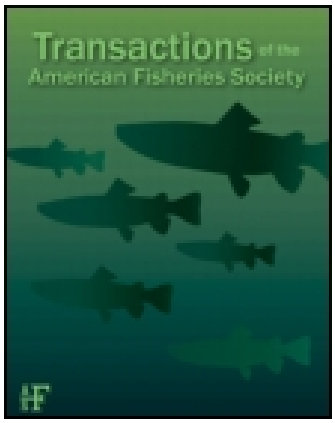

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Genetic Population Structure and Origin of Life History Types in Chinook Salmon in British Columbia, Canada

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Abstract.—We used protein electrophoresis to examine genetic population structure and origin of life history types of chinook salmon *Oncorhynchus tshawytscha* in British Columbia, Canada. Among 31 allozyme loci resolved in 91 samples from 63 populations of chinook salmon in rivers and hatcheries throughout British Columbia, population heterozygosities averaged 0.084 (range 0.048–0.108) and were typical of values for populations in other regions. A hierarchical gene diversity analysis indicated that 91.3% of the total allele-frequency diversity was attributable to within-population variability; the remaining 8.7% was attributable to geographic variability among populations, which was partitioned into among-river (3.3%), among-area (3.5%), and among-region (1.9%) components. Two major groups of populations appeared in the principal components analysis and in cluster analysis of genetic distances. A coastal group included populations in four subgroups: Central coast, Georgia Strait, lower Fraser River, and west Vancouver Island. An inland group included six subgroups: Nass River, Skeena River, north Thompson River, upper and mid-Fraser River, south Thompson River, and lower Thompson River. The geographic extents of the inland and coastal groups largely coincided with the geographic distributions of stream- and ocean-type juvenile forms and may reflect postglacial colonization by two ancestral lineages that survived in Pleistocene refugia. The presence of genetically undifferentiated stream-type fish in coastal streams populated by ocean-type fish may reflect either postglacial life history differentiation from ancestral ocean-type fish or life history flexibility of ocean-type fish.

Genetic studies of chinook salmon *Oncorhynchus tshawytscha* in British Columbia have been of particular interest to evolutionary biologists, because the diversity of life history patterns in this region provides an opportunity for understanding the origin of within-species variability. Various life history forms of chinook salmon spawn in about 260 rivers that are scattered throughout the province at locations ranging from just above the tidal limit to nearly 1,000 km inland (Aro and Shepard 1967). These forms are characterized by differences in the timing of juvenile outmigration from freshwater, in ocean distribution of maturing fish, in the timing of adult return to freshwater, in spawning timing, and in the geographic distributions of spawning populations (Fraser et al. 1982; Healey 1991). One of these traits, adult return timing, has been used to classify populations as management units, particularly in Washington, Oregon, Idaho, and California (e.g., WDF et al. 1993) and to interpret the results of genetic studies (e.g., Utter et al. 1989; Nielsen et al. 1994; Banks et al. 1996). Although adult run timing and other variables may provide useful categories for management, analyses of these variables may not provide sufficient information to understand the evolution of major lineages within chinook salmon.

Some authors have postulated that the length of juvenile freshwater residence, along with ocean distribution, and the geography of spawning populations delineate two evolutionary lineages or races along the west coast of North America, lineages that arose as a consequence of geographic isolation during Pleistocene glaciation (e.g., Healey 1991). An ocean-type lineage, consisting of fish that migrate to estuaries in their first year, contrasts with a stream-type lineage of fish that resides in freshwater for at least 1 year before migrating to marine waters. An extended estuarine residence is associated with ocean-type juveniles, and long-distance ocean migrations are associated with stream-type juveniles. The delineation between life history types, however, is not always clear. Individuals in some populations, particularly those in coastal areas, can show ocean- or stream-type life history traits (Healey 1991), which suggests mixing between evolutionary lineages, or phenotypic plasticity. Inheritance studies have shown that in at least some populations, early and late juvenile migration timings and other traits associated with ocean- and stream-type fish have a ge-

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netic as well as an environmental basis (Taylor 1988; Clarke et al. 1992, 1994).

Life history variability within a species may reflect adaptive convergence in similar habitats in different drainages. Taylor (1988, 1990b) has suggested that much of the life history variability in chinook salmon has resulted from adaptation to local environments. In a study of genetic variability in Alaskan and southern populations of chinook salmon, Gharrett et al. (1987) suggested that divergence in the timing of juvenile outmigration appeared to reflect natural selection after postglacial colonization, at least for populations in southeastern Alaska. However, in a study of chinook salmon in the Columbia River Basin, Waples et al. (1991) found that genetic relationships were concordant with juvenile migration timing and that significant genetic subdivision occurred within these two major life history groups.

In the present study, we surveyed allozyme variation in 63 river and hatchery populations of chinook salmon in British Columbia from 1981 to 1991. These genetic data have been used in previous studies to estimate the contributions of genetically distinct population groups to numerous commercial and recreational marine fisheries (e.g., Milner et al. 1985; Utter et al. 1987b; Shaklee et al. 1990b) and to study the migratory timing of adult chinook salmon caught in research fisheries in the lower Fraser (Waples et al. 1990) and lower Skeena rivers (G. A. Winans and D. J. Teel, Northwest Fisheries Science Center, unpublished data). In the analysis presented here, we estimated the distribution of genetic diversity among populations at three hierarchical levels: rivers, areas, and regions. We then inferred genetic relationships among populations of chinook salmon using cluster analyses, and we used these results to search for patterns of divergence that might be concordant with the distributions of ocean and stream life history types.

Methods

Samples.—A total of 91 samples were collected from 63 British Columbia rivers and hatcheries from 1981 to 1991. Forty localities were sampled in a single year, 18 locations over 2 years, and 5 locations over 3 years (Figure 1; Table 1). Spawning adults were sampled at hatcheries, and juveniles were collected from rearing ponds. Samples of hatchery broods included the progeny of at least 100 adult fish, except at Birkenhead Hatchery, where about 60 fish had been spawned. Wild juvenile fish were sampled in natal rivers with fyke nets or seines and were collected from several sites along a stream in order to avoid taking offspring from only a few matings. Wild adults were sampled on or near spawning grounds, typically over a period of 1 or 2 d, near the peak of the spawning run. Many samples were collected in conjunction with government or community enhancement projects, in which wild adult fish were captured on or near a spawning ground, transported to a hatchery, and spawned artificially. Progeny from these matings were reared until their release near the site of the adult capture. Many of our samples from these projects were juvenile fish. Most of the broods we sampled were the progeny of 100 to 300 adult fish. Several samples were taken from broods that were the progeny of 60 to 100 spawners (Table 1). In a few cases, in which efforts to supplement natural spawning have continued for several years, the captured adults may have included both naturally reared and hatchery-reared fish. Specimens were collected and stored as described by Aebersold et al. (1987), and specimens were shipped to the Northwest Fisheries Science Center for processing at the Manchester Marine Experimental Station in Manchester, Washington.

Electrophoresis.—Sample preparation and horizontal starch gel protein electrophoresis followed the method of Aebersold et al. (1987). The gel buffers and tissues used to resolve proteins are given in Waples et al. (1993). The guidelines outlined by Utter et al. (1987a) were used to infer genotypes from banding patterns on electrophoretic gels. Enzyme systems and locus designations for polymorphic loci are presented in Table 2. Nomenclature for locus names and alleles followed Shaklee et al. (1990a).

