)	1.000 (A–M)	0.004	0.045
Gpi-1	0.576 (L1)	1.000 (A–K,M)	0.040	0.245
Gpi-2	0.432 (K5)	1.000 (A–C,E–I,K–M)	0.169	0.310
Gpi-3	0.875 (B3)	1.000 (C,E–M)	0.022	0.060
Gr	0.420 (H6)	1.000 (C,D,F,G,I,K–M)	0.068	0.215
Idh-3,4	0.862 (E2)	1.000 (B,C,K,M)	0.080	0.040
Ldh-4	0.933 (B2)	1.000 (A–M)	0.009	0.037
Ldh-5	0.964 (E4)	1.000 (A–M)	0.008	0.017
Mdh-1,2	0.945 (K8)	1.000 (A–M)	0.003	0.023
Mdh-3,4	0.843 (C3)	1.000 (A–C,H,K,M)	0.040	0.025
Mpi	0.386 (H4)	0.990 (M3)	0.401	0.089
Pgm-1,2	0.903 (K3)	1.000 (A–M)	0.031	0.041
Pgk-2	0.062 (J2)	0.931 (H6)	0.420	0.153
Sod-1	0.530 (I2)	0.990 (M2)	0.345	0.086
Tapep-1	0.483 (G5)	1.000 (B,M)	0.226	0.134
Average	0.724	0.996	0.102	0.123

measures, and plots of principal component scores) assist in identifying patterns of allelic variability. The approximate location of each population is identified in Figure 2 on the basis of its inclusion in one of eight clusters (diverging beyond a genetic distance of 0.01) or major subgroupings (below a genetic distance of 0.01). A notable feature of Figure 2 is the geographic basis for much of the aggregation. For instance, clusters 1 and 2 represent downstream populations of the Columbia River, cluster 3 contains the two northernmost populations of Georgia Strait, and cluster 4 is comprised of coastal populations from Vancouver Island southward through Oregon. The nine population units shown in Figure 2 are explained in the following section and represent a synthesis of possible relationships among these 65 populations.

The two plots of principal components (Fig. 3) provide an alternative picture of the allelic variation based on different perspectives of the total variance in a multidimensional space. The first four principal components (PC), which account for almost 80% of the total genetic variation, also project a geographic picture of this variation in these plottings. Six of nine population groupings (described in the next section) are essentially resolved by PC1 and PC2. Two of the remaining units are resolved by PC3 and PC4.

We used three different hierarchies in the gene diversity analysis to give a more detailed examination beyond the data on gene diversity presented in Table 4 (Table 5). The hierarchies based on geographic and temporal clusters are discussed at this point; the hierarchy based on population unit clusters is discussed following the synthesis of these units. The geographic hierarchy was based on the locations of the samples using two regions (inland and coastal) with six areas within the inland region and seven areas within the coastal region (see Table 1).

The within-population component of gene diversity (i.e., the mean average heterozygosity) in each hierarchy was 87.7% of the total diversity (i.e., the expected heterozygosity based on the mean allele frequencies). The remaining 12.3% of the total diversity was the index of gene diversity, G(st) resulting from population subdivision (see also Table 5). Most of the gene diversity in the geographic hierarchy was due to genetic differences between populations within areas (4.6%) and areas within regions (6.2%). The regional component contrasting inland populations of major drainages with populations from downstream tributaries and coastal drainages contributed only 1.5% of the total diversity. By far the largest portion of subdivision in the temporal

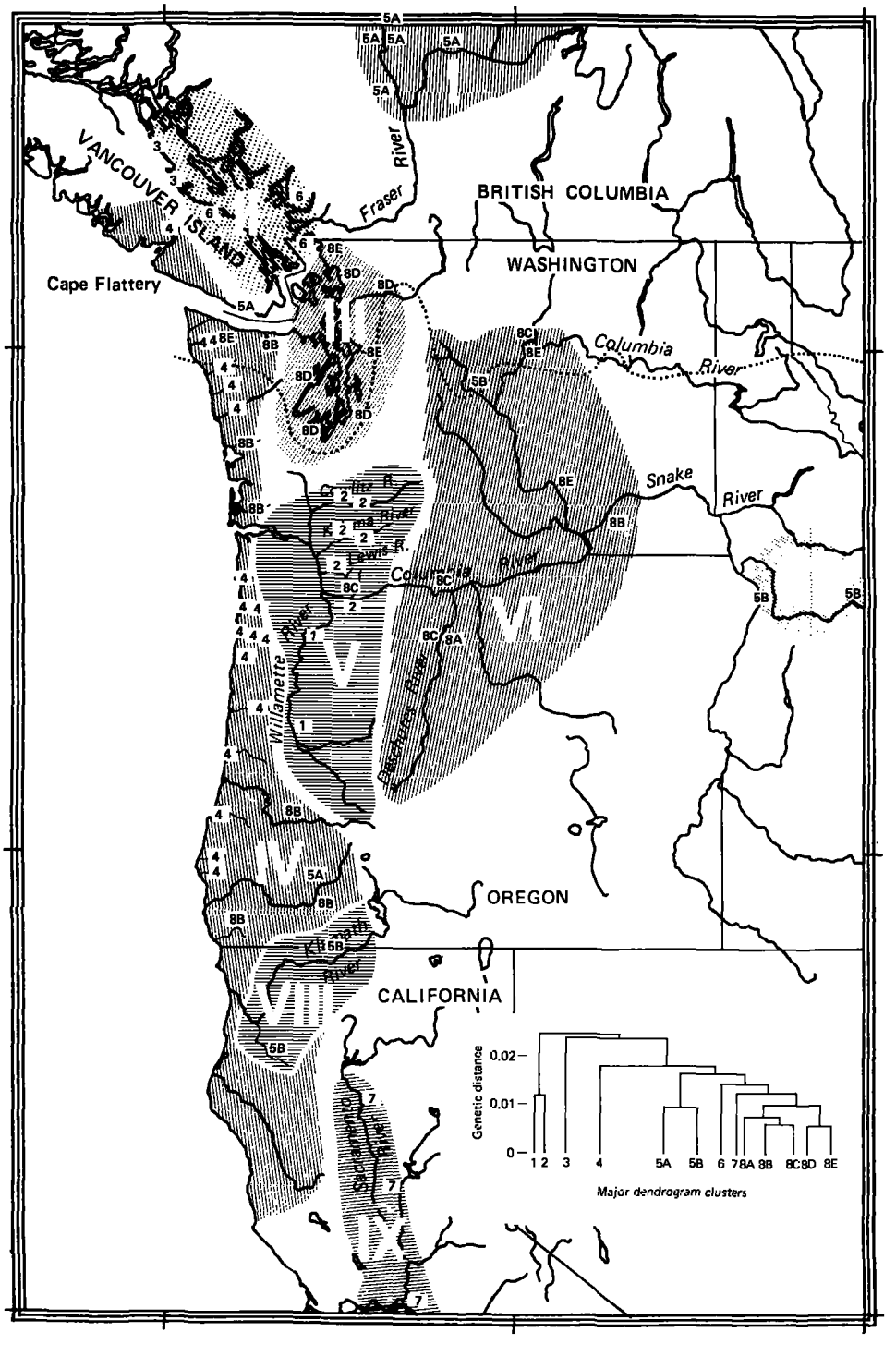

FIGURE 2.—Dendrogram and nine population units formulated from allele frequency data of this study. Populations are approximately located by numbered squares which identify membership in clusters on the superimposed genetic distance dendrogram. An exception is the most northern location of Unit I (Babine River) which lies beyond map range. Dotted line represents maximum glaciation during late Pleistocene (McPhail and Lindsey 1986).

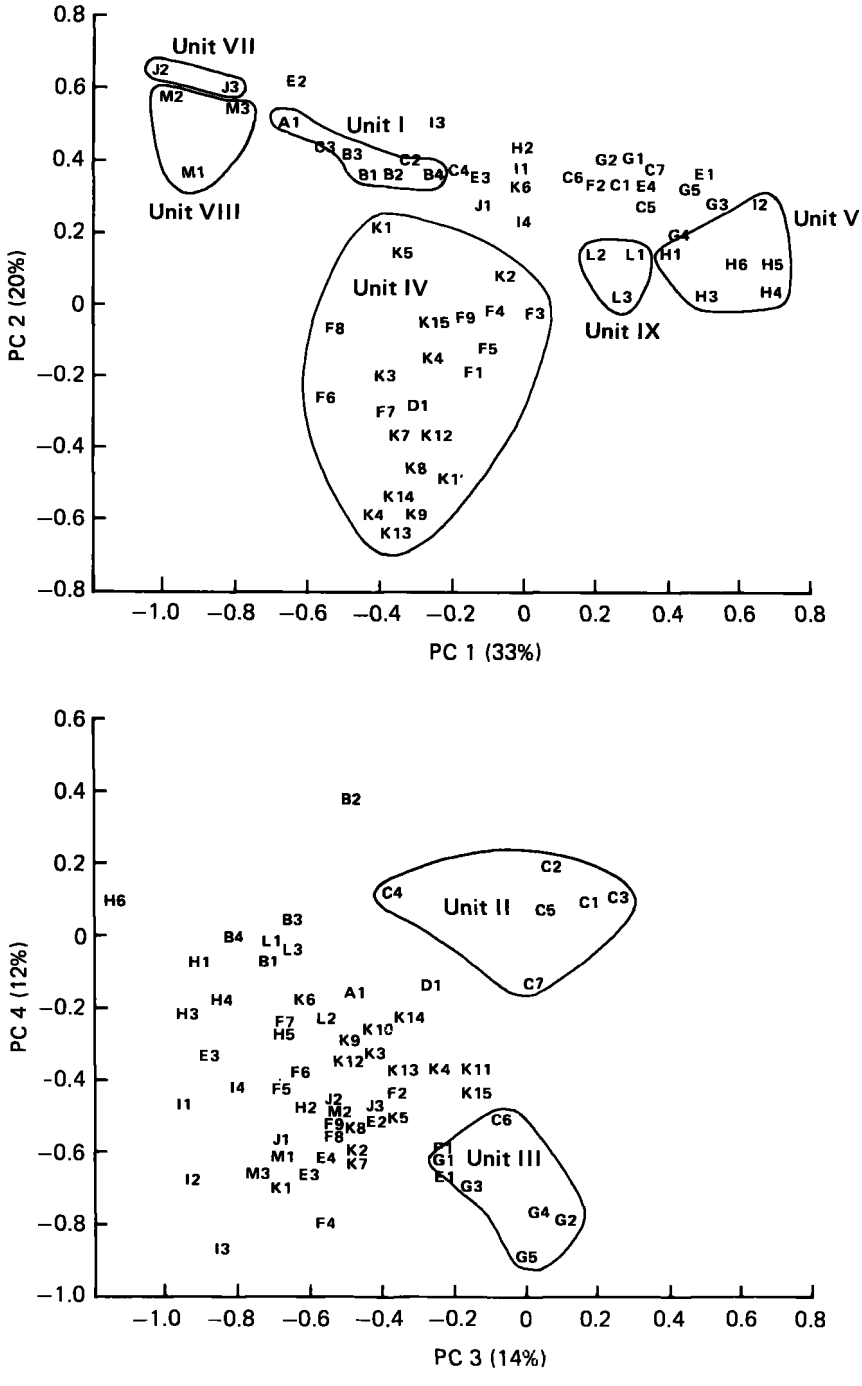

FIGURE 3.—Plots of scores for principal components 1 & 2 and 3 & 4 derived from allele frequencies in the Appendix. Major contributing loci include PC1 - Mpi, Pgk-2, Sod, and Tapep-1; PC2 - Ah, Dpep-1, Gpi-2, and Pgm-1,2; PC3 - Aat-3, Gr, and Tapep-1; PC4 - Mpi.

