Analysis of contemporary genetic structure of even-broodyear populations of Asian and western Alaskan pink salmon, *Oncorhynchus gorbuscha*

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Abstract—Even-year pink salmon (*Oncorhynchus gorbuscha*) populations from the Russian Far East and Japan exhibit genetic structure that reflects their geographic relationships. Extension of genetic analysis to include data from Bering Sea and northern Gulf of Alaska populations shows a combined genetic structure with three prominent groupings that correspond to the three North Pacific Ocean basins—the Sea of Okhotsk, the Bering Sea, and the Gulf of Alaska—and that are consistent with geographic, geologic history, and oceanographic features. Analysis of 35 Asian collections at 39 variable allozyme loci (54 total) allowed examination of population structure of even-year pink salmon. Although most (98.5%) of the genetic variation occurred within collections (populations), the 1.5% attributable to among-collection divergence was sufficient to detect population structure and provide a basis for some stock separation. Differences between western Kamchatka populations and eastern Sakhalin Island populations indicate that little gene flow occurs between those regions and argues against an interregional fluctuating stock model.

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Pink salmon (*Oncorhynchus gorbuscha*) are the most abundant Pacific salmon species and spawn along most of the Pacific rim coastline north of 40°N latitude (Heard, 1991). The species is unique among salmonids in having a determinate life cycle. Adults return to their natal streams to spawn at 2 years of age, which has resulted in separate broodlines in even and odd years (Heard, 1991). Most of the range supports spawning runs of both broodlines, although they may differ in numbers. The southern part of the North American Pacific coast has only small even-year runs; and in western Alaska, even-year runs are much more abundant than odd-year runs (Heard, 1991). The pattern of a numerically dominant broodline in many areas has changed since early this century, perhaps in response to changes in fishing intensity (Takagi et al., 1981) or climate cycles (Mantua et al., 1997). Optimum management and conservation of the pink salmon resource requires thorough knowledge of their biology, including population structure, relationships among populations, and the extent of genetic exchange among local populations and between geographically distinct regions. Genetic divergence among groups of salmon also may provide a basis for stock identification by fish managers (Beacham et al., 1985; Pella and Milner, 1987).

Although DNA-based analyses have become available in recent years (e.g. Park and Moran, 1994), allozyme analysis remains a powerful method for pink salmon studies because they exhibit variability at a number of loci. From allozyme data, marked broodline differences have been demonstrated between pink salmon populations from the Russian Pacific coast (Gagalchii, 1986; Glubokovsky et al., 1989; Kartavtsev, 1991; Zhivotovsky et al., 1989; Kartavtsev et al., 1992) and from the North American Pacific coast (Aspinwall, 1974; McGregor, 1983; Beacham et al., 1988). Although based on few allozyme loci, genetic divergence within each broodline also has been observed among pink salmon collections from many regions of Russia (Gagalchii, 1986; Glubokovsky et al., 1989);

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more extensive allozyme surveys show divergence within broodlines in several North American regions (Beacham et al., 1985, 1988; Gharrett et al., 1988; Shaklee et al., 1991). Genetic divergence is usually attributed to random genetic drift, adaptation to local environmental conditions, or both, which can occur because salmon home to their natal streams to spawn (for an overview, see Allendorf et al., 1987).

The genetic compositions of populations are also molded by other events in their evolutionary histories. If populations share multiple genetic characteristics, then they may share a common origin (colonization or gene flow) or may be derived from different ancestral lines that have experienced homogenizing selection pressures (similar historical environments). The far North Pacific Ocean, Bering Sea, and Sea of Okhotsk are of special interest in the evolution of salmon population structure because these basins encountered the most extreme environmental conditions during the late Pleistocene Epoch. During the last 100,000 years, the environment ranged from extremely favorable (modern conditions) to extremely harsh, which in some areas undoubtedly led to extirpation of many salmon populations. Comparison of the nature and extent of genetic variation within regions to variation among regions is one means of exploring the recent history of a species. Reports of genetic variation among chum salmon (*O. keta*; Wilmot et al., 1994; Winans et al., 1994; Seeb and Crane, 1999), sockeye salmon (*O. nerka*; Varnavskaya et al., 1994a, 1994b; Wilmot et al, 1994), and pink salmon (Gharrett et al., 1988; Varnavskaya and Beacham, 1992; Shaklee and Varnavskaya 1994) are mostly limited to a single region with few reference populations from other regions, or they skip across intervening regions. In addition for sockeye salmon, there are relatively few informational loci and the variation among populations within a region is often large. Consequently, it is difficult to formulate a coherent picture for any Pacific salmon species. The data available for a broader range of Asian populations (Glubokovsky et al., 1989) are based on too few loci to provide a strong basis for broader comparisons.

One advantage of studying pink salmon is that they are distributed almost continuously throughout the northern region. Tagging studies indicate that pink salmon from streams in large contiguous areas of the coast make similar movements and may occupy the same areas within the high seas during portions of their ocean migrations (Takagi et al., 1981). Although it is not clear to what extent this movement pattern reflects either a shared history or shares physical effects (such as the direction of prevailing currents), populations within a region presumably experience similar marine environments. The few genetic data that address the relatedness of even-year pink salmon from both Pacific coasts are limited by the number of genetic characters examined or by geographic area (Gharrett et al., 1988; Zhivotovsky et al., 1989; Shaklee and Varnavskaya, 1994).

Our study analyzed numerous allozyme loci in populations from the even-year broodline of pink salmon from Asian waters and compared those data with data from western Alaska populations (Gharrett et al., 1988). The study included most of the geographic groups identified by Takagi et al., (1981). We substantially expanded the number of allozyme loci sampled in Asian even-year populations to determine the genetic structure of those populations and to investigate the genetic relatedness within and among large areas of the pink salmon range. The questions we addressed are 1) Is there evidence of genetic structure for even-year pink salmon populations? 2) How does the genetic structure of Asian even-year pink salmon relate to the adjacent western Alaskan and Aleutian island populations? and 3) How does the genetic structure of Western Alaska and Asian pink salmon relate to geographic and oceanographic features and to recent geological history?