Data analysis.—Genotypic frequencies of polymorphic loci for each sample were examined for departures from expected Hardy-Weinberg proportions using chi-square goodness-of-fit tests, with Levene's (1949) correction for small sample sizes. A locus was considered polymorphic if more than one allele was observed in at least one sample. When a locus had more than two alleles, so that the expected frequency of occurrence of rare genotypes was less than 1.0, we pooled less frequent alleles and calculated frequencies for three classes of genotypes: homozygotes for the most frequent allele, heterozygotes for the most frequent allele and one other allele, and all other genotypes. This pooling reduced the number of tests in which the test statistic might not follow the chi-square distribution (Sokal and Rohlf 1981). Hardy-Weinberg tests were performed on isoloci (comigrating pro-

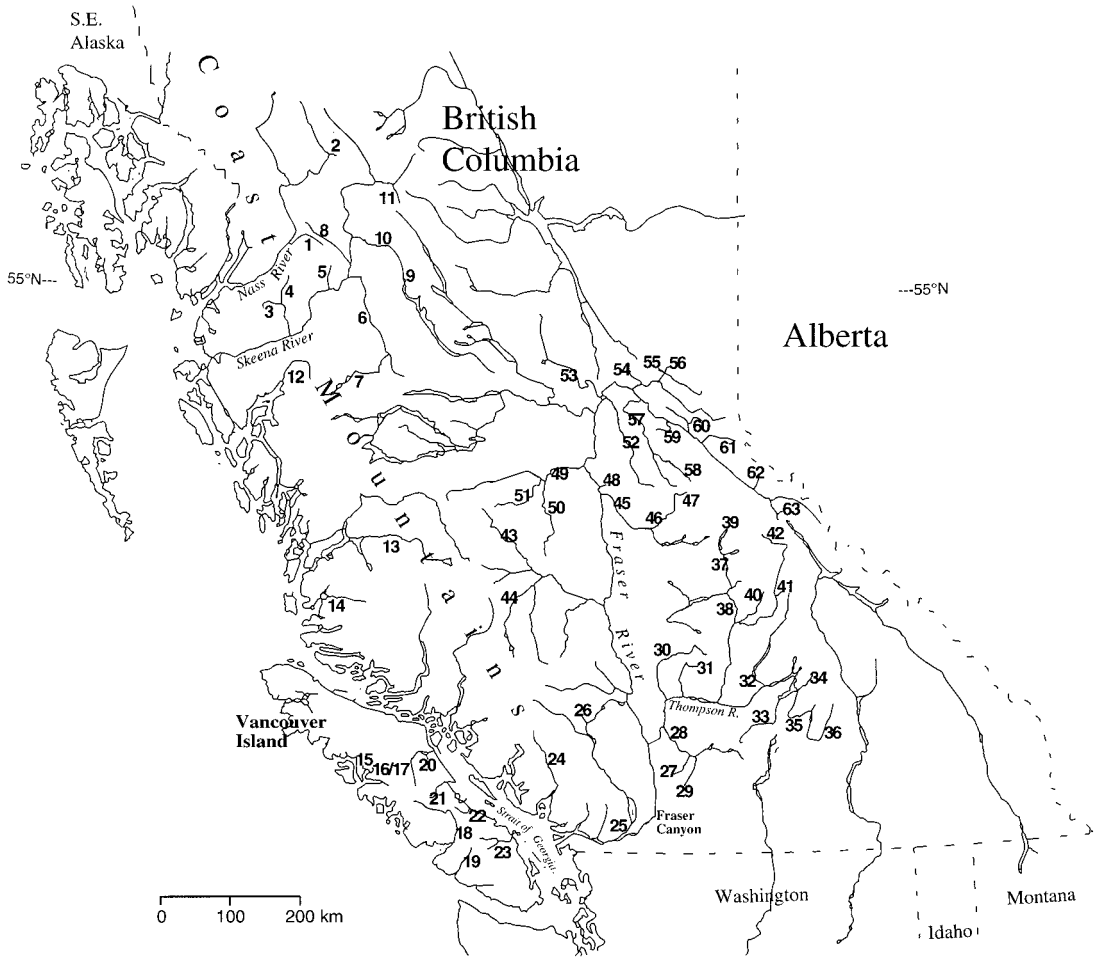

FIGURE 1.—Locations of 63 chinook salmon populations in British Columbia. Numbers correspond to population names in Table 1.

tein products of duplicated loci) using the methods of Waples (1988).

We estimated allelic frequencies from genotypic frequencies. Allelic frequencies for isoloci were calculated as mean frequencies over both loci and were treated as a single tetrasomic locus in our analyses. In this form, the frequencies of isoloci (*sAAT-1,2** and *sMDH-B1,2**) can be compared to those reported by Utter et al. (1989) for chinook salmon populations that ranged from California through British Columbia. Allelic frequencies of samples taken in different years from the same location were combined. Waples (1990) recommended combining temporal samples to estimate population allelic frequencies ''unless there is reason to believe that temporal differences are too large to be attributable to sampling error and genetic drift.''

We used five methods to examine levels and patterns of genetic variation within and between 63 populations using 31 loci (*sAAT-1,2*; sAAT-3*; sAAT-4*; ADA-1*; ADA-2*; sAH*; FDHG*; GPI-A*; GPI-B1*; GR*; mIDHP-1*; mIDHP-2*; sIDHP-1*; sIDHP-2*; LDH-B1*; LDH-B2*; LDH-C*; sMDH-A1,2*; sMDH-B1,2*; MPI*; PEPA*; PEPB-1*; PEPD-2*; PEPLT*; PGDH*; PGK-2*; sSOD-1*; TPI-1*; TPI-2*; TPI-3*;* and *TPI-4**). First, average heterozygosity per locus (isoloci excluded) for each population was calculated using an unbiased estimator of expected heterozygosity (Nei 1978). Second, the proportion of $P_{0.95}$ loci was computed for each population. A locus was con-

sidered a $P_{0.95}$ locus if the frequency of the most common allele was less than or equal to 0.95. Third, gene diversity analysis (Chakraborty et al. 1982) was used to examine genetic variation at three geographic levels: populations (a putative breeding population in a river or hatchery) within areas (G_{SA}); areas (groups of nearby populations) within regions (G_{AR}); and regions (coastal versus inland populations) (G_{RT}) (Table 1). Fourth, a principal components analysis (PCA) was applied to a correlation matrix based on alleles occurring at frequencies of greater than 0.05 in one or more populations. The number of alleles (*k*) analyzed at a locus was *k* minus 1; therefore, we arbitrarily dropped the most common allele at each locus and used only less frequent alleles, for a total of 26 alleles from 21 loci. Fifth, chord distances (Cavalli-Sforza and Edwards 1967) were computed between all pairs of populations, and relationships among populations were depicted in a dendrogram, using the unweighted pair-group method with arithmetic averaging algorithm (Sneath and Sokal 1963). An a priori grouping of populations by area, based on geography (12 areas total; Table 1), was used to calculate a mean between-population within-area distance for each area. Chord distances were calculated with the BIOSYS program (Swofford and Selander 1981), and the cluster and PCA analyses were made using the NTSYS program (Rohlf 1993).

Results

Of the 31 loci screened, 25 were polymorphic, and 21 of these were at the $P_{0.95}$ level of polymorphism in at least one population (Table 2). Allelic frequencies for polymorphic loci are available from FishBase (www.fishbase.org). Eleven of the 25 polymorphic loci had three alleles per locus, and 14 had two alleles per locus. Three loci (*sAH*, MPI*,* and *PGK-2**) were variable in all populations examined. Six loci (*GPI-B1*, mIDHP-1*, mIDHP-2*, sMDH-A1,2*, PGDH*,* and *TPI-2**) were monomorphic in all populations.