TABLE 5.—Summary of distribution of relative gene diversity of chinook salmon in geographical and temporal hierarchies based on 65 individual or pooled populations and 25 polymorphic loci. Areas, regions, and seasons are given for each population in Table 1. Absolute values of gene diversity include mean average heterozygosity (Hs) - 0.1018 and total diversity (Ht) - 0.1161.

Geographic clusters	%	Temporal clusters	%	Population unit clusters	%
Within populations	87.7	Within populations	87.7	Within populations	87.7
Between populations, within areas	4.6	Between populations, within seasons	11.4	Between populations, within units	4.4
Between areas, within regions	6.2	Between seasons	0.9	Between units	7.9
Between regions	1.5				
Total	100.0		100.0		100.0

hierarchy resulted from differences between populations within seasons (11.6%), with only 0.7% of the total diversity being due to differences between seasons.

Interpretation of Observed Variation

We interpreted the overall data set primarily as a reflection of patterns and levels of gene exchange among populations. This interpretation does not exclude the possibility of some selective forces influencing the frequencies of some alleles and genotypes in some environments (e.g., Powers et al. 1983; Mork et al. 1984). However, empirical data from diverse animal species justify an assumption of predominant neutrality (Ihssen et al. 1981; Chakraborty et al. 1980; Eanes 1987). This assumption is strengthened when many polymorphic loci are examined and is particularly pertinent in anadromous salmonids where restricted population sizes accentuate the influence of genetic drift (Utter et al. 1980). The data presented here indicate that chinook salmon consist of a genetically complex network of populations throughout the geographic range of this study. This information yields some clear conclusions and suggests a number of additional possibilities that must await confirmation or rejection from additional studies.

One conclusion is that the time of return (i.e., season) is not a major factor in establishing relationships of stocks among areas. Both the geographic clustering in Figures 2 and 3 and the small between-seasons component of the temporal gene diversity analysis point away from the concept of a recent common ancestry of fish returning at the same time in different areas. This finding comes as no surprise based on published data of other anadromous salmonids (e.g., rainbow trout, Allendorf and Utter 1979). However, it is still commonly accepted that the chinook salmon is separated into temporally distinct "races" (e.g., McClane 1978). Although a strong genetic component for the time of return has been clearly demonstrated in anadromous salmonids (e.g., Helle 1981), and this is not debated here, it appears that genetic divergence into temporally distinct units tends to occur within an area from a common ancestral stock of chinook salmon.

In contrast to the lack of evidence for genetic structuring of time of return, a geographic basis for genetic structuring is apparent. The relatively large area component of gene diversity (over half of the between-population diversity in column 1 of Table 5) coupled with the predominantly geographic clusterings warrant an attempt to define different geographically discrete population units. Most units (Figure 2 and Appendix) incorporate one or more of the areas or drainage systems listed in Table 1. Inevitably, overlap occurs between these formulated population units and the a priori groupings of areas or drainages.

The Fraser River grouping (unit I) is necessarily limited to the upstream areas because no downstream populations were sampled. The single sample from the Babine River, tributary to the Skeena River and adjacent to drainages of the upper Fraser River, is also tentatively included in Unit I. The Babine population aggregates with those of the Fraser River in the dendrogram (cluster 5A) and the plots of PC1 and PC2. Most populations of Unit I (including the Babine) are distinguished by the presence of the *Gr-110* allele at a mean frequency of 0.05. This allele was not included in the Appendix or in most analyses because of the incomplete data sets from some coastal populations. The *Gr-(110)* allele was not observed in other populations that aggregate in the dendrogram and PC plots with those of unit I; these populations include the San Juan River (southern Vancouver Island), the spring- and summer-run fish of the Snake River, and the Klamath River.

The population unit of Georgia Strait (unit II) comprises populations forming clusters 3 and 6 in the dendrogram, plus the San Juan River population. These six populations aggregate adjacently in the plottings of PC3 and PC4. Populations of Unit II typically have relatively high allele frequencies of *Aat-3 (90)*, *Pkg-2 (90)*, and *Tapep-1 (130)*, although exceptions occur at each locus. Carl and Healey (1984) reported similar high frequencies for allelic variations of Aat-3 and Tapep in a study of chinook salmon populations of the Nanaimo River which flows from Vancouver Island into Georgia Strait.

Populations in the Puget Sound unit (Unit III), bounded to the north by the population from the South Fork of the Nooksack River, aggregate fairly clearly in both the dendrogram (clusters 8D and 8E) and the plots of PC3 and PC4. The cohesiveness among the fall-run populations vary likely reflects both genetic isolation and present (or very recent) gene flow through transfers among hatcheries. Like unit II, populations of unit III also have high allele frequencies for *Tapep-1 130*; in fact, it has the highest mean frequencies for this allele among the nine population units that were formulated. However, the mean frequencies of the common (i.e., 100) alleles for Aat-3 and Pgk-2 are much higher in unit III than in unit II. No influence of reported transfers of lower Columbia River fish to Puget Sound hatcheries (e.g., Ricker 1972) is apparent from the graphic projections or the allelic data.

An extended grouping of coastal populations (unit IV) ranges from northern California (see Utter et al. 1980) to Robertson Creek on the west coast of Vancouver Island. Populations of the Columbia, Klamath, and Sacramento Rivers are excluded from unit IV. This unit is distinguished by high frequencies of the *Gpi-2 (60)* allele and (in most instances) some Pgm variation. Most populations appear either in clusters 4 or 8B of the dendrogram and aggregate distinctly in the plottings of PC1 and PC2. Two populations are retained in Unit IV for geographic consistency which do not congregate with other populations of this unit; the spring run returning to the Soleduck River on the Washington coast, and the Lobster Creek population returning to the upper Rogue River on the Oregon coast. The outlying of the Soleduck spring-run population appears to be related to its heterogeneous origins. Records indicate that this run originated from crosses of fish from the Cowlitz River (lower Columbia River) and Umpqua River (Oregon coast) with some contribution from the spring run of the Dungeness River, a drainage entering the Strait of Juan de Fuca (C. Johnson[5]). An explanation for the outlying of the Lobster Creek population is less apparent and requires further investigation.

Two individual and four paired hatchery populations sampled from the lower Columbia River form a geographically and genetically discrete unit (unit V). This group represents the most divergent pair of clusters (1 and 2) on the dendrogram and generally aggregates distinctly in the plotting of PC1 and PC2. Populations of unit V are particularly distinguished by high allele frequencies of *Gr (85)* and *Mpi (109)*. Unit V is bounded upstream by the U.S. Fish and Wildlife Service Spring Creek Hatchery population (Spring Creek Hatchery is located on the pool impounded by Bonneville Dam). The pairing of four of the six populations is consistent with high levels of gene flow resulting from an extensive history of transplantation among the populations of the lower Columbia River (Simon 1972; Howell et al. 1985). This group's distinctness from other groups is also consistent with a minimal impact of transplantations of these populations beyond the lower Columbia River on indigenous populations in other areas (e.g., Cowlitz spring-run fish to the Snake River, C. Burley[6]; Kalama fall-run fish to Puget Sound, mentioned above).

The upper Columbia River unit (unit VI)—more than any of the other groupings—is composed of genetically diverse elements placed together more on the basis of geographic convenience rather than genetic unity. Unit VI is somewhat loosely bounded downstream by populations of the Klickitat and Deschutes Rivers; both rivers enter the Columbia River near The Dalles Dam. Unit VI's component populations include individuals of mixed ancestral origins, along with others of presumably pure lineage. Two populations known to have mixed ancestral origin are those of the U.S. Fish and Wildlife Service Carson and Leavenworth Hatcheries. The Carson Hatchery population (located on the Wind River which drains into the Bonneville pool) was derived from interceptions of spring-run fish destined for areas of the upper Columbia and Snake Rivers. The Leavenworth population (combined with Carson in the analyses) has been largely maintained by continued infusions from fish of the Carson Hatchery (Howell et al. fn. 5). The Ice Harbor population—another group of mixed ancestral origins—is composed of fall-run fish destined for different areas within the Snake River that were intercepted at Ice Harbor Dam near the mouth of the Snake

[5]C. Johnson, Washington Department of Fisheries, General Administration Bldg., Olympia, WA 98504, pers. commun. May 1985.
[6]C. Burley, U.S. Fish and Wildlife Service, 9317 Highway 99, Vancouver, WA 98665, pers. commun. May 1985.

River. This population is included in unit VI because of its geographic proximity and genetic similarity to populations of unit VI contrasted with its distinctness from spring- and summer-run populations of the upper Snake River.

Populations of purer lineage within unit VI aggregate within cluster 8 of the dendrogram. The spring-run population returning to the Lewis River lies geographically within unit V, entering the Columbia River below Bonneville Dam. This population is included in unit VI because it is genetically distinct from other downstream populations and more typical of certain spring- and fall-run fish within Unit VI (i.e., Klickitat, Deschutes, and Winthrop populations) with which it closely aggregates on the dendrogram (cluster 8C) and the plots of PC1 and PC2.

The similarity of the populations from Wells Dam and Priest Rapids Dam in unit VI is presumably a reflection of the two groups being different temporal segments of the same major run. All fish migrating past Priest Rapids Dam prior to 13 August are permitted to pass upstream and sequentially constitute the spring- and summer-runs of the upper Columbia River. The latter segment of this migration arriving at Wells Dam is captured and spawned for hatchery production. Most arrivals at Priest Rapids Dam later than 14 August are intercepted and spawned there (Chris Carlson[7]). This process inevitably results in considerable gene flow between these two artificially maintained populations.

The Snake River unit (unit VII) contains the two combined populations of McCall Hatchery-Johnson Creek and Rapid River Hatchery-Valley Creek-Sawtooth-Red River, all managed by the Idaho Department of Fish and Game; all populations are from the Salmon River drainage of central Idaho. This unit is distinguished by very low average heterozygosities (see Winans in press) and by high frequencies of the *Pgk-2 (90)* allele.

The Klamath River populations (unit VIII) are geographically isolated from, but genetically similar to those of the Snake River. However, populations of unit VIII lack variation of Idh-3,4 contrasted with a mean frequency of 0.925 for the *Idh-3,4 (100)* allele in unit VII. Klamath River populations, like those of unit VII, are characterized by very low average heterozygosities. This characteristic contrasts sharply with most adjacent coastal populations for which the highest heterozygosities among all populations are observed. Allele frequency data from the Shasta and Scott river populations, two wild populations of the Klamath River are statistically identical with frequencies in the Iron Gate Hatchery sample; these data were recently collected which precluded their use in most of the analyses of this study. Thus the low heterozygosity of Klamath River populations cannot be attributed to effects of hatchery management (see Allendorf and Ryman 1987).