Materials and methods

Tissue samples from returning adult spawners were collected 1) from four river systems on southern Sakhalin Island (Dolinka, Lutoga, Monetka, and Ochepukha rivers) between 6 August and 19 September 1990; 2) from two river systems in the Magadan region of Russia (Tauy River on 26 July 1990 and Uglekanka River on 3 September 1990); 3) from seven river systems on the Kamchatka Peninsula (Utka, Pymta, Kol, Bistraya, Vorovskaya, Karaga, and Ossora rivers) between 29 July and 3 September 1990 (Fig. 1); 4) at hatcheries on three streams in Japan (Kushiro, Tokushibetsu, and Yurappu Rivers) between 21 and 29 September 1990; and 5) in five collections taken at different times during the return to a hatchery in Sawmill Bay in Prince William Sound, Alaska, between 27 August and 8 September 1988. There are no natural spawning runs of pink salmon in Japan; consequently, the hatchery samples are all that were available to represent Japan. Also, the samples from Prince William Sound, in the center of the North American range are intended to provide an idea of the extent of difference between Asian and North American pink salmon for the entire suite of allozyme loci examined in the Asian fish. The Znamenka River, a tributary of the Ochepukha River, was sampled repeatedly and considered separately in some analyses.

Pieces of heart, eye, liver, and skeletal muscle were sampled in the field and frozen on wet ice, frozen gel-packs, or dry ice until they were transferred to temporary storage at –20°C or to liquid nitrogen dewars at –196°C. Long-term storage was maintained at –85°C. The samples were analyzed by using horizontal starch-gel electrophoresis (Utter et al., 1974). Eight different gel buffers were used (Table 1). Proteins were revealed by using standard staining recipes (Aebersold et al., 1987). All allozyme data were collected at the NMFS Auke Bay Laboratory. An Excel™ file of allele frequency data can be downloaded by anonymous ftp from *ftp://wwwabl.afsc.noaa.gov* in file *SIDA/pink_salmon/evenasia*.

Variability at isoloci (Allendorf and Thorgaard, 1984) was assigned to one of the loci, and the other was treated as monomorphic, which for low frequencies (P<about 0.15) has little influence on the analysis (Gharrett and Thomason, 1987). The genotypic frequencies observed at each

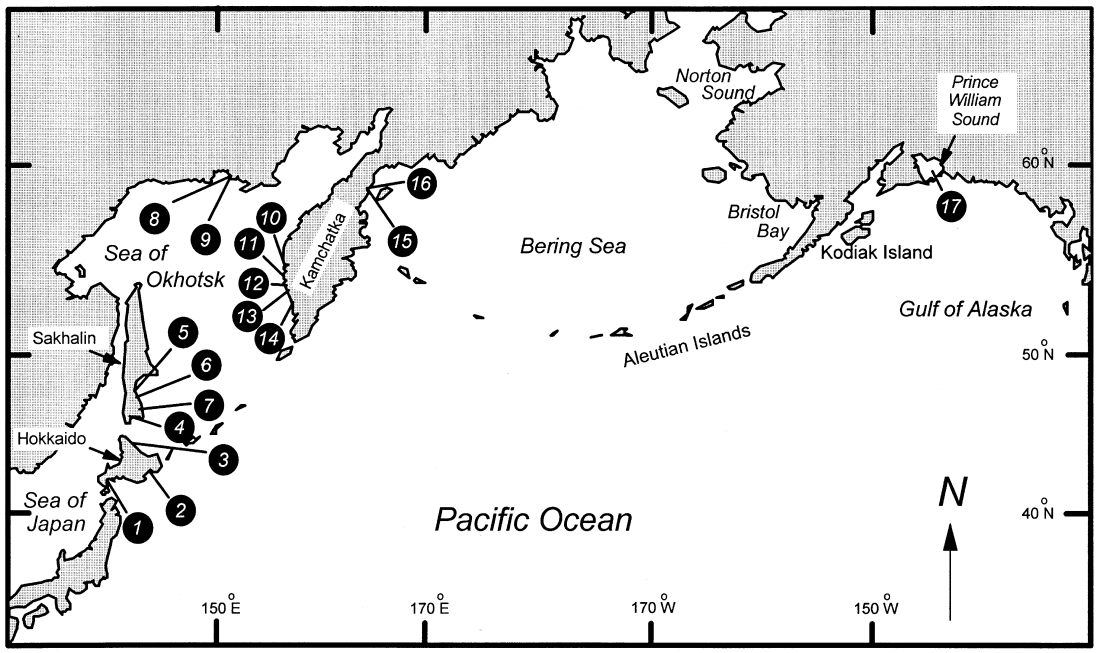

Figure 1

Map of location sites where fish were collected for tissue samples. Unless otherwise indicated, one collection of fish from the lower river was made. Japan: 1 = Yurappu River, Yacumo Hatchery (22 Sep 1990), 2 = Kushiro Hatchery (29 Sep 1990), 3 = Tokushibetsu Hatchery (17 Sep 1990). Sakhalin Island, Russia: 4 = Lutoga River, lower river (13 and 17 Jul 1990) and hatchery (29 Jul 1990 and 8 Nov 1990), 5 = Dolinka River (6 and 16 Aug 1990), 6 = Ochepukha River, lower river (8 and 22 Aug, and 3 Sep 1990) and upper river (6 and 9, and 11 Sep 1990) and Znamenka River, a major tributary of Ochepukha River (13, and 26 Aug 1990, 3, 6, , 9, 11, 13, 17, and 19 Sep 1990), 7 = Monetka River (18 and 19 Jul 1990). Magadan region, Russia: 8 = Tauy River (26 Jul 1990), 9 = Uglekanka River (3 Aug 1990). Western Kamchatka Peninsula, Russia: 10 = Vorovskaya River (31 Jul 1990), 11 = Kol River (30 Jul 1990), 12 = Pymta River (29 Jul 1990), 13 = Utka River (29 Jul 1990), 14 = Bistraya River (3 Aug 1990). Eastern Kamchatka Peninsula, Russia: 15 = Ossora River (28 Jul 1990), 16 = Karaga River (2 Aug 1990). Alaska: 17 = Prince William Sound, Armin F. Koernig Hatchery, Evans Island, Sawmill Bay, five collections in 1990.

locus were tested for departure from expected Hardy-Weinberg equilibrium frequencies by using a Pearson χ^2-goodness-of-fit test. Alleles were pooled to eliminate classes with expected values of less than four. Isoloci could not be tested for Hardy-Weinberg equilibrium because single-locus data were not available.