We tested observed genotypic proportions at polymorphic loci (up to 25) in 91 samples for departures from expected Hardy-Weinberg proportions. Significant ($P < 0.05$) deviations were detected in 51 of 1,267 tests (4.0%). This number of significant tests is close to the number expected by chance for this rejection level. There were no consistent trends in the distribution of significant tests by sample, sample type (wild versus hatchery, juvenile versus adult), or locus. Therefore, we accepted the null hypothesis that the samples were drawn from disscrete panmictic populations.

The percentage of $P_{0.95}$ loci and average heterozygosity per locus for each population over 31 loci are presented in Table 1. The percentage of $P_{0.95}$ loci ranged from 12.9% in Puntledge River to 35.5% in Kitimat River, with a mean for all populations of 25.0%. Mean percentage of $P_{0.95}$ loci for areas ranged from 20.6% in the south Thompson River to 31.2% in the Central coast. Average heterozygosity ranged from 0.048 in Birkenhead River to 0.108 in Harrison River, with a mean for all populations of 0.084. The average heterozygosity for areas ranged from 0.058 in the Nass River to 0.094 in the lower Thompson River. The gene diversity analysis of the 63 samples resulted in a total gene diversity of 0.085 (H_T) and an average sample diversity of 0.077 (H_S), indicating that 91.3% of the total genetic diversity was attributable to within-sample variability and that 8.7% was attributable to variability among samples (Table 3). About 3.3% of the total gene diversity was due to variability among populations within areas, 3.5% of the total was due to variability among areas within regions, and 1.9% was due to variability between populations in inland and coastal regions.

Some alleles were confined to particular groups of populations. For example, *sAAT-3*90* occurred in all populations from Vancouver Island, Georgia Strait, and the Central coast, but it was not found in Fraser or Nass river populations (Figure 2). *sAAT-4*63* occurred at high frequencies in the Fraser and Skeena river populations, with frequencies greater than 0.40, but it was absent in populations on west Vancouver Island and was found in only one Georgia Strait population (Big Qualicum Hatchery).

The first two eigenvectors of the PCA explained about 31.6% of the total variation (Table 4; Figure 3). Large negative loadings on PC1 for *sAAT-4*63* and *GR*110* contrasted with large positive loadings for *sAAT-3*90* and *PEPB-1*130* on PC1. Large negative loadings on PC2 for *PGK-2*100* and *GR*85* contrasted with the large positive loadings for *PEPA*90* on PC2.

A scatterplot of scores for PC1 and PC2 (Figure 3) showed a clear geographic pattern. Populations from the Central coast, west Vancouver Island, Georgia Strait, and the lower Fraser River had positive PC1 scores, whereas inland populations from the Nass and Skeena rivers and from the Fraser River above the Fraser Canyon had negative PC1 scores. PC2 separated populations in north and central British Columbia from coastal populations to the south. Populations in the Nass and Skeena

TABLE 1.—Sample information and indices of genetic variability for chinook salmon in British Columbia. Map codes refer to Figure 1. Sources are hatchery (H) and wild (W). Life-history type is stream type (S), ocean type (O), and intermediate (I). Age is adult fish (A) and juvenile fish (J). Brood year of juvenile fish is 1 year prior to year sampled. Indices of variability are based on data for 31 loci except for heterozygosity, which excluded 3 isoloci. Indices of genetic variability are $\%P_{0.95}$ = percentage of $P_{0.95}$ loci, H = heterozygosity, and D = average chord distance from other populations in the area.

Map code	Area (region) and locality	Sample source	Life history type[a]	Age	Number of fish	Year sampled	$\%P_{0.95}$	H	D
	Nass River (inland)								
1	Cranberry	W	S	A, A	93	88, 89	22.6	0.064	0.059
2	Damdochax	W	S	A	75	88	19.4	0.051	0.059
	Area mean						21.0	0.058	0.059
	Lower Skeena River (inland)								
3	Kitsumkalum	W[b]	S	A, A, A	281	88, 89, 91	32.3	0.082	0.076
4	Cedar	W[b]	S	A	100	91	32.3	0.102	0.076
	Area mean						32.3	0.092	0.076
	Upper Skeena River (inland)								
5	Kitwanga	W	S	A	111	91	22.6	0.076	0.061
6	Bulkley	W[b]	S	J,[c] A	192	89, 91	19.4	0.085	0.085
7	Morice	W	S	A	100	91	22.6	0.065	0.056
8	Kispiox	W[b]	S	J[c]	80	89	25.8	0.080	0.061
9	Fort Babine	H	S	J	80	90	29.0	0.078	0.052
10	Babine	W[b]	S	A, A	113	82, 88	25.8	0.064	0.068
11	Bear	W	S	A	100	91	25.8	0.072	0.049
	Area mean						24.4	0.075	0.062
	Central Coast (coastal)								
12	Kitimat	W[b]	I	J, A	190	85, 88	35.5	0.085	0.073
13	Atnarko	W[b]	I	J, A, A	329	85, 90, 91	29.0	0.077	0.065
14	Wannock	W[b]	O	A, A	180	88, 91	29.0	0.084	0.087
	Area mean						31.2	0.081	0.075
	West Vancouver Island (coastal)								
15	Sucwoa	W	O	J	40	85	25.8	0.078	0.053
16	Conuma	H	O	J	100	85	22.6	0.075	0.050
17	Conuma	W	O	J	40	85	29.0	0.079	0.050
18	Robertson	H	O	A, J	200	81, 85	22.6	0.086	0.059
19	Nitinat	W	O	J	100	85	19.4	0.065	0.051
	Area mean						23.9	0.076	0.052
	Georgia Strait (coastal)								
20	Quinsam	H	O	A, J	194	81, 85	25.8	0.093	0.089
21	Puntledge	H	O	J	100	85	12.9	0.071	0.090
22	Big Qualicum	H	O	J, J	185	81, 85	25.8	0.098	0.089
23	Nanaimo	H	O	J	100	85	19.4	0.085	0.080
24	Squamish	W[b]	O	J	150	85	25.8	0.087	0.097
	Area mean						21.9	0.086	0.089
	Lower Fraser River (coastal)								
25	Harrison	W[b]	O	J	150	85	29.0	0.108	0.125
26	Birkenhead	H	S	J,[c] J[c]	180	85, 87	16.1	0.048	0.125
	Area mean						22.6	0.078	0.125
	Lower Thompson River (inland)								
27	Spius	W[b]	S	J	78	87	22.6	0.090	0.058
28	Nicola	W[b]	S	J	196	87	22.6	0.082	0.056
29	Coldwater	W[b]	S	A, J	162	82, 87	22.6	0.088	0.054
30	Bonaparte	W[b]	S	J	80	87	32.3	0.095	0.060
31	Deadman	W[b]	S	J	120	87	22.6	0.092	0.060
	Area mean						24.5	0.094	0.058
	South Thompson River (inland)								
32	Adams	W	I	A	80	87	29.0	0.102	0.065
33	Salmon	W[b]	S	J, J, J	260	85, 87, 88	29.0	0.101	0.064
34	Eagle	W[b]	S	J, J, J	260	85, 87, 88	25.8	0.090	0.054
35	Lower Shuswap	W[b]	I	J	80	87	19.4	0.088	0.055
36	Middle Shuswap	W[b]	I	J	120	87	25.8	0.093	0.057
	Area mean						25.8	0.091	0.059

TABLE 1.—Continued.