The three samples from the Sacramento River drainage form a distinct geographic and genetic unit (unit IX). These samples cluster together in the dendrogram (cluster 7) and in PC1 and PC2. As mentioned above, these populations are distinguished by high frequencies of the *Gpi-1(H)* allele.

An analysis of gene diversity within and between the nine proposed population units (Table 5, column 3), provides further support for the reality of these genetic subdivisions. It is appropriate that almost two-thirds of the total gene diversity due to population structuring (7.9/12.3 = 64.2%) occurred between the population units. Furthermore, the diversity between populations within the units was smaller than the diversity between populations within areas (Table 5, column 1) calculated prior to the synthesis of the units.

Relationships and Origins of Population Units

The common genetic and geographic attributes of populations within units have been stressed, but relationships between units also require consideration. The geographic areas of the Fraser River, Georgia Strait, and Puget Sound (units I, II, and III) were completely glaciated during the late Pleistocene, and therefore must have been entirely repopulated within roughly the last 15,000 years (McPhail and Lindsey 1986). Those areas of the Columbia River sampled in this study were outside of the ice sheet, although the upper third of the drainage was glaciated. However, downstream populations (units V and VI) were doubtlessly affected by massive runoffs and temporary impoundments resulting from sudden releases of glacial Lake Missoula initially occurring some 18,000 years ago (Bunker 1982); most of the Snake River drainage (unit VII), entering the mid-Columbia River from the south, was presumably unaffected by these events above its lower reaches. The coastal region (Unit IV) from the Chehalis River (Washington) southward, and the entire Sacramento-San Joaquin River drainage (unit III), were likewise free of glaciation during the late Pleistocene.

Much of the presently observed genetic diversity almost certainly existed during the Pleistocene. The

[7]Chris Carlson, Grant County Public Utility District, P.O. Box 878, Ephrata, WA 98823, pers. commun. March 1986.

broad geographic range and high heterozygosity of the coastal populations support the long-term existence of unit IV in which cohesiveness among populations appears to have been maintained through some degree of gene flow (Soule 1976; Campton and Utter 1987). Ecological as well as geographic barriers to extensive gene flow from the coastal area apparently existed in the Columbia, Klamath, and Sacramento drainages. However, the presence of the *Gpi-2(60)* allele—typical of coastal populations—in some populations of units V, VI, VIII, and IX suggests some degree of introgression from coastal populations. Natural obstructions of the mid-Columbia River such as Cascade Falls and Celilo Falls (presently obscured by Bonneville and The Dalles Dams, respectively) may have restricted migration between populations of the lower Columbia River and those of the upper Columbia and Snake Rivers.

The relationship of the Snake River populations of unit VII to other groups within and beyond the Columbia River is unclear. Its most distinguishing feature is its very low average heterozygosity ($\bar{H}$ = 0.04), an attribute shared with the Klamath River populations ($\bar{H}$ = 0.029) (unit VIII) with which it also aggregates in the dendrogram and the principal component projections. In spite of this similarity, we favor an explanation that both Snake River and Klamath River populations had independent origins. The high frequencies of common (i.e., 100) alleles over the present sampling of loci are interpreted as reflecting loss of variation through genetic drift accentuated by periodic bottlenecks and restricted gene flow (see also Winans in press). This explanation is consistent with the inland locations of both drainages. In addition, both drainages continued to flow within their present courses during the Pleistocene. Thus, similarity is presently interpreted as an artifact based on minimal allelic variation detected over most of the loci sampled. However, drift coupled with isolation should lead to divergent frequencies of some alternate alleles with an adequate sampling of variable loci. If such differences are not observed as additional genetic marks continue to be detected in chinook salmon, then a zoogeographical explanation based on gene flow or recent ancestry must be pursued for Snake River and Klamath River populations.

Following glacial regression, the newly habitable regions appear to have been repopulated from diverse sources. Origins of the northern portions of the coastal unit can be readily explained by immigrations from more southern coastal streams. However, populations of units I, II, and III apparently arose from other sources based on their virtual absence of Gpi-2 variation. Seeding of the Fraser River from sources including the upper Columbia River and Snake River units, and of Georgia Strait and Puget Sound drainages from the lower Columbia River or Alaska, are possibilities that seem more likely. The *Aat-3 (85)* allele is recorded in most Alaskan populations studied by Gharrett et al. (1987) at frequencies up to 0.32. The highest frequencies of this allele occur in populations from Vancouver Island suggesting immigration from northern refugia.

Comparisons with Sympatric Salmonid Species

It is of interest to compare the present data set with similar information from other anadromous salmonid species within the same geographic range. These species presently share habitats and have been subjected to the same geological processes throughout their periods of common habitation. Thus, some common patterns of genetic population structuring may be anticipated. However, differences among species in life histories and long-term distributions may likewise result in unique population structures. Similar data sets have been collected from four species within this range: rainbow trout, *Salmo gairdneri*; coastal cutthroat trout, *S. clarki*; chum salmon, *O. keta*; and sockeye salmon, *O. nerka*.

Investigations of rainbow trout include both anadromous (i.e., steelhead) and nonmigratory populations (Huzyk and Tsuyuki 1974; Allendorf 1975; Allendorf and Utter 1979; Allendorf et al. 1980; Busack et al. 1980; Chilcote et al. 1980; Parkinson 1984; Wishard et al. 1984). A geographic basis for population structure is also apparent in this species and allelic similarities persist among indigenous populations of a particular region regardless of migratory tendencies, times of migration, or local environments. Apparent population units for chinook salmon and rainbow trout differ, however. A single major population unit of rainbow trout comprising the upper Fraser River, the upper Columbia River, and the Snake River contrasts with at least three distinct groupings for chinook salmon. A clear distinction between coastal streams of Washington and Oregon from those of the lower Columbia River, Puget Sound, and Georgia Strait is also not apparent in rainbow trout as it is in chinook salmon.

Distribution of sockeye salmon over the geographic range of this study is less continuous than that of chinook salmon because of the more stringent

ecological requirements of sockeye salmon during their freshwater life history. This irregular distribution is accompanied by greater geographic heterogeneity of allelic distributions, perhaps reflecting severe founder events and restricted gene flow (Utter et al. 1984). One population of sockeye salmon on the Quinault River (Washington coast) deviated strongly from all other groups sampled, but the possibility of a coastal unit of sockeye salmon, analogous to that of chinook salmon (i.e., unit IV), appears unlikely. Allele frequencies from Lake Ozette on the Washington coast (W. K. Hershberger[8]) were typical of noncoastal populations. Populations north of the Skeena River (approximately the position of "A" in Figure 1) are distinguished by the presence of Ldh-4 variation which is virtually absent from more southern groups (Utter et al. 1980; Withler 1985), presumably reflecting postglacial repopulation from a more northern refuge.

Studies of population groups of chum salmon and coastal cutthroat trout within Puget Sound and Georgia Stait suggest similar genetic structures to that observed in chinook salmon. Populations of chum salmon from south Puget Sound were distinguishable from those of north Puget Sound and Georgia Strait (Okazaki 1981). Populations of Georgia Strait and the lower Fraser River were likewise distinguishable from populations immediately north of Georgia Strait (Beacham et al. 1985). Intensive subsampling of cutthroat trout within Hood Canal and north Puget Sound indicated strong and consistent differences between these regions (Campton and Utter 1987).

More comprehensive comparisons will be possible as data accumulate on these and other species of anadromous salmonids. Both the similarities and the differences observed are of considerable interest in gaining further insights into the determinants of allele frequency variation, zoogeography, behavior, and management of these species.

Effects of Hatchery Operations

Further consideration of the effects of hatchery operations is also warranted. Hatchery operations and transplanted hatchery fish do not appear to have drastically altered the geographic distributions of protein coding alleles among the major population units. There is presently little question that hatchery operations have homogenized allele frequencies among many fall chinook hatcheries of the lower Columbia River (Simon 1972). However, the temporally isolated spring and fall populations of this region retain a greater similarity to one another than to populations of other regions. Thus it seems probable that the allele frequencies of unit V approximate those existing prior to the present century in spite of this region's large predominance of hatchery fish. Hatchery populations established from (and still reflecting) exotic origins (e.g., Carson and Leavenworth Hatcheries) have not noticeably perturbed the allelic distributions of adjacent populations having indigenous origins (Utter et al. 1987[9]). Where they exist (e.g., unit IV), indigenous wild and hatchery populations within a unit are generally separated by small genetic distances, reflected by close aggregations in the dendrogram and principal component clusters.

Infrequent alleles do not strongly affect genetic distance or heterozygosity, but their loss in hatchery stocks relative to comparable wild populations is a good indication of an inadequate number of spawning individuals used to establish or maintain a hatchery stock (Allendorf and Ryman 1987). A comparison was therefore made of the average number of alleles per locus and heterozygosity between seven hatchery and six wild samples from the Oregon coast, the most extensive collection of hatchery and wild samples within a restricted geographic range made in this study (two statistically indistinguishable combined populations each involving a hatchery and a wild sample were excluded). The mean values were very similar (heterozygosity—hatchery 0.137, wild 0.132; alleles per locus—hatchery 1.74, wild 1.68) and were not significantly different. Presumably, sufficient numbers of breeders have been used in Oregon coastal hatcheries to prevent losses of heterozygosity or alleles. However, the data provide no information concerning possible losses of genetically distinct geographic or temporal segments as a result of hatchery practices along the Oregon coast.

The present data set also pertains to additional aspects of hatchery management. Evidence continues to accumulate from numerous sources that individual populations of anadromous salmonids represent gene pools that are uniquely adapted to a particular location and spawning time (see Ricker 1972). Stocks transferred to areas beyond those to which they are locally adapted perform poorly

[8]W. K. Hershberger, Univ. of Washington, Seattle, WA 98195, pers. commun. December 1985.

[9]Utter, F., P. Aebersold, M. Griswold, G. Milner, N. Putas, J. Szeles, D. Teel, and G. Winans. 1987. Biochemical genetic variation of chinook salmon stocks of the mid-Columbia River. Processed Report 87-19, 22 p. Northwest and Alaska Fisheries Center, Seattle, WA 98112.

relative to indigenous populations (Withler 1982; Altukhov and Salmenkova 1987; Reisenbichler 1988). Transfers from maladapted populations not only waste effort and resource, but also carry the risk of disrupting locally adapted genomes through interbreedings (Reisenbichler and McIntyre 1977; Shields 1982). Sets of data such as those reported here are valuable in outlining at least the maximum distribution of locally adapted gene pools and thereby provide guidelines for stock transfers. In the absence of any other data, it would be inadvisable to translocate populations between sites such as the lower Columbia River and the Washington or Oregon coasts.

Stock transfers within major genetic units should also be performed with caution. Each of the individual or pooled populations within the nine units is also genetically distinct for some loci sampled in this study from other populations within the unit; they are therefore divergent from such populations at a much larger number of additional loci throughout the genome. It is pertinent to recall that a considerable amount of the total gene diversity results from population subdivision (4.4/12.3 = 35.8%) resided within the population units (Table 5, column 3). Likewise, slight or no divergence between two populations based on samplings of polymorphic protein-coding loci does not necessarily mean these populations are identically adapted (discussed in Utter 1981). For example, two groups of rainbow trout in the Snake River drainage having similar allele frequencies at five polymorphic loci are adapted to drastically different local environments and life history patterns (Wishard et al. 1984).