Homogeneity of allele frequencies was examined by using log-likelihood ratio analysis (*G*-test, Sokal and Rohlf, 1995); tests were performed among collections within a river, among rivers within a region, and among regions. The regions were Japan (Hokkaido Island), Sakhalin Island, western Kamchatka, eastern Kamchatka, and Alaska (Prince William Sound). Significance of tests that indicated low probability ($P<0.05$) based on χ^2 distributions and that had small expected numbers in rare classes (<4) were confirmed by using a Monte-Carlo procedure analogous to the one described by Roff and Bentzen (1989). Significance of multiple tests was corrected according to Cooper (1968). Heterogeneity within and among regions was compared by using an approximate *F*-statistic:

$$F_{df\,among,\,df\,within} = (G_{among}/df_{among})/(G_{within}/df_{within}).$$

Neighbor-joining trees (Saitou and Nei, 1987) were constructed by using chord distances (Cavalli-Sforza and Edwards, 1967; Wright, 1978). Genetic variability within and among streams, regions, and continents was partitioned hierarchically by gene diversity analysis (Chakraborty and Leimar, 1987) and analysis of variance (Weir and Cockerham, 1984; Weir, 1996). Average unbiased heterozygosities and their standard errors were calculated according to Nei (1978).

The five collections from Prince William Sound were, in a strict sense, temporal collections from the mixed fishery in the Sound and were not intended to represent collections from discrete drainages. Nevertheless, for convenience of analysis, they were treated as unique collections from a single system in the genetic distance and gene diversity analyses.

Results

A total of 54 genetic loci were scored. The 17 loci with frequencies of the common allele less than 0.95 in at least

Table 1

Loci analyzed in even-year pink salmon broodlines from Japan, Russia, and Alaska, their enzyme numbers and designations (Shaklee et al., 1990), the tissue(s) and buffer(s) in which they were scored, and the level of variability observed.

Enzyme	Enzyme number	Locus	Tissue[1]	Buffer[2]	Level of variability[3]
Aconitate hydratase	4.2.1.3	*sAH**	L	8	2
		*mAH-1**	H	4,5,6	2
		*mAH-2**	H	4,5,6	3
		*mAH-3**[4,5]	H,M	4,5,6	2
		*mAH-4**[4,5]	H,M	4,5,6	3
Alanine aminotransferase	2.6.1.2	*ALAT**[4]	M	2	2
Aspartate aminotransferase	2.6.1.1	*sAAT-1,2**[4]	M,H	4,6	2
		*sAAT-3**[4,5]	E	7	3
		*sAAT-4**	L	8	3
		*mAAT-1**[4]	M,H	4,6	1
		*mAAT-2**	L	8	1
Creatine kinase	2.7.3.2	*CK-A1**[4,5]	M	1	2
		*CK-A2**[4,5]	M	1	2
		*CK-B**	E	7	2
		*CK-C1**	E	7	3
		*CK-C2**	E	7	2
Formaldehyde dehydrogenase	1.2.1.1	*FDHG**[4]	H	2	2
Fumarate hydratase	4.2.1.2	*FH**	M	4	3
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**[4,5]	M	1	2
		*GPI-B1,2**[4,5]	M	1	2
Glutathione reductase	1.6.4.2	*GR**[4]	E	4,5	3
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**[4,5]	M	2,3	3
Guanine deaminase	3.5.4.3	*GDA**	L	7,8	3
L-Iditol dehydrogenase	1.1.1.14	*IDDH**	L	7	2
Isocitrate dehydrogenase	1.1.1.42	*mIDHP-1**[4]	M,H	4	1
		*mIDHP-2**[4]	M,H	4	1

continued

one collection were *sAAT-3**, *sAAT-4**, *mAH-2**, *mAH-4**, *CK-C1**, *FH**, *GDA**, *G3PDH-1**, *GR**, *LDH-A1**, *sMDH-A1**, *sMDH-B2**, *mMEP-1**, *PEP-LT**, *PEPB**, *PEPD-2**, and *PGDH**. At 22 other variable loci, the frequency of the common allele was greater than 0.95 in all collections: *sAAT-1,2**, *mAH-1**, *sAH**, *mAH-3**, *ALAT**, *CK-A1**, *CK-A2**, *CK-B**, *CK-C2**, *FDHG**, *GPI-A**, *GPI-B2**, *IDDH**, *mIDHP-1**, *LDH-B1**, *LDH-B2**, *MPI**, *PEPD-1**, *PGM-2**, *TPI-2**, and *TPI-4**. The remaining 15 loci were monomorphic for the same allele in all collections.

The allelic frequencies observed are generally comparable to data for the few loci published by Russian geneticists (Altukhov et al., 1983; Salmenkova and Omelchenko, 1983; Zhivotovsky et al., 1989; Kartavtsev, 1991; Kartavtsev et al., 1992) except that we observed the *PGDH*95* allele in all regions. Detection of that allele requires careful adjustment of the buffer pH, otherwise it migrates with the common allele. The pH at which Gharrett et al. (1988) analyzed *PGDH** did not distinguish that allele from the **100* allele.