Map code	Area (region) and locality	Sample source	Life history type[a]	Age	Number of fish	Year sampled	$\%P_{0.95}$	H	D
	North Thompson River (inland)								
37	Clearwater	W[b]	S	A, J	145	82, 85	25.8	0.087	0.062
38	White Horse Bluff	W[b]	S	J	80	87	32.3	0.103	0.063
39	Horseshoe	W[b]	S	J	80	87	25.8	0.086	0.062
40	Raft	W[b]	S	J[c]	100	85	19.4	0.090	0.074
41	Finn	W[b]	S	J	160	87	19.4	0.075	0.087
42	North Thompson	W[b]	S	J	200	87	29.0	0.099	0.070
	Area mean						25.3	0.089	0.070
	Mid Fraser River (inland)								
43	Chilcotin	W[b]	S	J	80	88	29.0	0.088	0.055
44	Chilko	W[b]	S	A, J	169	82, 87	32.3	0.088	0.063
45	Quesnel	W[b]	S	J, J, J	340	85, 87, 88	29.0	0.092	0.054
46	Lower Cariboo	W[b]	S	J[c]	160	87	29.0	0.096	0.067
47	Upepr Cariboo	W[b]	S	J[c], J[c]	180	85, 87	25.8	0.089	0.054
48	Cottonwood	W[b]	S	J, J	220	85, 87	25.8	0.083	0.065
49	Blackwater	W[b]	S	J, J	240	85, 87	29.0	0.084	0.050
50	Nazko	W[b]	S	J	80	87	25.8	0.090	0.056
51	Baezaeko	W[b]	S	J[c], J	220	85, 87	29.0	0.091	0.063
	Area mean						28.3	0.091	0.059
	Upper Fraser River (inland)								
52	Willow	W	S	J, J	252	85, 87	22.6	0.083	0.050
53	Salmon	W	S	J	71	87	29.0	0.094	0.045
54	Seebach—McGregor	W	S	J	100	85	29.0	0.083	0.048
55	James—McGregor	W	S	J	100	85	25.8	0.079	0.048
56	Fontoniko—McGregor	W	S	J	100	85	22.6	0.078	0.054
57	Bowron	W[b]	S	J, J	270	85, 87	29.0	0.087	0.042
58	Indianpoint—Bowron	W	S	J	100	85	19.4	0.072	0.055
59	Slim	W	S	J	80	87	25.8	0.085	0.050
60	Walker—Torpy	W	S	J	80	87	29.0	0.091	0.055
61	Morkill	W	S	J	80	87	29.0	0.075	0.048
62	Horsey	W	S	J	80	87	29.0	0.087	0.059
63	Swift	W	S	A	80	87	29.0	0.093	0.072
	Area mean						26.6	0.090	0.052

[a] Data from Taylor (1989) and personal communications from fishery biologists of the Canadian Department of Fisheries and Oceans.
[b] Sample taken in conjunction with enhancement project.
[c] Brood sampled was the progeny of 60 to 100 adult fish.

rivers and in rivers along the Central coast had high PC2 scores. Populations in west Vancouver Island and along Georgia Strait had lower PC2 scores. Within the Fraser River, PC2 also separated inland and northernmost populations from lower river and southern populations. Populations in the mid- and upper Fraser River had higher PC2 scores than did populations in Harrison, south Thompson, and lower Thompson rivers. Most populations in the north Thompson River had intermediate PC2 scores. One geographical exception was the Birkenhead Hatchery population in the lower Fraser River, which had a relatively high PC2 score. The scatterplot showed that in addition to these broad patterns of PC1 and PC2 scores, most populations clustered with other populations from the same major drainage or area. In many cases, these clusters were distinct from one another.

Unweighted pair-group method with arithmetic averaging algorithm analysis of chord distances between the 63 populations (Figure 4) showed similar relationships. Two large clusters were joined at a genetic distance of 0.126. The first group contained populations north of the Wannock River of the Central coast and Fraser River populations above Fraser Canyon. The other cluster contained the populations from west Vancouver Island and the Georgia Strait areas and two lower Fraser River populations.

Each of these two clusters contained subgroups (D = 0.074–0.083 between subgroups) that included populations in the same drainage or area. However, a few genetic outliers also appeared. For example, Cedar River and Bulkley River populations did not cluster closely with others from the Skeena River, and the Finn Creek population was not part of the north Thompson River cluster. Populations in the Birkenhead Hatchery and Harrison River of the lower Fraser River clustered relatively distantly with the southern coastal populations.

TABLE 2.—Enzymes and study results for 25 polymorphic loci in samples of British Columbia chinook salmon.

Enzyme name	Enzyme Commission number[a]	Locus	Number of populations polymorphic	Range of common allele frequency
Aspartate amino transferase	2.6.1.1	*sAAT-1,2**	30	1.000–0.930
		*sAAT-3**	19	1.000–0.779
		*sAAT-4**	55	1.000–0.415
Adenosine deaminase	3.5.4.4	*ADA-1**	54	1.000–0.680
		*ADA-2**	7	1.000–0.957
Aconitate hydratase	4.2.1.3	*sAH**	63	0.994–0.528
Formaldehyde dehydrogenase (glutathione)	1.2.1.1	*FDHG**	14	1.000–0.942
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**	52	1.000–0.800
Glutathione reductase	1.6.4.2	*GR**	58	1.000–0.622
Isocitrate dehydrogenase	1.1.1.42	*sIDHP-1**	37	1.000–0.918
		*sIDHP-2**	38	1.000–0.854
Lactate dehydrogenase	1.1.1.27	*LDH-B1**	8	1.000–0.933
		*LDH-B2**	9	1.000–0.925
		*LDH-C**	14	1.000–0.958
Malate dehydrogenase	1.1.1.37	*sMDH-B1,2**	51	1.000–0.847
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	63	0.894–0.341
Dipeptidase	3.4.–.–	*PEPA**	42	1.000–0.887
Tripeptide aminopeptidase	3.4.–.–	*PEPB-1**	53	1.000–0.560
Proline dipeptidase	3.4.13.9	*PEPD-2**	8	1.000–0.992
Leucyl-L-tyrosine peptidase	3.4.–.–	*PEPLT**	49	1.000–0.740
Phosphoglycerate kinase	2.7.2.3	*PGK-2**	63	0.650–0.006
Superoxide dismutase	1.15.1.1	*sSOD-1**	60	1.000–0.650
Triose-phosphate isomerase	5.3.1.1	*TPI-1**	3	1.000–0.988
		*TPI-3**	10	1.000–0.878
		*TPI-4**	24	1.000–0.929

[a] IUBMBNC (1992).

The largest average chord distances (Table 1) were found between two populations in the lower Fraser River (0.125). Other areas had much smaller average distances, which ranged from 0.052 for west Vancouver Island and upper Fraser River to 0.089 for Georgia Strait.

Discussion

Genetic Variation within Populations

The levels of genetic diversity in chinook salmon in British Columbia do not indicate that populations have experienced strong reductions in

TABLE 3.—Components of genetic diversity in chinook salmon for 13 highly polymorphic loci. H_T = total expected heterozygosity; H_S = average within-sample heterozygosity; G_{SA} = relative differentiation among populations within areas; G_{AR} = relative differentiation among areas within regions; G_{RT} = relative differentiation between regions (coastal vs. inland populations); $(1 - G_{ST})$ = within-population variation.