CONCLUDING OBSERVATIONS

Three points require emphasis following this initial outline of population units. First, it warrants restating that each of the nine units represents a genetically heterogeneous grouping. It is important that this heterogeneity be recognized and maintained within the respective units.

Second, these units are based on limited data within the range of sampling and, in some instances, on arbitrary decisions; the units are intended to be modified as more information accumulates and therefore to serve as guidelines for further investigation. For purposes of clarification, allelic data beyond those listed in the Appendix have been introduced at various places in the text. Additional alleles and polymorphic protein-coding loci are continually being identified through ongoing investigations, and further clarification is inevitable as these data accumulate. Genetic data other than from protein-coding loci are accumulating on chinook salmon populations within the geographic range of this study. Such genetic data show differences among populations in mitochondrial DNA (E. Bermingham[10]), and life history variables (Nicholas and Hankin 1988; Schreck et al. 1986), and provide complementary insights that will ultimately result in a much more detailed understanding of genetic structuring of these chinook salmon populations.

Third, numerous distinct population units exist in North America beyond the sampling area of this study (e.g., Gharrett et al. 1987) and nothing is known of Asiatic populations. The nine units presented here, then, are viewed as a necessary part of a much more complete picture of the genetic structure of chinook salmon that will ultimately emerge.

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APPENDIX A

Allele frequencies and average heterozygosities for 65 individual and pooled populations of naturally reproducing and hatchery stocks of chinook salmon. Hatchery stocks are identified by (\$). The map code refers to Figure 1.