Tests of conformance to Hardy-Weinberg expectations for genotypic frequencies were made for 126 locus-collection combinations. Of these, four did not conform ($P<0.05$); this is fewer than would be expected at random. However, the sample size for most tests was small; therefore only large deviations from Hardy-Weinberg expectations would have been detected. Homogeneity within and among drainages, geographic regions, and continents or marine basins was tested by using 28 loci at which more than 5 variant alleles were observed (Table 2). Four rivers on Sakhalin Island were the only drainages from which multiple, temporally stratified collections were sampled during the spawning season. The numerous samples collected within the Ochepukha River system permitted treatment of its Znamenka tributary as a fifth separate system. Only a subset of loci was scored in some collections, but at least one collection from each river was scored for the entire set of loci. No overall heterogeneity ($P>0.05$) was observed for any Sakhalin drainage, and only a few loci suggested heterogeneity (Table 2), which vanishes when corrections

Table 1 (continued)

Enzyme	Enzyme number	Locus	Tissue[1]	Buffer[2]	Level of variability[3]
Lactate dehydrogenase	1.1.1.27	*LDH-A1*[4,5]*	M	1	3
		LDH-A2[4,5]*	M	1	1
		LDH-B1[4]*	H	1	2
		*LDH-B2**	L	1	2
		LDH-C[4,5]*	E	7	1
Malate dehydrogenase	1.1.1.37	*sMDH-A1,2**	L	6	3
		sMDH-B1,2[4,5]*	M	2,3	3
Malic enzyme	1.1.1.40	*mMEP-1*[4,5]*	M	3,4	3
Mannose-6-phosphate isomerase	5.3.1.8	*MPI*[4,5]*	H	2	2
Peptidase:					
Cytosol non-specific dipeptidase (glycyl-leucine)	3.4.–.–	*PEPA*[4]*	M	2	1
Tripeptide aminopeptidase (zinc enzyme) (leucyl-glycyl-glycine)	3.4.–.–	*PEPB*[4]*	M	1	3
Leucyl-tyrosine peptidase	3.4.–.–	*PEP-LT**	M	2,4	3
Phosphoglucomutase	5.4.2.2	*PGM-2*[4,5]*	M	3	2
Phogluconate dehydrogenase	1.1.1.44	*PGDH*[4,5]*	E	3	3
Phosphoglycerate kinase	2.7.2.3	*PGK-1**	L	8	1
		*PGK-2**	L	8	1
X-proline dipeptidase	3.4.13.9	*PEPD-1*[4,5]*	M	2	2
		PEPD-2[4,5]*	M	2	3
Superoxide dismutase	1.15.1.1	*sSOD-1*[4,5]*	L	7	1
		*mSOD**	H	1,2	1
Triose-phosphate isomerase	5.3.1.1	*TPI-1*[4]*	E	7	1
		TPI-2[4]*	E	7	2
		TPI-3[4]*	E	7	1
		TPI-4[4]*	E	7	2

[1] E = eye; H = heart; L = liver; M = muscle; preferred tissue listed first.

[2] 1 = lithium hydroxide (Ridgway et al., 1970);
2 = Tris-EDTA-borate (Boyer et al., 1963);
3 = amine citrate, pH 6.1 (Clayton and Tretiak, 1972);
4 = Tris-citrate, pH 7.0 (Shaw and Prasad, 1970);
5 = Tris-citrate discontinuous (Schaal and Anderson, 1974);
6 = amine-citrate-EDTA, pH 7.2 (modified from Clayton and Tretiak, 1972);
7 = Tris-glycine (Holmes and Masters, 1970);
8 = amine-citrate, pH 6.8 (modified from Clayton and Tretiak, 1972).

[3] 1 = monomorphic;
2 = low (frequency of most prevalent allele >0.95);
3 = high (frequency of most prevalent allele ≤0.95).

[4] Loci included in 36-locus version of neighbor-joining tree and gene diversity analysis.

[5] Loci included in 21-locus version of neighbor-joining tree.

are made for multiple testing. This is especially notable for the series of collections from the Znamenka (9 collections, P=0.43) and Ochepukha (6 collections, P=0.52) rivers. No heterogeneity was detected among Sakhalin drainages (G=131.01, 127 df; P=0.39).

The three Japanese (Hokkaido) collection sites were the Tokushibetsu River on the Sea of Okhotsk coast, the Kushiro River facing the northwestern Pacific Ocean, and the Yurappu River southwest of the Kushiro River on Hokkaido's eastern coast. The synthetic Yurappu stock is derived in large part from Okhotsk coast stocks, including the Tokushibetsu stock. The genetic profile of the Yurappu stock resembles that of the Tokushibetsu stock except at *sAAT-3** (P=0.018, analysis not shown), which suggests a founder effect or subsequent divergence. The Yurappu sample was not used in subsequent analyses. Overall heterogeneity was observed between the Kushiro and Tokushibetsu Rivers (G=48.87, 33 df; P=0.037) (Table 2), although tests at the four loci suggest heterogeneity was not significant after correction for multiple testing.

Table 2

Hierarchical homogeneity tests. Levels are among collections within streams, among streams within drainages, among drainages within a region, among Asian regions, and between Asia and Prince William Sound, Alaska. Degrees of freedom of tests at lower levels of hierarchy may differ from (be lower than) those necessary for the overall hierarchical analysis. — indicates that no test was possible because there were data for only one collection. The hierarchical nature of the analysis precludes multiple testing corrections in the table because several different hypotheses are possible.