Locus	H_T	H_S	G_{SA}	G_{AR}	G_{RT}	$(1 - G_{ST})$
*sAAT-3**	0.053	0.047	0.036	0.035	0.034	0.895
*sAAT-4**	0.335	0.285	0.045	0.032	0.072	0.851
*ADA-1**	0.145	0.134	0.046	0.018	0.013	0.923
*sAH**	0.224	0.206	0.039	0.015	0.026	0.919
*GR**	0.262	0.240	0.027	0.045	0.014	0.915
*sIDHP-2**	0.052	0.049	0.024	0.031	0.003	0.943
*LDH-B2**	0.011	0.011	0.014	0.040	0.002	0.944
*MPI**	0.441	0.417	0.032	0.020	0.001	0.946
*PEPB-1**	0.144	0.121	0.040	0.054	0.069	0.837
*PEPLT**	0.099	0.093	0.048	0.015	0.000	0.936
*PGK-2**	0.402	0.356	0.022	0.091	0.000	0.887
*sSOD-1**	0.186	0.177	0.036	0.009	0.006	0.949
*TPI-3**	0.013	0.012	0.016	0.042	0.004	0.938
Mean(25 loci)	0.085	0.077	0.033	0.035	0.019	0.913

size, nor do they indicate that chinook salmon have experienced founder effects. Chinook salmon in British Columbia contained intermediate levels of within-population genetic variation in comparison with populations in other regions. We found 21 $P_{0.95}$ loci in British Columbia chinook salmon that were similar to values for chinook salmon in California and Oregon (34 of 78 loci; Bartley et al. 1992), in the Snake River (24 of 63 loci; Waples et al. 1993), and in the upper Columbia River (18 of 32 loci; Utter et al. 1995).

Estimates of heterozygosity for British Columbia populations of chinook salmon appear to be intermediate to those for populations in other areas. Our estimates of population heterozygosity averaged 0.084 (range: 0.048–0.108; 31 loci) and were similar to those of Utter et al. (1989), who found a mean heterozygosity for 10 British Columbia chinook salmon populations of 0.085 (25 loci). In contrast, populations of chinook salmon along the Oregon coast had a mean population heterozygosity of 0.122 (Utter et al. 1989). However, populations located toward the edge of the range of this species tend to have smaller heterozygosities. For example, heterozygosities for populations in the Snake River averaged 0.040, and those in the Klamath River averaged 0.029 (Utter et al. 1989). The various levels of genetic diversity in chinook salmon populations may reflect population size or population stability. If so, chinook populations in British Columbia appear to have had population histories that were free of severe population bottlenecks.

Variability among Populations

One goal of this study was to examine allele-frequency variability among populations of chinook salmon in British Columbia. We found strong differences among populations at all levels of the geographic hierarchy that we examined. The proportion of genetic variability among populations (8.7%) is typical for groups of populations in other areas. Smaller among-population diversities were found by Gharrett et al. (1987) for Alaskan chinook salmon (5.9%) and by Waples et al. (1993) for Snake River populations (3.4%). However, the samples from these studies encompassed smaller geographic ranges and contained fewer genetically differentiated life history types than do samples in the present study. High levels of among-population diversity were reported by Bartley et al. (1992) for California and Oregon populations (10.6%) and by Utter et al. (1989) for populations from the Pacific Northwest (12.3%), most likely because these studies included samples from larger areas.

Slightly less than one-third of the total among-population gene diversity occurred within areas, the smallest unit of the geographic hierarchy that we examined. In general, populations within areas appeared to be genetically distinct from, although clearly related to, one another. In some cases, the areas we defined were quite large, and isolation by distance may account for genetic differences among populations. However, in other cases, genetic distances were pronounced among populations that spawned in different locations within the same drainage. Differences in adult migration and spawn timing, in addition to spatial separation, provided a likely mechanism to limit gene flow between these populations. For example, the Kitsumkalum River and Cedar River populations in the lower Skeena River do not cluster closely together, although both rivers are part of the Kitsumkalum River subbasin. The two populations have quite different timings for both adult migration and spawning. The Cedar River has an adult spring-run population with individuals that spawn largely in July and August. Fish return to the Kitsumkalum River in summer and spawn mostly in September. In the lower Fraser River, the two populations we sampled are genetically distinct and are also characterized by very different adult life histories (Fraser et al. 1982). Fish return to the Harrison River in fall and spawn in October and November, later than other Fraser River populations. In contrast, the Birkenhead Hatchery population originated from spring-run fish that are among the earliest migrating and spawning chinook salmon in the Fraser River.

Over greater geographic distances, the pattern of genetic differentiation among populations is largely congruent with geographic relationships. In some cases, groups of populations can be characterized by frequencies of individual alleles. Results of PCA and cluster analyses that use multilocus information further depict genetic relationships that have geographic coherence. Distinct groups of populations can be identified in the Nass River, the Skeena River, the Central coast, the west coast of Vancouver Island, the east coast of Vancouver Island and the southern mainland, the lower Thompson River, the south Thompson River, the north Thompson River, and the mid- and upper Fraser River. In many cases, genetic groups are also identifiable on a larger geographic scale. For example, the Thompson River genetic groups clus-