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Ah					Ada-1		Aat-1,2	
		100	86	116	108	69	100	83	100	85
A1	Babine	0.986	0.014	0	0	0	0.986	0.014	1.000	0
B1	Tete Jaune	0.882	0.118	0	0	0	0.986	0.014	1.000	0
B2	Clearwater	0.786	0.214	0	0	0	0.900	0.100	1.000	0
B3	Chilco	0.922	0.078	0	0	0	0.969	0.031	1.000	0
B4	Stuart–Nechako	0.958	0.042	0	0	0	0.894	0.106	1.000	0
C1	$Big Qualicum	0.838	0.162	0	0	0	0.953	0.047	1.000	0
C2	$Puntledge	0.610	0.390	0	0	0	0.975	0.025	0.990	0.010
C3	$Quinsam	0.366	0.629	0.005	0	0	0.995	0.005	0.997	0.003
C4	$San Juan	0.820	0.160	0	0.020	0	1.000	0	0.987	0.013
C5	$Capilano	0.763	0.237	0	0	0	0.909	0.091	0.967	0.033
C6	Nooksack SF	0.780	0.220	0	0	0	0.870	0.130	0.995	0.005
C7	Nooksack NF	0.810	0.190	0	0	0	0.927	0.073	0.922	0.078
D1	$Robertson Ck.	0.806	0.194	0	0	0	1.000	0	0.981	0.019
E1	$Wells Dam	0.800	0.200	0	0	0	1.000	0	1.000	0
E2	$Carson–$Leavenworth	0.987	0.010	0.003	0	0	0.969	0.031	1.000	0
E3	$Winthrop	0.920	0.070	0.010	0	0	0.973	0.027	1.000	0
E4	$Priest Rapids	0.825	0.175	0	0	0	0.985	0.015	1.000	0
F1	$Soleduck (sum)	0.959	0.036	0.005	0	0	1.000	0	0.929	0.071
F2	$Soleduck (spr)	0.848	0.152	0	0	0	0.995	0.005	0.998	0.003
F3	$Naselle	0.908	0.092	0	0	0	0.980	0.020	0.965	0.035
F4	$Humptulips	0.920	0.080	0	0	0	1.000	0	0.975	0.025
F5	$Quinault	0.920	0.080	0	0	0	0.985	0.015	0.975	0.025
F6	Queets	0.959	0.032	0.009	0	0	0.985	0.015	0.994	0.006
F7	Hoh	0.930	0.040	0.030	0	0	1.000	0	0.994	0.006
F8	$Soleduck (f)	0.837	0.133	0.031	0	0	1.000	0	1.000	0
F9	$Elwha	0.920	0.080	0	0	0	0.980	0.020	1.000	0
G1	$Skykomish	0.860	0.135	0.005	0	0	0.865	0.135	0.980	0.020
G2	$Skagit	0.838	0.162	0	0	0	0.959	0.041	0.985	0.015
G3	$Hood Canal	0.918	0.077	0.005	0	0	0.903	0.097	0.888	0.112
G4	$Deschutes	0.842	0.158	0	0	0	0.953	0.047	0.913	0.088
G5	$Green R.–$Sammish	0.903	0.097	0	0	0	0.973	0.027	0.966	0.034
H1	$Cowlitz–$Kalama	0.845	0.149	0.006	0	0	0.975	0.025	1.000	0
H2	$Lewis R. (spr)	0.910	0.080	0	0	0.010	0.980	0.020	0.995	0.005
H3	$Cowlitz–$Kalama	0.855	0.131	0.014	0	0	0.993	0.007	1.000	0
H4	$Lewis R. (f)	0.800	0.200	0	0	0	0.980	0.020	1.000	0
H5	$Washougal R.	0.850	0.120	0.030	0	0	1.000	0	0.995	0.005
H6	$Eagle Ck.–$McKenzie R.	0.782	0.190	0.029	0	0	1.000	0	1.000	0
I1	$Klickitat R.	0.930	0.070	0	0	0	0.980	0.020	0.995	0.005
I2	$Spring Ck.–$Big Ck.	0.990	0.010	0	0	0	1.000	0	1.000	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0	0	1.000	0	0.996	0.004
I4	Deschutes	0.867	0.102	0.031	0	0	0.990	0.010	1.000	0
J1	Ice Harbor	0.874	0.111	0.003	0.013	0	0.998	0.003	1.000	0
J2	McCall–Johnson Ck.	1.000	0	0	0	0	0.953	0.047	0.981	0.019
J3	$Rapid R.–Valley Ck.	0.994	0.006	0	0	0	0.969	0.031	0.997	0.003
K1	$Cole R.–Hoot Owl Ck.	0.957	0.043	0	0	0	1.000	0	0.998	0.002
K2	$Rock Ck.	0.890	0.105	0.005	0	0	1.000	0	0.990	0.010
K3	$Cedar Ck.	0.760	0.087	0.036	0.010	0.107	1.000	0	0.987	0.013
K4	$Trask R. (spr)	0.735	0.110	0.020	0.020	0.115	1.000	0	0.978	0.023
K5	Chetco	0.890	0.110	0	0	0	0.990	0.010	0.990	0.010
K6	Lobster Ck.	0.930	0.070	0	0	0	1.000	0	0.975	0.025
K7	$Elk R.	0.800	0.185	0.015	0	0	0.950	0.050	0.950	0.050
K8	Sixes R. estu.	0.850	0.105	0.035	0.010	0	0.985	0.015	0.968	0.032
K9	Coquille R. estu.	0.883	0.113	0	0.004	0	0.965	0.035	0.949	0.051
K10	Siuslaw Bay	0.790	0.136	0.049	0.006	0.019	0.976	0.024	0.959	0.041
K11	$Salmon R.	0.737	0.076	0.152	0.035	0	1.000	0	0.990	0.010
K12	$Nestucca R.–$Alsea R.	0.811	0.064	0.113	0.001	0.012	0.969	0.031	0.976	0.024
K13	$Cedar Ck.	0.610	0.215	0.120	0	0.055	0.995	0.005	0.944	0.056
K14	$Trask R.–Tillamook Bay	0.730	0.141	0.113	0.003	0.013	0.968	0.032	0.991	0.009
K15	Nehalem estu.	0.685	0.236	0.079	0	0	0.984	0.016	0.990	0.010
L1	$Feather R.	0.720	0.240	0.040	0	0	1.000	0	1.000	0
L2	$Coleman–$Nimbus	0.815	0.173	0.007	0.005	0	1.000	0	0.992	0.008
L3	$Feather R.–$Mokelumne	0.797	0.195	0.005	0.002	0	1.000	0	0.999	0.001
M1	$Trinity R.	1.000	0	0	0	0	1.000	0	1.000	0
M2	$Iron Gate	0.995	0	0	0.005	0	1.000	0	0.997	0.003
M3	$Trinity (f)	1.000	0	0	0	0	1.000	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Aat-3		Dpep-1		Dpep-2		Gpi-1		
		100	90	100	90	100	105	100	60	H
A1	Babine	0.957	0.043	0.972	0.028	1.000	0	1.000	0	0
B1	Tete Jaune	1.000	0	0.987	0.013	1.000	0	1.000	0	0
B2	Clearwater	1.000	0	1.000	0	1.000	0	1.000	0	0
B3	Chilco	1.000	0	0.979	0.021	0.939	0.061	1.000	0	0
B4	Stuart–Nechako	1.000	0	0.963	0.037	1.000	0	1.000	0	0
C1	$Big Qualicum	0.829	0.171	0.935	0.065	1.000	0	1.000	0	0
C2	$Puntledge	0.735	0.265	0.995	0.005	1.000	0	1.000	0	0
C3	$Quinsam	0.831	0.169	0.974	0.026	1.000	0	1.000	0	0
C4	$San Juan	0.990	0.010	0.970	0.030	1.000	0	1.000	0	0
C5	$Capilano	0.803	0.197	0.985	0.015	1.000	0	1.000	0	0
C6	Nooksack SF	0.990	0.010	0.918	0.082	1.000	0	1.000	0	0
C7	Nooksack NF	1.000	0	0.980	0.020	1.000	0	1.000	0	0
D1	$Robertson Ck.	0.911	0.089	1.000	0	1.000	0	1.000	0	0
E1	$Wells Dam	1.000	0	0.980	0.020	1.000	0	0.859	0	0.141
E2	$Carson–$Leavenworth	1.000	0	0.993	0.007	1.000	0	1.000	0	0
E3	$Winthrop	1.000	0	1.000	0	1.000	0	1.000	0	0
E4	$Priest Rapids	1.000	0	0.995	0.005	1.000	0	0.824	0	0.176
F1	$Soleduck (sum)	0.995	0.005	0.745	0.255	1.000	0	1.000	0	0
F2	$Soleduck (spr)	0.995	0.005	0.970	0.030	1.000	0	1.000	0	0
F3	$Naselle	1.000	0	0.843	0.157	0.995	0.005	1.000	0	0
F4	$Humptulips	1.000	0	0.840	0.160	1.000	0	1.000	0	0
F5	$Quinault	1.000	0	0.890	0.110	1.000	0	0.995	0.005	0
F6	Queets	1.000	0	0.833	0.167	0.954	0.046	0.996	0.004	0
F7	Hoh	1.000	0	0.905	0.095	0.995	0.005	0.980	0.020	0
F8	$Soleduck (f)	1.000	0	0.740	0.260	1.000	0	1.000	0	0
F9	$Elwha	0.979	0.021	0.890	0.110	1.000	0	1.000	0	0
G1	$Skykomish	0.967	0.033	0.980	0.020	1.000	0	1.000	0	0
G2	$Skagit	1.000	0	0.925	0.075	1.000	0	1.000	0	0
G3	$Hood Canal	0.995	0.005	0.923	0.077	1.000	0	1.000	0	0
G4	$Deschutes	1.000	0	0.893	0.107	1.000	0	1.000	0	0
G5	$Green R.–$Sammish	1.000	0	0.876	0.124	1.000	0	1.000	0	0
H1	$Cowlitz–$Kalama	1.000	0	0.949	0.051	1.000	0	0.895	0	0.105
H2	$Lewis R. (spr)	1.000	0	1.000	0	1.000	0	1.000	0	0
H3	$Cowlitz–$Kalama	1.000	0	0.913	0.087	1.000	0	1.000	0	0
H4	$Lewis R. (f)	1.000	0	0.830	0.170	1.000	0	1.000	0	0
H5	$Washougal R.	1.000	0	0.850	0.150	0.990	0.010	1.000	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	1.000	0	1.000	0	0
I1	$Klickitat R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0.987	0.013	1.000	0	1.000	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0.972	0.028	1.000	0	1.000	0	0
I4	Deschutes	0.989	0.011	0.898	0.102	1.000	0	1.000	0	0
J1	Ice Harbor	0.996	0.004	0.967	0.033	1.000	0	0.842	0	0.158
J2	McCall–Johnson Ck.	1.000	0	1.000	0	1.000	0	1.000	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0.994	0.006	1.000	0	1.000	0	0
K1	$Cole R.–Hoot Owl Ck.	0.972	0.028	0.908	0.092	1.000	0	0.890	0	0.110
K2	$Rock Ck.	0.955	0.045	0.925	0.075	1.000	0	1.000	0	0
K3	$Cedar Ck.	0.995	0.005	0.652	0.348	1.000	0	1.000	0	0
K4	$Trask R. (spr)	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K5	Chetco	1.000	0	0.855	0.145	1.000	0	1.000	0	0
K6	Lobster Ck.	1.000	0	0.850	0.150	1.000	0	1.000	0	0
K7	$Elk R.	1.000	0	0.732	0.268	1.000	0	1.000	0	0
K8	Sixes R. estu.	1.000	0	0.655	0.345	1.000	0	1.000	0	0
K9	Coquille R. estu.	1.000	0	0.652	0.348	1.000	0	1.000	0	0
K10	Siuslaw Bay	1.000	0	0.701	0.299	1.000	0	1.000	0	0
K11	$Salmon R.	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0.708	0.292	1.000	0	1.000	0	0
K13	$Cedar Ck.	0.995	0.005	0.700	0.300	1.000	0	1.000	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0.704	0.296	1.000	0	1.000	0	0
K15	Nehalem estu.	0.980	0.020	0.770	0.230	1.000	0	1.000	0	0
L1	$Feather R.	1.000	0	0.890	0.110	1.000	0	0.576	0	0.424
L2	$Coleman–$Nimbus	1.000	0	0.869	0.131	1.000	0	0.705	0	0.295
L3	$Feather R.–$Mokelumne	1.000	0	0.905	0.095	1.000	0	0.689	0	0.311
M1	$Trinity R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
M2	$Iron Gate	1.000	0	0.995	0.005	1.000	0	1.000	0	0
M3	$Trinity (f)	1.000	0	1.000	0	1.000	0	1.000	0	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles						
		Gpi-2		Gpi-3			Gr	
		100	60	100	105	93	100	85
A1	Babine	1.000	0	0.917	0.083	0	0.973	0.027
B1	Tete Jaune	1.000	0	0.932	0.068	0	0.958	0.042
B2	Clearwater	1.000	0	0.989	0.011	0	0.856	0.144
B3	Chilco	1.000	0	0.875	0.125	0	0.939	0.061
B4	Stuart–Nechako	1.000	0	0.933	0.067	0	0.860	0.140
C1	$Big Qualicum	1.000	0	1.000	0	0	1.000	0
C2	$Puntledge	1.000	0	0.995	0.005	0	1.000	0
C3	$Quinsam	1.000	0	1.000	0	0	0.995	0.005
C4	$San Juan	1.000	0	1.000	0	0	0.970	0.030
C5	$Capilano	1.000	0	1.000	0	0	1.000	0
C6	Nooksack SF	1.000	0	0.880	0.120	0	0.990	0.010
C7	Nooksack NF	1.000	0	0.950	0.050	0	0.908	0.092
D1	$Robertson Ck.	0.755	0.245	1.000	0	0	1.000	0
E1	$Wells Dam	1.000	0	0.970	0.030	0	0.980	0.020
E2	$Carson–$Leavenworth	1.000	0	1.000	0	0	0.993	0.007
E3	$Winthrop	1.000	0	0.984	0.016	0	0.918	0.082
E4	$Priest Rapids	1.000	0	1.000	0	0	0.975	0.025
F1	$Soleduck (sum)	0.613	0.387	1.000	0	0	1.000	0
F2	$Soleduck (spr)	1.000	0	1.000	0	0	1.000	0
F3	$Naselle	0.788	0.212	1.000	0	0	1.000	0
F4	$Humptulips	0.755	0.245	0.970	0	0.030	0.990	0.010
F5	$Quinault	0.700	0.300	0.980	0.020	0	1.000	0
F6	Queets	0.671	0.329	0.996	0.004	0	1.000	0
F7	Hoh	0.542	0.458	0.995	0.005	0	1.000	0
F8	$Soleduck (f)	0.553	0.447	0.980	0.020	0	1.000	0
F9	$Elwha	0.684	0.316	0.975	0.025	0	0.995	0.005
G1	$Skykomish	1.000	0	0.955	0.045	0	0.995	0.005
G2	$Skagit	1.000	0	0.995	0.005	0	1.000	0
G3	$Hood Canal	1.000	0	1.000	0	0	1.000	0
G4	$Deschutes	0.916	0.084	0.990	0.010	0	1.000	0
G5	$Green R.–$Sammish	1.000	0	0.993	0.003	0.003	0.990	0.010
H1	$Cowlitz–$Kalama	1.000	0	1.000	0	0	0.822	0.179
H2	$Lewis R. (spr)	1.000	0	1.000	0	0	0.908	0.092
H3	$Cowlitz–$Kalama	0.916	0.084	1.000	0	0	0.795	0.205
H4	$Lewis R. (f)	1.000	0	1.000	0	0	0.820	0.180
H5	$Washougal R.	1.000	0	1.000	0	0	0.800	0.200
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	0	0.420	0.580
I1	$Klickitat R.	1.000	0	1.000	0	0	0.760	0.240
I2	$Spring Ck.–$Big Ck.	1.000	0	1.000	0	0	0.663	0.337
I3	$Warm Spr.–$Round Butte	1.000	0	1.000	0	0	1.000	0
I4	Deschutes	1.000	0	0.990	0	0.010	0.949	0.051
J1	Ice Harbor	0.929	0.071	1.000	0	0	1.000	0
J2	McCall–Johnson Ck.	1.000	0	1.000	0	0	1.000	0
J3	$Rapid R.–Valley Ck.	1.000	0	1.000	0	0	1.000	0
K1	$Cole R.–Hoot Owl Ck.	0.842	0.158	1.000	0	0	0.997	0.003
K2	$Rock Ck.	0.755	0.245	1.000	0	0	0.925	0.075
K3	$Cedar Ck.	0.698	0.302	1.000	0	0	1.000	0
K4	$Trask R. (spr)	0.553	0.447	1.000	0	0	0.961	0.039
K5	Chetco	0.827	0.173	1.000	0	0	1.000	0
K6	Lobster Ck.	1.000	0	1.000	0	0	0.960	0.040
K7	$Elk R.	0.520	0.480	1.000	0	0	1.000	0
K8	Sixes R. estu.	0.434	0.566	1.000	0	0	1.000	0
K9	Coquille R. estu.	0.441	0.559	0.991	0.009	0	1.000	0
K10	Siuslaw Bay	0.545	0.455	1.000	0	0	1.000	0
K11	$Salmon R.	0.682	0.318	1.000	0	0	1.000	0
K12	$Nestucca R.–$Alsea R.	0.525	0.475	0.997	0.003	0	1.000	0
K13	$Cedar Ck.	0.432	0.568	1.000	0	0	1.000	0
K14	$Trask R.–Tillamook Bay	0.435	0.565	1.000	0	0	1.000	0
K15	Nehalem estu.	0.783	0.217	1.000	0	0	1.000	0
L1	$Feather R.	1.000	0	1.000	0	0	1.000	0
L2	$Coleman–$Nimbus	0.945	0.055	1.000	0	0	1.000	0
L3	$Feather R.–$Mokelumne	0.900	0.100	1.000	0	0	1.000	0
M1	$Trinity R.	0.859	0.141	1.000	0	0	1.000	0
M2	$Iron Gate	1.000	0	1.000	0	0	0.995	0.005