	*sAAT-4**		*sAH**		*GDA**		*FDHG**		*sAAT-3**		*CK-C1**		*PGDH**		*TPI-2**	
Collection site	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df
Asia																
Hokkaido	0.96	1	1.46	1	0.66	4	1.8	2	0.48	1	1.36	1	8.79[a]	3	0	1
Sakhalin																
Dolinka	—		—		—		—		—		—		0.71	3	—	
Lutoga	—		1.81	1	3.55	4	0.82	2	0.03	1	—		7.49	9	0	1
Monetka	—		1.64	1	5.45	4	0.01	2	0.01	1	0.02	1	6.89[a]	3	0	1
Ochepukha																
Other	—		—		—		—		—		—		7.01	15	—	
Znamenka	—		0	1	3.14	4	0.09	2	0.002	1	—		25.31	24	0	1
Within Ochepukha	—		0	1	3.14	4	0.09	2	0.002	1	—		32.32	39	0	1
Between Ochepukha	—		4.67[a]	1	1.01	4	4.74[a]	2	0.001	1	0.70	1	4.42	3	0	1
Total Ochepukha	—		4.67	2	4.15	8	4.82	4	0.003	2	0.70	1	36.74	42	0	2
Within Sakhalin	—		8.12	4	13.15	16	5.65	8	0.03	4	0.72	2	51.83	57	0	4
Among Sakhalin	—		1.21	3	10.84	12	7.33	6	0.96	3	7.53	3	6.40	9	0	3
Total Sakhalin	—		9.34	7	23.99	28	12.98	14	1	7	8.25	5	58.22	66	0	7
Northern Sea of Okhotsk	—		—		—		0.20	2	—		—		3.29	3	0	1
Western Kamchatka	—		0	2	10.07	8	8.03	8	10.61[a]	4	1.08	2	11.67	12	0	4
Eastern Kamchatka	—		0	1	6.28	4	0.02	2	1.31	1	0.14	1	3.19	3	0	1
Within Asia	0.96	1	10.80	11	41.00	44	23.04	28	13.40	13	10.84	9	85.16	87	0	14
Among Asia	6.64[b]	1	3.04	3	39.75[d]	12	19.89[a]	8	56.59[d]	3	3.00	3	65.95[d]	12	0	4
Total Asia	7.60[a]	2	13.84	14	80.75[a]	56	42.93	36	69.99[d]	16	13.84	12	151.11[d]	99	0	18
North America																
Prince William Sound	7.8	4	2.45	4	10.02	16	3.20	8	3.96	4	4.90	4	18.58[a]	12	3.38	4
Total within	15.40[a]	6	16.29	18	90.77	72	46.13	44	73.95[d]	20	18.74	16	169.69[d]	111	3.38	22
Between Alaska and Asia	0.95	1	0	1	107.53[d]	4	23.51[d]	2	269.38[d]	1	8.83[b]	1	43.12[d]	3	39.30[d]	1
Total for collections	16.34[a]	7	16.29	19	198.30[d]	76	69.64[a]	46	343.33[d]	21	27.57	17	212.81[d]	114	42.68[b]	23

	*TPI-4**		*mAH-4**		*G3PDH-1**		*GPI-B2**		*GPI-A**		*LDH-A1**		*LDH-B1**	
Collection site	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df
Asia														
Hokkaido	5.30[a]	1	0	2	0.14	3	1.33	3	2.9	2	0	3	1.45	2
Sakhalin														
Dolinka	—		—		0.02	3	—		—		—		—	
Lutoga	0.07	1	2.76	2	1.69	9	0	3	1.01	2	1.05	3	1.05	2
Monetka	1.39	1	1.73	2	0.47	3	1.45	3	0	2	0	3	0	2
Ochepukha														
Other	—		—		3.16	15	—		—		—		—	
Znamenka	1.39	1	0.76	2	12.71	24	0	3	1.39	2	1.43	3	0	2
Within Ochepukha	1.39	1	0.76	2	15.88	39	0	3	1.39	2	1.43	3	0	2
Between Ochepukha	0.81	1	0.20	2	0.01	3	0	3	0.83	2	0.22	3	2.20	2
Total Ochepukha	2.20	2	0.97	4	15.89	42	0	6	2.22	4	1.65	6	2.20	4
Within Sakhalin	3.66	4	5.45	8	18.06	57	1.45	12	3.23	8	2.70	12	3.25	8
Among Sakhalin	1.41	3	5.41	6	4.54	9	3.93	9	2.22	6	6.76	9	2.14	6
Total Sakhalin	5.06	7	10.86	14	22.60	66	5.38	21	5.45	14	9.47	21	5.39	14
Northern Sea of Okhotsk	0.19	1	0.64	2	0.33	3	0.19	3	0.19	2	—		0	2

continued

Table 2 (continued)

Collection site	*TPI-4** G	df	*mAH-4** G	df	*G3PDH-1** G	df	*GPI-B2** G	df	*GPI-A** G	df	*LDH-A1** G	df	*LDH-B1** G	df
Western Kamchatka	8.87	4	7.85	8	14.91	12	13.24	12	6.60	8	2.99	12	2.07	8
Eastern Kamchatka	1.67	1	2.53	2	0.003	3	1.58	3	0	2	2.47	3	0	2
Within Asia	21.10	14	21.88	28	37.98	87	21.72	42	15.14	28	14.92	39	8.91	28
Among Asia	17.06[b]	4	14.21	8	10.69	12	13.85	12	9.58	8	7.59	12	1.60	8
Total Asia	38.16[b]	18	36.08	36	48.66	99	35.56	54	24.72	36	22.51	51	10.5	36
North America														
Prince William Sound	0	4	2.98	8	7.32	12	3.17	12	6.55	8	13.31[b]	12	6.78	8
Total within	38.16[a]	22	39.06	44	55.98	111	38.73	66	31.27	44	35.82	63	17.28	44
Between Alaska and Asia	7.36[b]	1	28.86[d]	2	42.64[d]	3	28.71[d]	3	6.12[a]	2	23.20[d]	3	4.09	2
Total for collections	45.52[b]	23	67.93[a]	46	98.62	114	67.44	69	37.39	46	59.02	66	21.37	46