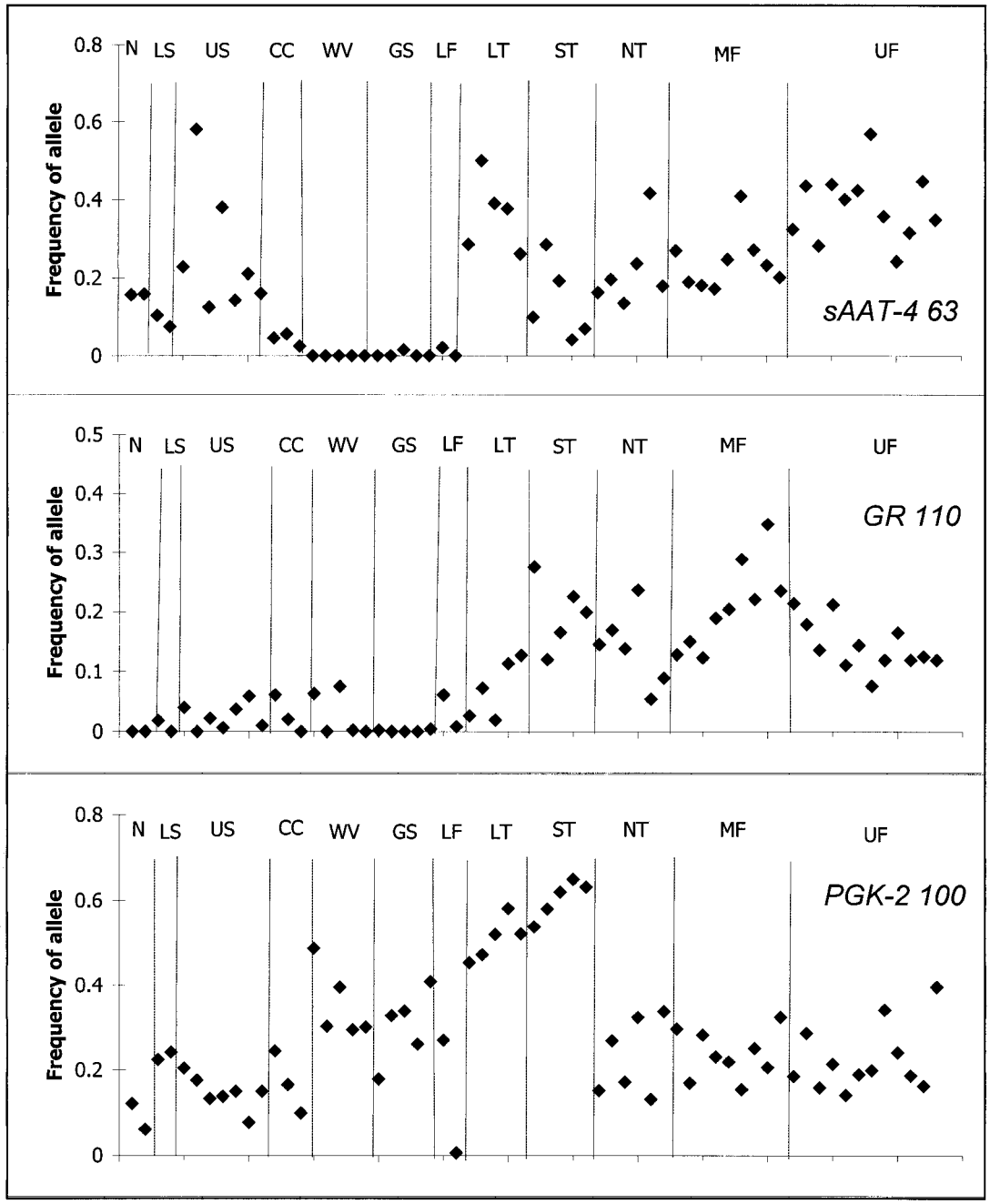

FIGURE 2.—Frequencies for six alleles in 63 chinook salmon populations in British Columbia. Samples are arranged in the order listed in Table 1. Areas are Nass River (N), lower Skeena River (LS), upper Skeena River (US), Central coast (CC), west Vancouver Island (WV), Georgia Strait (GS), lower Fraser River (LF), lower Thompson River (LT), south Thompson River (ST), north Thompson River (NT), mid-Fraser River (MF), and upper Fraser River (UF).

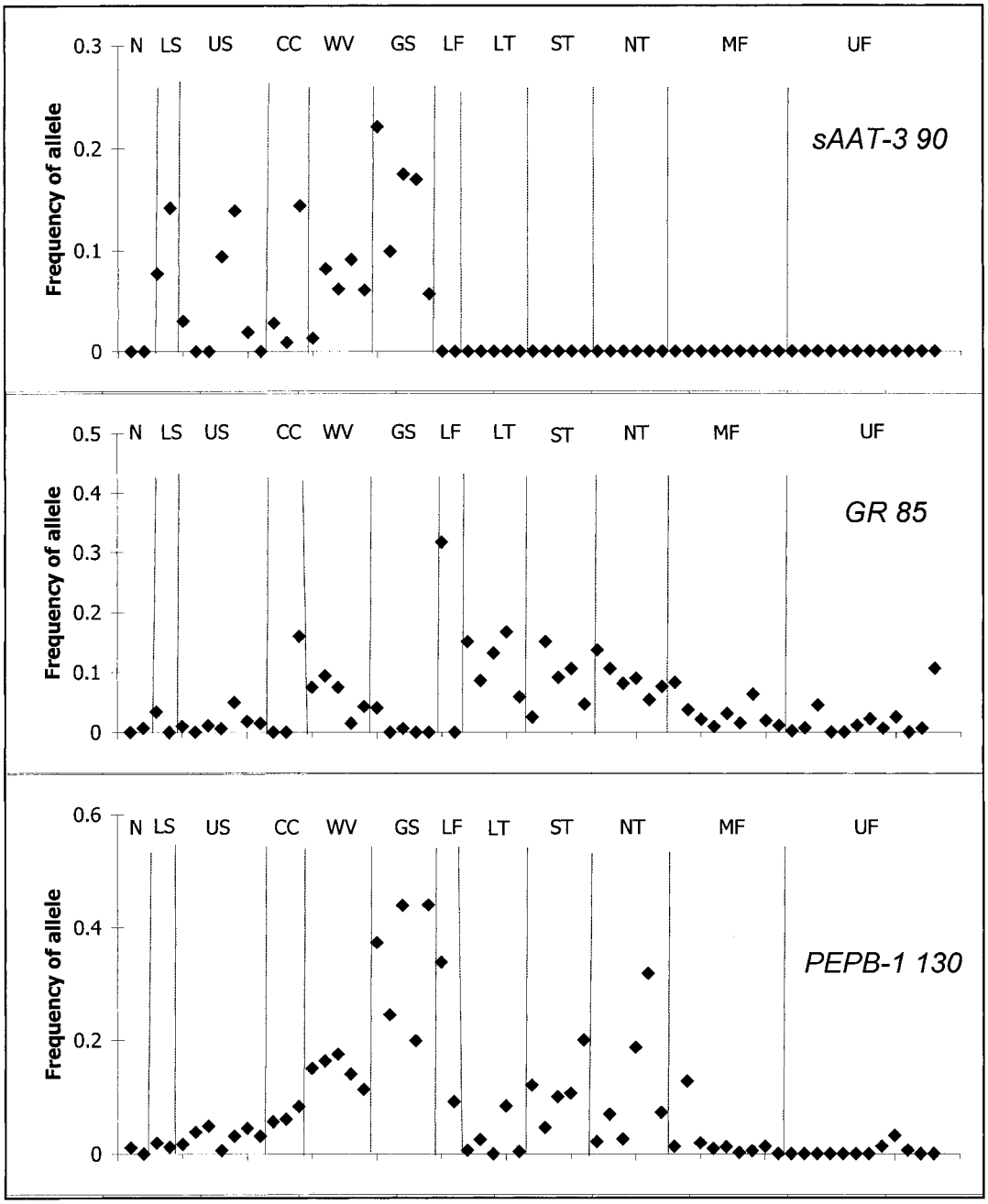

FIGURE 2.—Continued.

ter together and are most genetically similar to populations from the mid-Fraser River.

Variability among Regions

On a broader level, the PCA and dendrogram revealed two large genetic groups of populations of British Columbia chinook salmon. The first group contained populations in the Skeena and Nass rivers, along with those in the Fraser River above the Fraser Canyon. These rivers transverse the Coast Mountains and drain inland regions. A second genetic group contained populations in riv-

TABLE 4.—Factor scores of principal component analysis (PCA).

Allele	Factor 1	Factor 2
*sAAT-1,2*85*	0.58	0.35
*sAAT-3*90*	0.70	0.08
*sAAT-4*63*	−0.76	0.14
*ADA-1*83*	−0.58	0.15
*sAH*86*	0.56	−0.39
*FDHG*143*	0.44	0.59
*GPI-A*105*	−0.48	0.35
*GPI-A*93*	0.17	−0.04
*GR*85*	0.07	−0.52
*GR*110*	−0.68	−0.23
*sIDHP-1*74*	−0.10	−0.26
*sIDHP-2*127*	0.48	−0.28
*sIDHP-2*50*	−0.11	−0.15
*LDH-B1*48*	0.09	0.54
*LDH-B2*71*	−0.16	−0.22
*sMDH-B1,2*121*	0.50	−0.36
*sMDH-B1,2*70*	−0.36	−0.24
*MPI*109*	0.03	−0.43
*PEPA*90*	0.11	0.67
*PEPB-1*130*	0.66	−0.47
*PEPLT*110*	0.00	0.16
*PGK-2*100*	−0.05	−0.62
sSOD-1−260*	0.48	0.14
*sSOD-1*580*	−0.43	−0.06
*TPI-3*96*	0.44	0.53
*TPI-4*104*	−0.19	0.31
Eigenvalue	4.74	3.49
% Variation explained	18.2	13.4

ers draining coastal regions and in the western slopes of the Coast Mountains.