M3	$Trinity (f)	1.000	0	1.000	0	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles							
		Idh-3,4				Ldh-4			
		100	127	74	142	100	112	134	71
A1	Babine	0.947	0.007	0.046	0	1.000	0	0	0
B1	*Tete Jaune*	1.000	0	0	0	1.000	0	0	0
B2	Clearwater	0.967	0.006	0.011	0.017	0.933	0	0	0.067
B3	Chilco	0.985	0.005	0.010	0	1.000	0	0	0
B4	Stuart–Nechako	0.976	0.009	0.002	0.012	1.000	0	0	0
C1	$Big Qualicum	1.000	0	0	0	1.000	0	0	0
C2	$Puntledge	0.995	0.005	0	0	1.000	0	0	0
C3	$Quinsam	1.000	0	0	0	1.000	0	0	0
C4	$San Juan	1.000	0	0	0	1.000	0	0	0
C5	$Capilano	0.970	0.013	0.018	0	1.000	0	0	0
C6	Nooksack SF	0.984	0.016	0	0	1.000	0	0	0
C7	Nooksack NF	1.000	0	0	0	1.000	0	0	0
D1	$Robertson Ck.	0.980	0.020	0	0	1.000	0	0	0
E1	$Wells Dam	0.875	0.125	0	0	1.000	0	0	0
E2	$Carson–$Leavenworth	0.862	0.002	0.136	0	0.973	0.027	0	0
E3	$Winthrop	0.965	0.010	0.025	0	0.996	0.004	0	0
E4	$Priest Rapids	0.908	0.090	0.003	0	1.000	0	0	0
F1	$Soleduck (sum)	0.874	0.111	0.003	0.013	1.000	0	0	0
F2	$Soleduck (spr)	0.958	0.037	0.005	0	1.000	0	0	0
F3	$Naselle	0.987	0.010	0	0.003	1.000	0	0	0
F4	$Humptulips	0.985	0.010	0	0.005	1.000	0	0	0
F5	$Quinault	0.903	0.090	0.003	0.005	1.000	0	0	0
F6	Queets	0.892	0.108	0	0	1.000	0	0	0
F7	Hoh	0.908	0.093	0	0	1.000	0	0	0
F8	$Soleduck (f)	0.990	0.010	0	0	1.000	0	0	0
F9	$Elwha	0.898	0.095	0.003	0.005	1.000	0	0	0
G1	$Skykomish	0.958	0.008	0	0.035	1.000	0	0	0
G2	$Skagit	0.960	0.010	0.010	0.020	1.000	0	0	0
G3	$Hood Canal	0.957	0.003	0.005	0.036	1.000	0	0	0
G4	$Deschutes	0.942	0.055	0.003	0	1.000	0	0	0
G5	$Green R.–$Sammish	0.968	0.009	0.002	0.022	1.000	0	0	0
H1	$Cowlitz–$Kalama	0.915	0.055	0.030	0	1.000	0	0	0
H2	$Lewis R. (spr)	0.925	0.005	0.070	0	0.980	0.020	0	0
H3	$Cowlitz–$Kalama	0.971	0.012	0.017	0	1.000	0	0	0
H4	$Lewis R. (f)	0.933	0.022	0.044	0	1.000	0	0	0
H5	$Washougal R.	0.955	0.015	0.030	0	1.000	0	0	0
H6	$Eagle Ck.–$McKenzie R.	0.868	0.126	0.006	0	1.000	0	0	0
I1	$Klickitat R.	0.900	0.070	0.030	0	1.000	0	0	0
I2	$Spring Ck.–$Big Ck.	0.990	0.008	0.002	0	1.000	0	0	0
I3	$Warm Spr.–$Round Butte	0.865	0	0.135	0	1.000	0	0	0
I4	Deschutes	0.969	0.031	0	0	1.000	0	0	0
J1	Ice Harbor	0.977	0.023	0	0	1.000	0	0	0
J2	McCall–Johnson Ck.	0.913	0	0.087	0	1.000	0	0	0
J3	$Rapid R.–Valley Ck.	0.937	0.006	0.057	0	0.972	0.028	0	0
K1	$Cole R.–Hoot Owl Ck.	0.962	0.038	0	0	0.994	0.003	0.003	0
K2	$Rock Ck.	0.977	0.023	0	0	1.000	0	0	0
K3	$Cedar Ck.	0.995	0.003	0.003	0	1.000	0	0	0
K4	$Trask R. (spr)	0.995	0.005	0	0	1.000	0	0	0
K5	Chetco	0.985	0.015	0	0	1.000	0	0	0
K6	Lobster Ck.	0.978	0.022	0	0	0.940	0	0.060	0
K7	$Elk R.	0.973	0.027	0	0	0.990	0	0	0.010
K8	Sixes R. estu.	0.972	0.028	0	0	0.970	0.005	0.010	0.015
K9	Coquille R. estu.	1.000	0	0	0	0.961	0	0.003	0.009
K10	Siuslaw Bay	0.994	0.003	0.003	0	1.000	0	0	0
K11	$Salmon R.	0.975	0.025	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.981	0.016	0.001	0.001	0.999	0	0	0.001
K13	$Cedar Ck.	0.947	0.053	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	0.963	0.037	0	0	1.000	0	0	0
K15	Nehalem estu.	0.947	0.053	0	0	1.000	0	0	0
L1	$Feather R.	0.940	0.060	0	0	1.000	0	0	0
L2	$Coleman–$Nimbus	0.950	0.050	0	0	1.000	0	0	0
L3	$Feather R.–$Mokelumne	0.945	0.055	0	0	1.000	0	0	0
M1	$Trinity R.	1.000	0	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	0	1.000	0	0	0
M3	$Trinity (f)	1.000	0	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles									
		Ldh-5			Mdh-1,2			Mdh-3,4			
		100	90	70	100	120	27	100	121	70	83
A1	Babine	1.000	0	0	1.000	0	0	1.000	0	0	0
B1	Tete Jaune	1.000	0	0	1.000	0	0	1.000	0	0	0
B2	Clearwater	1.000	0	0	1.000	0	0	0.989	0.006	0.006	0
B3	Chilco	1.000	0	0	1.000	0	0	0.990	0	0.010	0
B4	Stuart–Nechako	1.000	0	0	1.000	0	0	0.936	0	0.064	0
C1	$Big Qualicum	1.000	0	0	1.000	0	0	1.000	0	0	0
C2	$Puntledge	1.000	0	0	1.000	0	0	0.948	0.037	0.015	0
C3	$Quinsam	0.966	0.034	0	1.000	0	0	0.843	0.103	0.054	0
C4	$San Juan	1.000	0	0	1.000	0	0	0.990	0.010	0	0
C5	$Capilano	0.995	0.005	0	1.000	0	0	1.000	0	0	0
C6	Nooksack SF	1.000	0	0	1.000	0	0	0.965	0.030	0.005	0
C7	Nooksack NF	1.000	0	0	1.000	0	0	0.965	0	0.035	0
D1	$Robertson Ck.	1.000	0	0	1.000	0	0	0.993	0.008	0	0
E1	$Wells Dam	0.980	0.020	0	1.000	0	0	0.970	0.010	0.020	0
E2	$Carson–$Leavenworth	1.000	0	0	1.000	0	0	0.978	0.022	0	0
E3	$Winthrop	1.000	0	0	1.000	0	0	0.990	0.010	0	0
E4	$Priest Rapids	0.964	0.015	0.020	1.000	0	0	0.955	0.030	0.015	0
F1	$Soleduck (sum)	1.000	0	0	1.000	0	0	0.963	0.003	0.035	0
F2	$Soleduck (spr)	1.000	0	0	1.000	0	0	0.975	0.015	0.010	0
F3	$Naselle	1.000	0	0	1.000	0	0	0.944	0.040	0.015	0
F4	$Humptulips	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F5	$Quinault	1.000	0	0	1.000	0	0	0.988	0.013	0	0
F6	Queets	1.000	0	0	1.000	0	0	0.963	0.037	0	0
F7	Hoh	1.000	0	0	1.000	0	0	0.993	0.003	0.003	0.003
F8	$Soleduck (f)	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F9	$Elwha	1.000	0	0	1.000	0	0	0.968	0.015	0.017	0
G1	$Skykomish	0.980	0.020	0	1.000	0	0	0.990	0	0.010	0
G2	$Skagit	0.990	0.010	0	1.000	0	0	0.993	0	0.008	0
G3	$Hood Canal	1.000	0	0	1.000	0	0	0.967	0	0.033	0
G4	$Deschutes	1.000	0	0	1.000	0	0	0.992	0	0.008	0
G5	$Green R.–$Sammish	0.990	0.010	0	1.000	0	0	0.991	0.003	0.005	0
H1	$Cowlitz–$Kalama	1.000	0	0	1.000	0	0	0.988	0.013	0	0
H2	$Lewis R. (spr)	0.990	0.010	0	1.000	0	0	0.965	0.035	0	0
H3	$Cowlitz–$Kalama	0.997	0.003	0	1.000	0	0	0.983	0.017	0	0
H4	$Lewis R. (f)	1.000	0	0	1.000	0	0	1.000	0	0	0
H5	$Washougal R.	1.000	0	0	1.000	0	0	0.990	0.010	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	0	1.000	0	0	0.963	0.037	0	0
I1	$Klickitat R.	1.000	0	0	1.000	0	0	0.970	0.030	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0.995	0.005	0	1.000	0	0	0
I4	Deschutes	1.000	0	0	1.000	0	0	0.985	0.010	0.005	0
J1	Ice Harbor	0.995	0.003	0.003	1.000	0	0	0.985	0.005	0.010	0
J2	McCall–Johnson Ck.	0.976	0.024	0	1.000	0	0	0.998	0.002	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0	1.000	0	0	0.995	0.005	0	0
K1	$Cole R.–Hoot Owl Ck.	0.988	0.012	0	0.989	0	0.011	0.992	0.008	0	0
K2	$Rock Ck.	1.000	0	0	1.000	0	0	0.968	0.030	0.003	0
K3	$Cedar Ck.	0.975	0.025	0	1.000	0	0	0.995	0.005	0	0
K4	$Trask R. (spr)	0.985	0.015	0	1.000	0	0	0.990	0.010	0	0
K5	Chetco	1.000	0	0	0.998	0.003	0	0.955	0.045	0	0
K6	Lobster Ck.	1.000	0	0	1.000	0	0	0.975	0.025	0	0
K7	$Elk R.	1.000	0	0	0.998	0	0.003	0.983	0.017	0	0
K8	Sixes R. estu.	1.000	0	0	0.945	0.027	0.027	0.993	0.008	0	0
K9	Coquille R. estu.	0.996	0.004	0	0.987	0.011	0.002	0.996	0.004	0	0
K10	Siuslaw Bay	0.982	0.018	0	0.997	0.003	0	0.982	0.018	0	0
K11	$Salmon R.	1.000	0	0	1.000	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0	0.999	0.001	0	1.000	0	0	0
K13	$Cedar Ck.	1.000	0	0	1.000	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0	0.999	0.001	0	0.985	0.015	0	0
K15	Nehalem estu.	1.000	0	0	1.000	0	0	1.000	0	0	0
L1	$Feather R.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
L2	$Coleman–$Nimbus	1.000	0	0	1.000	0	0	0.968	0.032	0	0
L3	$Feather R.–$Mokelumne	1.000	0	0	1.000	0	0	0.977	0.023	0	0
M1	$Trinity R.	1.000	0	0	1.000	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	1.000	0	0	0.997	0.003	0	0
M3	$Trinity (f)	1.000	0	0	1.000	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles								
		Mpi				Pgm-1,2			Pgk-2	
		100	109	95	113	−100	−70	−84	100	90
A1	Babine	0.730	0.270	0	0	1.000	0	0	0.095	0.905
B1	Tete Jaune	0.689	0.311	0	0	1.000	0	0	0.421	0.579
B2	Clearwater	0.535	0.465	0	0	1.000	0	0	0.178	0.822
B3	Chilco	0.633	0.367	0	0	1.000	0	0	0.194	0.806
B4	Stuart–Nechako	0.592	0.408	0	0	1.000	0	0	0.383	0.617
C1	$Big Qualicum	0.400	0.600	0	0	1.000	0	0	0.292	0.708
C2	$Puntledge	0.690	0.310	0	0	0.980	0.020	0	0.229	0.771
C3	$Quinsam	0.887	0.113	0	0	0.997	0.002	0	0.151	0.849
C4	$San Juan	0.540	0.460	0	0	0.995	0.005	0	0.180	0.820
C5	$Capilano	0.444	0.556	0	0	1.000	0	0	0.479	0.521
C6	Nooksack SF	0.729	0.271	0	0	1.000	0	0	0.521	0.479
C7	Nooksack NF	0.480	0.520	0	0	1.000	0	0	0.277	0.723
D1	$Robertson Ck.	0.595	0.405	0	0	0.997	0.002	0	0.307	0.693
E1	$Wells Dam	0.670	0.330	0	0	1.000	0	0	0.590	0.410
E2	$Carson–$Leavenworth	0.867	0.133	0	0	1.000	0	0	0.105	0.895
E3	$Winthrop	0.702	0.298	0	0	1.000	0	0	0.505	0.495
E4	$Priest Rapids	0.705	0.295	0	0	1.000	0	0	0.643	0.357
F1	$Soleduck (sum)	0.652	0.338	0.010	0	1.000	0	0	0.345	0.655
F2	$Soleduck (spr)	0.630	0.365	0.005	0	1.000	0	0	0.490	0.510
F3	$Naselle	0.709	0.250	0.005	0.036	0.982	0.012	0.005	0.638	0.362
F4	$Humptulips	0.806	0.194	0	0	0.950	0.045	0.005	0.600	0.400
F5	$Quinault	0.613	0.325	0	0.062	0.970	0.023	0.008	0.575	0.425
F6	Queets	0.713	0.279	0	0.008	0.974	0.025	0	0.333	0.667
F7	Hoh	0.610	0.390	0	0	0.947	0.042	0.011	0.484	0.516
F8	$Soleduck (f)	0.810	0.190	0	0	1.000	0	0	0.365	0.635
F9	$Elwha	0.675	0.290	0.035	0	0.985	0.015	0	0.399	0.601
G1	$Skykomish	0.695	0.305	0	0	1.000	0	0	0.495	0.505
G2	$Skagit	0.768	0.232	0	0	1.000	0	0	0.559	0.441
G3	$Hood Canal	0.608	0.392	0	0	1.000	0	0	0.689	0.311
G4	$Deschutes	0.673	0.317	0.010	0	1.000	0	0	0.649	0.351
G5	$Green R.–$Sammish	0.720	0.280	0	0	1.000	0	0	0.663	0.337
H1	$Cowlitz–$Kalama	0.460	0.515	0.025	0	1.000	0	0	0.722	0.278
H2	$Lewis R. (spr)	0.700	0.280	0.020	0	1.000	0	0	0.378	0.622
H3	$Cowlitz–$Kalama	0.467	0.497	0.037	0	0.995	0.005	0	0.810	0.190
H4	$Lewis R. (f)	0.380	0.490	0.130	0	0.990	0.005	0.005	0.816	0.184
H5	$Washougal R.	0.450	0.550	0	0	1.000	0	0	0.750	0.250
H6	$Eagle Ck.–$McKenzie R.	0.458	0.542	0	0	1.000	0	0	0.931	0.069
I1	$Klickitat R.	0.730	0.260	0.010	0	1.000	0	0	0.570	0.430
I2	$Spring Ck.–$Big Ck.	0.596	0.356	0.048	0	1.000	0	0	0.863	0.137
I3	$Warm Spr.–$Round Butte	0.871	0.129	0	0	1.000	0	0	0.356	0.644
I4	Deschutes	0.704	0.296	0	0	1.000	0	0	0.633	0.367
J1	Ice Harbor	0.793	0.207	0	0	1.000	0	0	0.548	0.452
J2	McCall–Johnson Ck.	0.953	0.047	0	0	1.000	0	0	0.062	0.938
J3	$Rapid R.–Valley Ck.	0.910	0.090	0	0	1.000	0	0	0.139	0.861
K1	$Cole R.–Hoot Owl Ck.	0.868	0.132	0	0	0.992	0.008	0	0.470	0.531
K2	$Rock Ck.	0.740	0.260	0	0	1.000	0	0	0.485	0.515
K3	$Cedar Ck.	0.717	0.283	0	0	0.992	0.008	0	0.378	0.622
K4	$Trask R. (spr)	0.710	0.290	0	0	0.962	0.038	0	0.449	0.551
K5	Chetco	0.790	0.210	0	0	0.980	0.020	0	0.388	0.612
K6	Lobster Ck.	0.550	0.450	0	0	1.000	0	0	0.223	0.777
K7	$Elk R.	0.773	0.227	0	0	0.972	0.023	0.005	0.457	0.543
K8	Sixes R. estu.	0.725	0.275	0	0	0.938	0.040	0.023	0.480	0.520
K9	Coquille R. estu.	0.591	0.409	0	0	0.915	0.050	0.035	0.412	0.588
K10	Siuslaw Bay	0.605	0.395	0	0	0.924	0.073	0.003	0.524	0.476
K11	$Salmon R.	0.677	0.323	0	0	0.920	0.067	0.013	0.279	0.721
K12	$Nestucca R.–$Alsea R.	0.639	0.361	0	0	0.944	0.054	0.002	0.466	0.534
K13	$Cedar Ck.	0.735	0.265	0	0	0.903	0.097	0	0.551	0.449
K14	$Trask R.–Tillamook Bay	0.652	0.346	0	0.003	0.918	0.079	0.003	0.432	0.568
K15	Nehalem estu.	0.780	0.220	0	0	0.918	0.067	0.015	0.438	0.563
L1	$Feather R.	0.510	0.490	0	0	1.000	0	0	0.540	0.460
L2	$Coleman–$Nimbus	0.586	0.414	0	0	0.991	0.009	0	0.592	0.408
L3	$Feather R.–$Mokelumne	0.487	0.513	0	0	0.988	0.011	0	0.651	0.349
M1	$Trinity R.	0.980	0.020	0	0	0.985	0.015	0	0.290	0.710
M2	$Iron Gate	0.975	0.025	0	0	0.942	0.058	0	0.146	0.854
M3	$Trinity (f)	0.990	0.010	0	0	0.997	0.002	0	0.350	0.650