Collection site	*LDH-B2** G	df	*PEPLT** G	df	*PGM-2** G	df	*PEPD-1** G	df	*PEPD-2** G	df	*FH** G	df	*GR** G	df
Asia														
Hokkaido	0	3	0.88	2	1.37	2	0	1	2.56	4	0	2	2.90	2
Sakhalin														
Dolinka	—		—		—		—		—		—		—	
Lutoga	1.05	3	—		1.05	2	0	1	1.52	8	0	2	0.35	2
Monetka	0	3	—		1.41	2	2.04	1	6.28[a]	4	2.78	2	2.95	2
Ochepukha														
Other	—		—		—		—		7.46	20	—		—	
Znamenka	1.39	3	—		1.39	2	4.25	3	11.10	28	5.25	2	0.08	2
Within Ochepukha	1.39	3	—		1.39	2	4.25	3	18.56	48	5.25	2	0.08	2
Between Ochepukha	3.01	3	—		0.81	2	1.10	1	5.81	4	2.44	2	0.03	2
Total Ochepukha	4.40	6	—		2.20	4	5.35	4	24.37	52	7.68	4	0.11	4
Within Sakhalin	5.45	12	—		4.66	8	7.39	6	32.16	64	10.46	8	3.41	8
Among Sakhalin	8.11	9	—		0.62	6	2.24	3	13.24[a]	12	6.49	6	3.67	6
Total Sakhalin	13.56	21	—		5.28	14	9.63	9	45.41	76	16.95	14	7.08	14
Northern Sea of Okhotsk	—		—		0	2	0	1	0.57	4	—		—	
Western Kamchatka	3.00	9	7.00	6	0	8	8.34	4	16.05	16	6.34	6	10.05	8
Eastern Kamchatka	0	3	1.30	2	0	2	0.27	1	0.81	4	0.72	2	0.18	2
Within Asia	16.56	36	9.17	10	6.65	28	18.24	16	65.40	104	24.00	24	20.21	26
Among Asia	5.23	12	9.78	6	10.08	8	6.45	4	74.59[d]	16	79.18[d]	8	76.78[d]	8
Total Asia	21.79	48	18.95	16	16.73	36	24.69	20	139.99	120	103.18[d]	32	96.98[d]	34
North America														
Prince William Sound	3.20	12	5.60	8	8.16	8	2.37	4	3.09	16	11.02	8	3.26	8
Total within	24.99	60	24.55	24	24.89	44	27.06	24	143.09	136	114.20[d]	40	100.24[d]	42
Between Alaska and Asia	12.25[b]	3	6.27[a]	2	2.94	2	0.32	1	18.69[c]	4	6.72[a]	2	33.91[d]	2
Total for collections	37.24	63	30.82	26	27.82	46	27.38	25	161.78	140	120.92[d]	42	134.15[d]	44

Collection site	*sMDH-A1,2** G	df	*sMDH-B1,2** G	df	*mMEP-1** G	df	*MPI** G	df	*PEPB** G	df	*mAH-2** G	df	Total for loci G	df
Asia														
Hokkaido	0.09	4	2.74	6	0.77	2	0.001	2	6.64[a]	2	4.30[a]	1	48.87[a]	62
Sakhalin														
Dolinka	—		1.95	6	5.95[a]	2	—		—		—		8.63	14
Lutoga	0.77	4	4.47	18	3.67	6	0.21	2	0.05	2	—		34.47	89

continued

Table 2 (continued)

Collection site	*sMDH-A1,2** G	df	*sMDH-B1,2** G	df	*mMEP-1** G	df	*MPI** G	df	*PEPB** G	df	*mAH-2** G	df	Total for loci G	df
Monetka Ochepukha	1.75	4	1.20	6	0.01	2	0.34	2	1.33	2	2.07	1	41.20	59
Other	—		25.79	30	3.28	10	—		—		—		46.70	90
Znamenka	0.11	4	37.29	48	4.14	16	1.35	2	8.47	6	0	1	121.04	186
Within Ochepukha	0.11	4	63.08	78	7.43	26	1.35	2	8.47	6	0	1	167.74	276
Between Ochepukha	0.03	4	6.60	6	1.25	2	1.87	2	3.16	2	—		45.91	58
Total Ochepukha	0.15	8	69.68	84	8.67	28	3.22	4	11.62	8	0	1	213.66	334
Within Sakhalin	2.67	16	77.30	114	18.30	38	3.77	8	13.01	12	2.07	2	297.94	496
Among Sakhalin	8.52	12	16.07	18	1.10	6	2.28	6	3.54	6	4.44	3	131.01	177
Total Sakhalin	11.19	28	93.37	132	19.40	44	6.05	14	16.55	18	6.51	5	428.95	673
Northern Sea of Okhotsk	0.60	4	0	6	0.66	2	0	2	9.55[b]	2	—		16.41	41
Western Kamchatka	0.16	12	18.47	24	4.87	8	5.21	8	6.08	8	6.55	3	190.11	220
Eastern Kamchatka	4.08	4	4.02	6	3.38	2	1.57	2	2.14	2	1.42	1	39.07	61
Within Asia	16.11	52	118.60	174	29.07	58	12.82	28	40.96	32	18.78	10	723.41	1057
Among Asia	74.76[d]	16	45.82[b]	24	8.14	8	15.98[a]	8	76.91[d]	8	15.69[b]	4	768.81[d]	236
Total Asia	90.87[a]	68	164.42	198	37.21	66	28.81	36	117.87[d]	40	34.47[b]	14	1492.22[d]	1293
North America														
Prince William Sound	5.67	16	13.22	24	4.12	8	6.27	8	11.49	8	8.31[a]	3	176.78[a]	247
Total within	96.53	84	177.64	222	41.33	74	35.08	44	129.36[d]	48	42.78	17	1669.01[d]	1540
Between Alaska and Asia	9.40	4	12.09	6	4.06	2	1.73	2	12.88[b]	2	2.33	1	717.87[d]	62
Total for collections	105.93	88	189.73	228	45.39	76	36.81	46	142.24[d]	50	45.11[c]	18	2386.85[d]	1602

[a]$P < 0.05$, [b]$P < 0.01$, [c]$P < 0.001$, [d]$P < 0.0001$.