Differentiation between these two genetic groups is particularly pronounced, over a relatively small geographic distance, within the Fraser River. The genetic similarity between lower Fraser River populations and coastal fish and the divergence from those fish above the Fraser Canyon have also been observed in steelhead *Oncorhynchus mykiss* (Parkinson 1984), coho salmon *Oncorhynchus kisutch* (Wehrhahn and Powell 1987; Small et al. 1998), and sockeye salmon *Oncorhynchus nerka* (Wood et al. 1994).

Our allozyme data agree with the genetic groupings of populations that were based on a study of minisatellite DNA in 30 stocks of British Columbia chinook salmon (Beacham et al. 1996). That study delineated a southern group composed of southern mainland, Vancouver Island, and Fraser River populations and a northern group containing populations from the northern mainland, the Skeena River, and the Yukon River. Although Beacham et al. (1996) placed inland Fraser River populations in the southern group, the authors presented results from a PCA in which populations from the mid- and upper Fraser River clustered more closely to Skeena River populations.

The separation of British Columbia chinook salmon into coastal and inland genetic groups is congruent with groupings based on chinook salmon life history forms. In coastal rivers as far north as the Nass River, populations are predominately ocean type (Taylor 1989, 1990a). Fish in these populations migrate to sea primarily as subyearlings, they tend to spend most of their ocean life in coastal waters, and they return to freshwater shortly prior to spawning, usually in the fall or summer (Healey 1991). In the upstream drainages of the Fraser, Skeena, and Nass rivers, populations are predominately stream type, and fish migrate downstream primarily as yearlings, move extensively offshore, and return to freshwater several months prior to spawning, usually in the spring or summer (Healey 1983; Taylor 1989, 1990a).

The geographic separation between ocean- and stream-type spawning populations is not complete, however, and several British Columbia coastal populations consist of stream-type individuals (Taylor 1989). Two of the populations we studied in mainland rivers having headwaters in the Coast Mountains are stream type. One was in the Squamish River of the lower Strait of Georgia. The other was the Birkenhead Hatchery in the lower Fraser River, which uses stream-type fish from the Birkenhead River for broodstock. Both populations clustered with the coastal ocean-type populations and were genetically dissimilar to inland stream-type populations.

Several British Columbia populations also contain substantial proportions of both ocean-type and stream-type chinook salmon, particularly in the south Thompson River and along the Central coast (Taylor 1989). Several populations in these areas were genetically intermediate between the coastal and inland populations. For example, in the PCA plot (Figure 3), populations in the Adams and Shuswap rivers, which are tributaries of the south Thompson River, and in the Atnarko and Kitimat rivers (from the Central coast) were positioned near the convergence of the coastal and inland genetic groups. These populations have frequencies of the *sAAT4*63* and *PEPB1*130* alleles that are intermediate between frequencies in southern coastal populations and those in inland populations. Although the PC1 values show the genetic affinities between the Atnarko and Kitimat populations and the southern coastal populations, the PC2 values and the dendrogram (Figure 4) indicate genetic similarities to populations in the Skeena and Nass rivers.

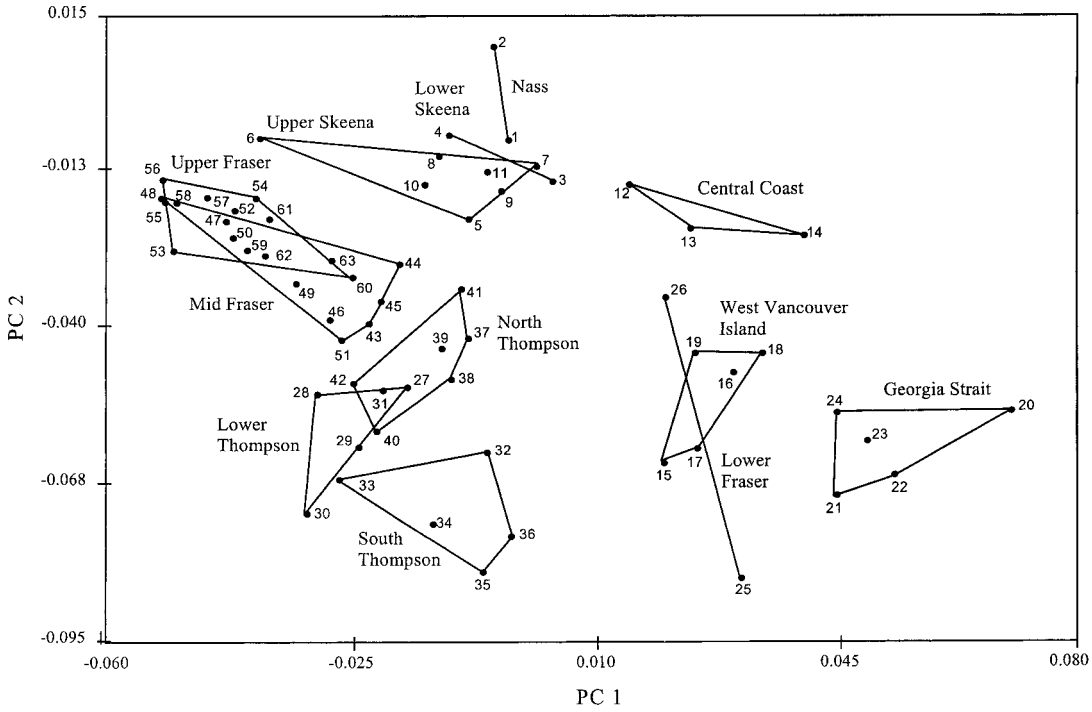

FIGURE 3.—Scatterplot of scores along the first two principal component (PC) axes for 63 chinook salmon populations in British Columbia. Location numbers are given in Table 1 and Figure 1. Populations within an area are identified with polygons where possible.

Zoogeography of Life History Types

The dichotomous distributions of ocean- and stream-type chinook salmon life history forms most likely reflect postglacial dispersals and colonizations (Healey 1983, 1991; Gharrett et al. 1987; Taylor 1990a). Most of British Columbia was covered with ice during the last glacial maximum and has been repopulated by chinook salmon within the last 13,000 years (McPhail and Lindsey 1986). Potential sources for recolonization include chinook salmon that survived in the Bering refugium to the north and in the Pacific and Columbia–Snake River refugia to the south (McPhail and Lindsey 1970; Gharrett et al. 1987). Ocean- and stream-type chinook salmon may have survived the glaciation in different refugia, and following retreat of the ice sheet, the two forms may have expanded into deglaciated areas in Washington, British Columbia, and Alaska.

The pattern of allozyme variability in British Columbia largely supports this hypothesis. If we can assume near-neutrality of the majority of allozyme alleles (Kimura 1968), our results imply long-standing genetic isolation between inland stream-type and coastal ocean-type populations of British Columbia chinook salmon. The genetic similarity among geographically isolated stream-type populations in the upper Fraser, Skeena, and Nass rivers suggests that these chinook salmon descended from a common ancestor. Such a pattern would not arise from convergent selection for a particular life history type. Previous genetic data indicate that the upper Fraser River may have been colonized by chinook salmon from the upper Columbia and Snake rivers (Utter et al. 1989). Stream-type populations from these rivers possess behaviors—spring or summer adult return-timing and juvenile residence in freshwater for at least a year—that would be needed to successfully colonize the upstream areas of large British Columbia rivers.