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles						
		Sod-1				Tapep-1		
		−100	−260	580	1260	100	130	45
A1	Babine	0.936	0.064	0	0	0.921	0.079	0
B1	Tete Jaune	0.931	0.056	0.014	0	1.000	0	0
B2	Clearwater	0.933	0.067	0	0	0.967	0.033	0
B3	Chilco	0.888	0.112	0	0	1.000	0	0
B4	Stuart–Nechako	0.865	0.135	0	0	0.991	0.009	0
C1	$Big Qualicum	0.794	0.206	0	0	0.565	0.435	0
C2	$Puntledge	0.931	0.053	0.016	0	0.803	0.197	0
C3	$Quinsam	0.892	0.098	0.010	0	0.839	0.161	0
C4	$San Juan	0.800	0.190	0.010	0	0.890	0.110	0
C5	$Capilano	0.778	0.157	0.066	0	0.617	0.383	0
C6	Nooksack SF	0.660	0.220	0.120	0	0.653	0.347	0
C7	Nooksack NF	0.570	0.340	0.090	0	0.620	0.380	0
D1	$Robertson Ck.	0.805	0.195	0	0	0.855	0.145	0
E1	$Wells Dam	0.540	0.460	0	0	0.640	0.360	0
E2	$Carson–$Leavenworth	0.821	0.179	0	0	0.872	0.128	0
E3	$Winthrop	0.736	0.264	0	0	0.992	0.008	0
E4	$Priest Rapids	0.550	0.450	0	0	0.793	0.207	0
F1	$Soleduck (sum)	0.725	0.260	0.015	0	0.712	0.288	0
F2	$Soleduck (spr)	0.621	0.379	0	0	0.755	0.245	0
F3	$Naselle	0.684	0.316	0	0	0.854	0.146	0
F4	$Humptulips	0.670	0.290	0.040	0	0.840	0.160	0
F5	$Quinault	0.784	0.206	0.010	0	0.899	0.101	0
F6	Queets	0.875	0.117	0.008	0	0.944	0.056	0
F7	Hoh	0.905	0.095	0	0	0.935	0.065	0
F8	$Soleduck (f)	0.796	0.204	0	0	0.970	0.030	0
F9	$Elwha	0.640	0.290	0.070	0	0.875	0.125	0
G1	$Skykomish	0.565	0.425	0.010	0	0.690	0.310	0
G2	$Skagit	0.707	0.283	0.010	0	0.495	0.505	0
G3	$Hood Canal	0.624	0.366	0.010	0	0.561	0.439	0
G4	$Deschutes	0.627	0.317	0.056	0	0.507	0.493	0
G5	$Green R.–$Sammish	0.625	0.365	0.010	0	0.483	0.517	0
H1	$Cowlitz–$Kalama	0.679	0.321	0	0	0.930	0.070	0
H2	$Lewis R. (spr)	0.620	0.380	0	0	0.875	0.125	0
H3	$Cowlitz–$Kalama	0.615	0.385	0	0	0.923	0.077	0
H4	$Lewis R. (f)	0.571	0.429	0	0	0.880	0.120	0
H5	$Washougal R.	0.560	0.440	0	0	0.780	0.220	0
H6	$Eagle Ck.–$McKenzie R.	0.782	0.213	0.006	0	0.925	0.075	0
I1	$Klickitat R.	0.690	0.310	0	0	0.950	0.050	0
I2	$Spring Ck.–$Big Ck.	0.530	0.470	0	0	0.777	0.223	0
I3	$Warm Spr.–$Round Butte	0.550	0.450	0	0	0.967	0.033	0
I4	Deschutes	0.735	0.265	0	0	0.939	0.061	0
J1	Ice Harbor	0.705	0.295	0	0	0.918	0.082	0
J2	McCall–Johnson Ck.	0.976	0.024	0	0	0.962	0.038	0
J3	$Rapid R.–Valley Ck.	0.944	0.056	0	0	0.886	0.114	0
K1	$Cole R.–Hoot Owl Ck.	0.776	0.221	0.003	0	0.937	0.063	0
K2	$Rock Ck.	0.665	0.330	0.005	0	0.825	0.175	0
K3	$Cedar Ck.	0.828	0.172	0	0	0.914	0.086	0
K4	$Trask R. (spr)	0.890	0.110	0	0	0.800	0.200	0
K5	Chetco	0.800	0.200	0	0	0.840	0.160	0
K6	Lobster Ck.	0.590	0.410	0	0	0.938	0.063	0
K7	$Elk R.	0.655	0.345	0	0	0.920	0.080	0
K8	Sixes R. estu.	0.780	0.220	0	0	0.900	0.100	0
K9	Coquille R. estu.	0.787	0.213	0	0	0.920	0.080	0
K10	Siuslaw Bay	0.841	0.152	0.006	0	0.866	0.134	0
K11	$Salmon R.	0.742	0.258	0	0	0.783	0.217	0
K12	$Nestucca R.–$Alsea R.	0.819	0.181	0	0	0.905	0.095	0
K13	$Cedar Ck.	0.840	0.160	0	0	0.915	0.085	0
K14	$Trask R.–Tillamook Bay	0.895	0.105	0	0	0.881	0.119	0
K15	Nehalem estu.	0.819	0.181	0	0	0.772	0.228	0
L1	$Feather R.	0.620	0.380	0	0	0.950	0.050	0
L2	$Coleman–$Nimbus	0.728	0.267	0.005	0	0.842	0.156	0.002
L3	$Feather R.–$Mokelumne	0.749	0.251	0	0	0.889	0.111	0
M1	$Trinity R.	0.980	0.020	0	0	1.000	0	0
M2	$Iron Gate	0.990	0.010	0	0	0.949	0.051	0
M3	$Trinity (f)	0.895	0.050	0.035	0.020	1.000	0	0