No overall heterogeneity was observed in tests among collections within each of the remaining geographic regions: northern Okhotsk coast, eastern Kamchatka, and western Kamchatka (Table 2). The northern Okhotsk and western Kamchatka collections each had a single locus that indicated heterogeneity, but neither test was significant after correction for multiple testing.

The Alaska (Prince William Sound) collections exhibited low heterogeneity over all loci (G=176.78, 147 df; P=0.047) (Table 2); tests at three loci suggested that heterogeneity was not significant after correction for multiple testing. Although not the focus of this paper, the overall heterogeneity suggests local genetic structure in even-year pink salmon within Prince William Sound.

The collections of even-year pink salmon within the Asian geographic regions were relatively homogeneous, but we found strong heterogeneity among regions (G=1492.22, 1257 df; $P<10^{-4}$) (Table 2). Of the nine loci that individually suggest heterogeneity, eight (*GDA**, *sAAT-3**, *PGDH**, *PEPD-2**, *FH**, *GR**, *sMDH-A1**, and *PEPB**) showed significant heterogeneity (P<0.05) after correction for multiple testing. The ratios of heterogeneities among regions to heterogeneity within regions (approximate F's) for each locus (not shown) were significant (P<0.05) for 13 of 28 loci, and comparisons of *GDA**, *sAAT-3**, *PGDH**, *PEPD-2**, *FH**, *GR**, *sMDH-A1**, *sMDH-B2**, and *PEPB** were highly significant (P<0.001).

At the next level of hierarchy, between continents, Asian samples (in aggregate) differed overall from the Alaska samples with which they were compared (G=717.87, 62 df; $P<<10^{-6}$) (Table 2); many of the loci examined contribute to the difference. After correction for multiple tests, *GDA**, *FDHG**, *sAAT-3**, *PGDH**, *TPI-2**, *mAH-4**, *G3PDH-1**, *GPI-B2**, *LDH-A1**, and *GR** were strongly significant (P<0.001). Of these loci, *GDA**, *sAAT-3**, *PGDH**, *mAH-4**, *G3PDH-1**, *LDH-A1**, and *GR** had appreciable variation (common allele <0.95) in at least some populations. These results suggest that at least seven allozyme loci may prove useful for distinguishing among even-year pink salmon stocks from different regions of the northern Pacific Ocean (Hawkins et al., 1998).

Data from 36 loci common to all regions were used to estimate pairwise chord distances (Cavalli-Sforza and Edwards, 1967) with which we constructed an unrooted neighbor-joining tree (Fig. 2). The tree supports a geographic basis for the variability observed among collections and suggests a geographic relationship among regions. Four clusters are evident along the tree axis: in linear order, they consisted of the collections from southern Okhotsk (Hokkaido Island and Sakhalin Island), western Kamchatka, eastern Kamchatka, and Alaska. The greatest distance was between the Alaska cluster and all the other collections. When the Magadan samples were included in a similar tree with data from 34 loci, they

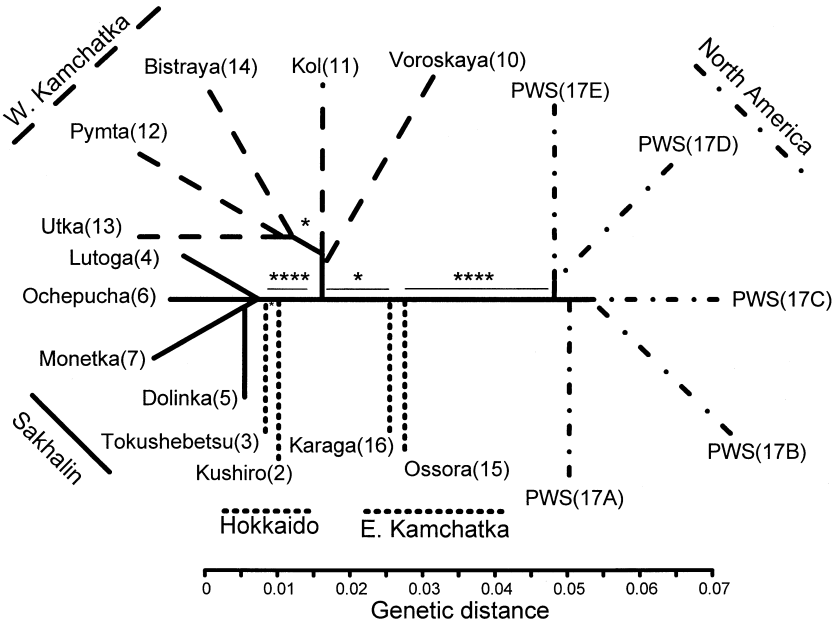

Figure 2

Neighbor-joining tree of even-year pink salmon broodlines from Japan, Russia, and Prince William Sound based on Cavalli-Sforza and Edwards (1967) chord distances from allele frequencies at 36 loci. Significance between nodes or for collections joined at nodes were tested within regions by using log-likelihood ratios (*G*-tests; Sokal and Rohlf, 1995) of the 36 loci to test homogeneity of branches joined at a node, and between basins by tests of homogeneity among the populations of the two adjacent regions. The numbers following the population names correspond to their locations in Figure 1. PWS = Prince William Sound.

clustered with the eastern and western Kamchatka collections (not shown). The arrangement of the other clusters remained as in Figure 2.

The variation at 36 loci common to all collections was partitioned by using gene diversity analysis (G_{ST}'s; Chakraborty and Leimar, 1987) and analysis of variance (θ_{ST}'s; Weir and Cockerham, 1984; Weir, 1996) (Table 3). Analysis of variance accounts for bias inherent in analyses that use finite samples from and small numbers of populations. Differences between the G_{ST}'s and θ_{ST}'s are most apparent at upper levels of the hierarchy where fewer groups are compared. Although biased, the G_{ST}'s have been widely used, so we summarize results of partitioning variation with G_{ST}'s but included θ_{ST}'s parenthetically. On average, variation within streams accounted for 97.2% (95.57%) of the total, with 0.63% (0.05%) attributable to differences among streams within regions, 0.65% (1.29%) to differences among regions within continents, and 1.52% (3.09%) to differences between continents.