The genetic study of Utter et al. (1989), however, included only a single sample north of Vancouver Island. Genetic analyses of populations in Alaska and in Asia, north of the glaciation, where stream-type juveniles predominate, may be particularly important. Recent allozyme studies of chinook salmon in Alaska and Asia (P. Crane, Alaska Department of Fish and Game, and C. Guthrie, National Marine Fisheries Service, personal com-

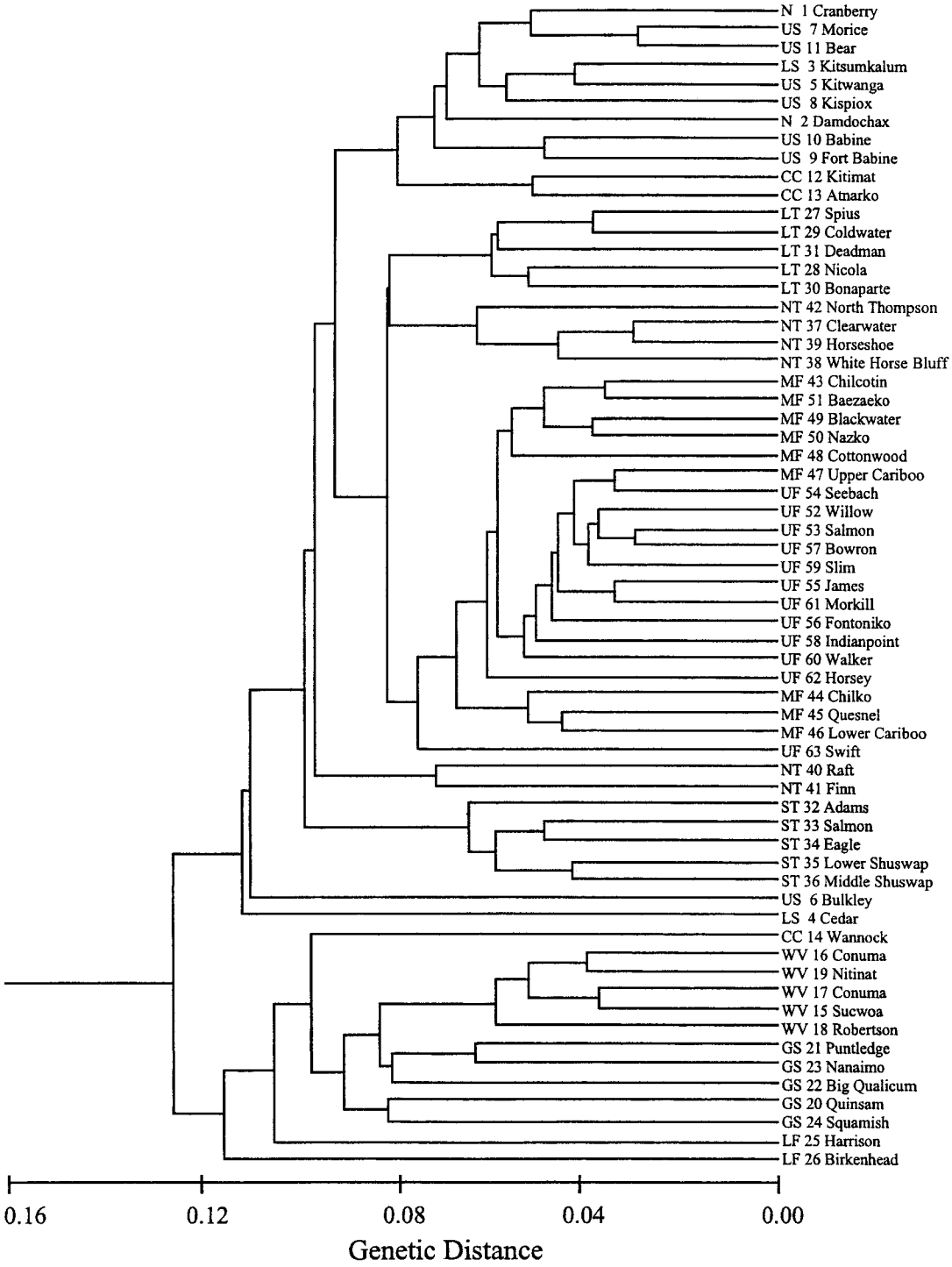

FIGURE 4.—Dendrogram of Cavalli-Sforza and Edwards (1967) chord distances (31 loci) among 63 chinook salmon populations in British Columbia (cophenetic correlation = 0.848). Areas are Nass River (N), lower Skeena River (LS), upper Skeena River (US), Central coast (CC), west Vancouver Island (WV), Georgia Strait (GS), lower Fraser River (LF), lower Thompson River (LT), south Thompson River (ST), north Thompson River (NT), mid-Fraser River (MF), and upper Fraser River (UF).

munications) will make these comparisons possible and may provide more insight into the origins of stream-type populations in inland British Columbia.

Genetic data indicate that southern British Columbia coastal rivers were colonized by chinook salmon from the Pacific refuge (Utter et al. 1989). If fish surviving in coastal rivers south of the ice sheet had chiefly ocean-type life histories, as is presently the case, a northward expansion along the coast would explain the distribution of ocean-type populations in southern British Columbia. The transition from ocean-type populations to stream-type populations at 55°N (Figure 1), without a corresponding change in environmental conditions, supports a zoogeographic explanation for the appearance of different life history types in British Columbia (Healey 1983; Taylor 1990a).

Life History Variability within Regions

The patterns of life history variability in some areas conflict with a strictly zoogeographic explanation for the origin of ocean- and stream-type forms. Healey (1991) thought these exceptions represented a serious inconsistency with the zoogeographic model. In British Columbia, some stream-type populations occur in areas that are otherwise inhabited by ocean-type populations, and many populations contain some individuals of both life history types. Populations with intermediate genetic and life history patterns in the south Thompson River and along the Central coast may be explained by mixing or hybridization of inland stream-type and coastal ocean-type lineages. However, other stream-type populations in southern British Columbia coastal rivers were genetically most closely related to ocean-type populations and appear to have been derived from the same ancestral ocean-type populations, which implies a postcolonization divergence in life history types.

Several studies have shown that life history patterns in chinook salmon can change rapidly. For example, ocean-type chinook salmon introduced in New Zealand have developed some stream-type behaviors over a period of about 30 generations (Quinn and Unwin 1993; Quinn et al. 1996). Also, in the Great Lakes, where fall-spawning chinook salmon were introduced, spring-spawning behavior has appeared in only a few generations (Kwain and Thomas 1984). Breeding experiments have shown that several behavioral and life history characteristics are controlled by the interaction between genetic and environmental variability (Taylor 1988, 1990b; Clarke et al. 1992, 1994). One trait, the response to photoperiod change, appears to be under the control of a single genetic locus (Clarke et al. 1992). Clarke et al. (1992) suggested that disruptive selection at this locus in ocean-type populations might have repeatedly produced stream-type responses to photoperiod. The close genetic affinity between stream- and ocean-type forms in coastal areas in our study and the occurrence of populations with a mix of individuals with different life history types support this hypothesis. Therefore, various life history patterns in chinook salmon appear to have arisen on long and short time scales.

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