APPENDIX A.—*Continued.*

Map code	Population	Heterozygosity	Dendrogram cluster	Population unit
A1	Babine	0.057	5A	1
B1	Tete Jaune	0.061	5A	1
B2	Clearwater	0.082	5A	1
B3	Chilco	0.071	5A	1
B4	Stuart–Nechako	0.090	5A	1
C1	$Big Qualicum	0.099	6	2
C2	$Puntledge	0.101	3	2
C3	$Quinsam	0.095	3	2
C4	$San Juan	0.074	5A	2
C5	$Capilano	0.118	6	2
C6	Nooksack SF	0.122	8E	3
C7	Nooksack NF	0.124	6	2
D1	$Robertson Ck.	0.105	4	4
E1	$Wells Dam	0.127	8E	6
E2	$Carson–$Leavenworth	0.067	5B	6
E3	$Winthrop	0.076	8C	6
E4	$Priest Rapids	0.118	8E	6
F1	$Soleduck (sum)	0.141	4	4
F2	$Soleduck (spr)	0.097	8E	4
F3	$Naselle	0.114	8B	4
F4	$Humptulips	0.112	8B	4
F5	$Quinault	0.119	4	4
F6	Queets	0.111	4	4
F7	Hoh	0.109	4	4
F8	$Soleduck (f)	0.098	4	4
F9	$Elwha	0.125	8B	4
G1	$Skykomish	0.114	8E	3
G2	$Skagit	0.101	8D	3
G3	$Hood Canal	0.122	8D	3
G4	$Deschutes	0.128	8D	3
G5	$Green R.–$Sammish	0.105	8D	3
H1	$Cowlitz–$Kalama	0.110	2	5
H2	$Lewis R. (spr)	0.113	8C	6
H3	$Cowlitz–$Kalama	0.103	2	5
H4	$Lewis R. (f)	0.113	2	5
H5	$Washougal R.	0.112	2	5
H6	$Eagle Ck.–$McKenzie R.	0.102	1	5
I1	$Klickitat R.	0.099	8C	6
I2	$Spring Ck.–$Big Ck.	0.093	2	5
I3	$Warm Spr.–$Round Butte	0.072	8A	6
I4	Deschutes	0.086	8C	6
J1	Ice Harbor	0.090	8B	6
J2	McCall–Johnson Ck.	0.035	5B	7
J3	$Rapid R.–Valley Ck.	0.045	5B	7
K1	$Cole R.–Hoot Owl Ck.	0.090	8B	4
K2	$Rock Ck.	0.112	8B	4
K3	$Cedar Ck.	0.111	4	4
K4	$Trask R. (spr)	0.124	4	4
K5	Chetco	0.100	8B	4
K6	Lobster Ck.	0.092	5A	4
K7	$Elk R.	0.130	4	4
K8	Sixes R. estu.	0.137	4	4
K9	Coquille R. estu.	0.134	4	4
K10	Siuslaw Bay	0.135	4	4
K11	$Salmon R.	0.128	4	4
K12	$Nestucca R.–$Alsea R.	0.125	4	4
K13	$Cedar Ck.	0.143	4	4
K14	$Trask R.–Tillamook Bay	0.132	4	4
K15	Nehalem estu.	0.131	4	4
L1	$Feather R.	0.124	7	9
L2	$Coleman–$Nimbus	0.123	7	9
L3	$Feather R.–$Mokelumne	0.119	7	9
M1	$Trinity R.	0.032	5B	8
M2	$Iron Gate	0.027	5B	8
M3	$Trinity (f)	0.027	5B	8

APPENDIX B

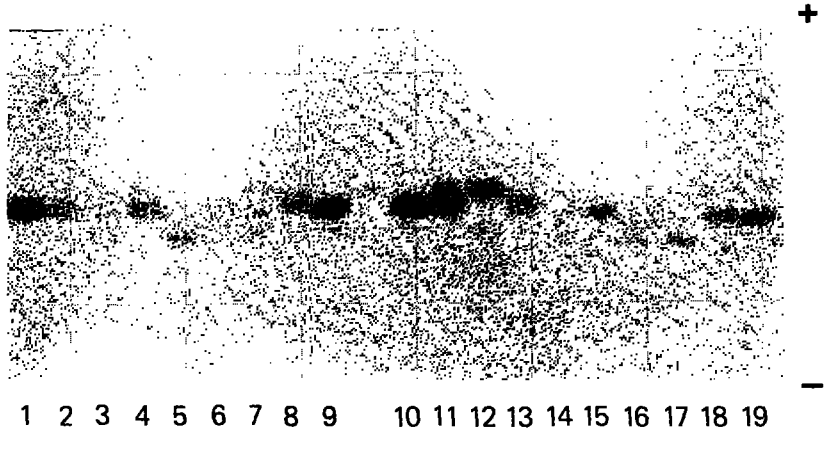
Previously Unreported Genetic Variants

Glutathione reductase (Gr) was the more readily interpreted of the two previously undescribed polymorphic enzymes observed for chinook salmon in this study. The phenotypic forms (App. Fig. 1) were those expected from a dimeric enzyme with three alleles and were consistent with known allelic variants of Gr observed in other vertebrates (e.g., man) (Harris and Hopkinson 1976). The assumption that this variation was a three-allele polymorphism was supported by the conformance of phenotypic ratios to those expected under Hardy-Weinberg equilibrium, the absolute repeatability of expression from independent extractions, and the parallel expression of different tissues (eye and skeletal muscle) from individuals expressing a given phenotype.

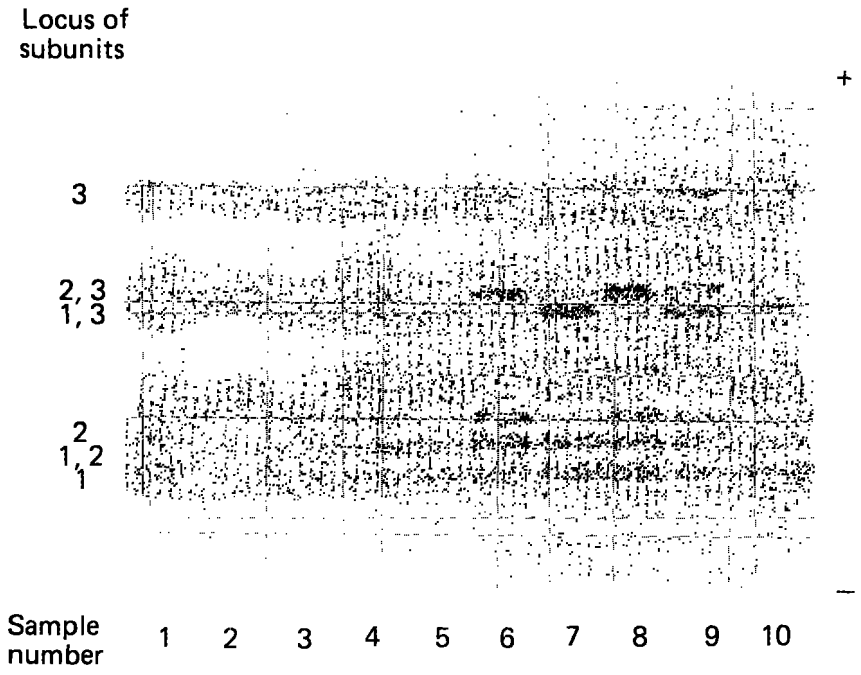
The previously undescribed glucose-6-phosphate isomerase (Gpi) variation was less readily explained. Individuals homozygous for the common alleles at each of the three Gpi loci express a six-banded phenotype that is directly interpreted as having three homodimeric and three heterodimeric bands (App. Fig. 2). An extension of this interpretation also explains additional numbers of bands which arise from allelic forms having different mobilities, or fewer bands resulting from either allelic forms of different loci having common mobilities or from null alleles. However, none of these explanations adequately describe the five-banded Gpi phenotypes that have been found with regularity in some collections.

One explanation that is consistent with the observed phenotypes is that the subunits encoded by a locus aggregate randomly, but that the aggregations for some interlocus combinations are precluded. Such inhibited combinations are common among duplicated loci of salmonids. For instance, subunits of Ldh-3 and Ldh-5 randomly aggregate, as do those of Ldh-3 and Ldh-4; however, Ldh-4 and Ldh-5 subunits do not aggregate (Wright et al. 1975). Mutations precluding aggregation (but not necessarily affecting electrophoretic mobility) must have arisen at some time between the duplication event and the present, and such mutations must have been polymorphic between their arising and their fixation (see Allendorf and Thorgaard 1984, for a review of gene duplication in salmonids).

The above model was tested when gametes and tissues were obtained from individuals of the Priest Rapids stock where five-banded Gpi phenotypes were commonly observed. Because of difficulty in unambiguously discerning common and presumed heterozygous phenotypes, the only informative crosses were those involving the single parent having a five-banded phenotype. The phenotypic ratios of the two matings involving this individual (App. Table 1) conform to those expected from a Men-



APPENDIX FIGURE 1.—Glutathione reductase phenotypes of chinook salmon from eye fluid extracts. Genotypes include 100/100 (samples 1, 2, 4, 9, 10, 15, 18, 19), 100/85 (samples 3, 6, 14, 16), 85/85 (samples 5, 17), 85/110 (sample 7), 110/100 (samples 8, 11, 13), 110/110 (sample 12).



APPENDIX FIGURE 2.—*Gpi-1(H)* variation in chinook salmon from extracts of skeletal muscle. Samples 2, 6, and 8 are H/H homozygotes. Genotypes of other samples are unknown for the *Gpi-1(H)* allele.

APPENDIX TABLE 1.—Observed and (in parentheses) expected numbers of chinook salmon progeny from parents of known Gpi-1 phenotype assuming Mendelian inheritance of subunits having differential heterodimer forming capabilities. Phenotypic designations are based on Figure 3.

Parental		Observed and (in parentheses) expected number of progeny for genotypes	
Phenotype male	Genotype female	100/100 or 100/H	H/H
H/H	?	41	46
	H/100	(43.5)	(43.5)
	100/100	(87)	(0)
H/H	?	139	0
	100/100	(139.0)	(0)
	H/100	(69.5)	(69.5)

delian variant affecting heterodimer formation between Gpi-1 and Gpi-3 subunits. We therefore conclude that individuals with such five-banded phenotypes are homozygous for an allele at the Gpi-1 or Gpi-3 loci that affects dimer formation between subunits of these loci. The present data give no information regarding which locus encodes the mutant subunit. However, the polymorphism has been recorded and analyzed as a third allele at the Gpi-1 locus [*Gpi-1(H)*] because of the low frequency of mobility variants at this locus, none of which occurred in populations where the allele affecting heteromeric combinations was observed. The correct locus could probably be identified through induced gynogenesis of eggs from females heterozygous for mobility variants at Gpi-1 and Gpi-3, and *Gpi-1(H)* heterozygotes. The gene-centromere distance for *Gpi-1(H)* would match that of the mobility variant of the appropriate locus assuming that gene-centromere distances differ for the loci encoding the mobility variants (e.g., see Thorgaard et al. 1983).

Because of the difficulty in distinguishing the common and the *Gpi-1(H)* heterozygous phenotypes the recorded allele frequencies are based on the square root of the *Gpi-1(H)* homozygous (i.e., five-banded) phenotypes under the assumption that the samples where these phenotypes are observed are in Hardy-Weinberg equilibrium. This assumption is supported by the preponderance of genotypic frequencies in Hardy-Weinberg equilibrium at other polymorphic loci. This restriction results in an inevitable underestimation of the frequency of this allele when its frequency is too low for homozygous expression at reasonable sample sizes.