We combined our data with available data (Altukhov et al., 1983; Salmenkova and Omelchenko, 1983; Zhivitovsky et al., 1989; Kartavtsev, 1991; Kartavtsev et al., 1992) to conduct a log-likelihood ratio analysis to test for homogeneity within and among Asian regions. The primary (variable) loci for which data were available were *PGDH** (omitting collections missing the **95* allele), *G3PDH-1**, and *MDH-B1,2**. These data included collections from Primorie, western Sakhalin Island, and the Kuril Islands in addition to the regions we reported (Table 4). There was no overall heterogeneity within regions and only a single test suggested heterogeneity. However, *PGDH** and *MDH-B1,2** exhibited strong heterogeneity ($P<10^{-4}$) among regions.

Data from an earlier study of genetic diversity in Alaska pink salmon (Gharrett et al., 1988) were included to produce an unrooted neighbor-joining tree based on 21 loci common (Appendix 1) to that study and the present one (Fig. 3). Data from all collections were condensed by region, except for Japan, where the collections were heterogeneous. Some regions were represented by a single collection; data for the Aleutian Islands collections were pooled because they exhibited no heterogeneity, but as a group differed from other Western Alaska regions (Gharrett et al., 1988). The Magadan collections were omitted from our analysis because data from several of the 21 loci were unavailable. As in the previous analysis, the tree showed a clear geographic basis for genetic variation. A cluster containing the Japan and Sakhalin Island collections adjoined the western Kamchatka group. A longer span joined the latter with a cluster consisting of the eastern Kamchat-

Table 3

Gene diversity analysis of even-year pink salmon broodlines. Relative gene diversities are estimated from the variable loci in the 36-locus set that these collections had in common. Estimates and standard deviations are jackknife estimates over loci and based on the total expected heterozygosity at each level of hierarchy (*G*'s; Chakraborty and Leimar, 1987) or analysis of variance (θ's; Weir, 1996) in parentheses.

Source	Number of collections	G_{ST} (θ_{SS})	G_{SL} (θ_S–θ_S)	G_{LR} (θ_S–θ_P)	G_{RT} (θ_P)
Asia	13	0.0150 ±0.0007	0.0051 ±0.0001	0.0099 ±0.0007	
		(0.0144 ±0.0011)	(0.0003 ±0.0001)	(0.0140 ±0.0012)	
Southern Sea of Okhotsk	6	0.0024 ±0.0001	0.0016 ±0.0001	0.0007 ±0.0001	
		(0.0000 ±0.0002)	(–0.0003 ±0.0001)	(0.0003 ±0.0001)	
Hokkaido	2	0.0022 ±0.0002			
		(–0.0008 ±0.0004)			
Southern Sakhalin	4	0.0014 ±0.0001			
		(–0.0002 ±0.0001)			
Western Kamchatka	5	0.0085 ±0.0003			
		(0.0019 ±0.0003)			
Eastern Kamchatka	2	0.0053 ±0.0005			
		(0.0030 ±0.0010)			
Alaska (Prince William Sound)	5	0.0089 ±0.0004			
		(0.0005 ±0.0005)			
Total	18	0.0280 ±0.0021	0.0063 ±0.0002	0.0065 ±0.0005	0.0152 ±0.0019
		(0.0443 ±0.0055)	(0.0005 ±0.0001)	(0.0129 ±0.0011)	(0.0309 ±0.0055)

Table 4

Log-likelihood ratio analysis of allozyme data available for Asian even-year pink salmon broodlines (Altukhov et al., 1983; Salmenkova and Omelchenko, 1983; Zhivotovsky et al., 1989; Kartavtsev, 1991; Kartavtsev et al., 1992; our paper). Data include three alleles or allele pools (*100, *95, and *90) at *PGDH** for 4587 individuals from 42 collections, two alleles or allele pools (*100 and all others) at *G3PDH** for 6398 fish from 53 collections, and three alleles or allele pools (*100, fast alleles, and slow alleles at *sMDH-B1,2** for 6336 individuals from 53 collections.

Region	*PGDH** *G* (df)	*G3PDH** *G* (df)	*MDHB-1,2** *G* (df)
Hokkaido	5.84 (2)	0.52 (1)	0.80 (2)
Primoriya	6.08 (6)	8.10 (4)	16.66* (8)
Western Sakhalin Island	0.71 (2)	1.04 (3)	6.03 (6)
Eastern Sakhalin Island	19.67 (16)	14.99 (12)	34.94 (24)
Kuril Islands	33.36 (26)	11.83 (13)	16.67 (26)
Northern Sea of Okhotsk	4.37 (4)	2.02 (5)	15.88 (10)
Western Kamchatka	7.50 (10)	8.53 (5)	9.42 (10)
Eastern Kamchatka	3.04 (2)	0.03 (2)	6.59 (4)
Total within region	80.58 (68)	47.07 (45)	107.00 (90)
Among regions	110.05*** (14)	13.92 (7)	50.21*** (14)
Total	190.61*** (82)	60.99 (52)	157.21** (104)

* = $P < 0.05$; ** = $P < 0.001$; *** = $P < 0.0001$.

ka, Aleutian Islands, Norton Sound, and Bristol Bay collections. A cluster consisting of Kodiak Island and Prince William Sound collections was separated from the other groups by the longest distance in this tree. The neighbor-joining tree suggested three large geographic aggregations of pink salmon populations which correspond to marine basins: the Sea of Okhotsk, the Bering Sea, and the Gulf of Alaska. Using those basins as the basis for gene diversity hierarchy, we partitioned the variation. We estimated the proportion of the total variation attributable to differ-

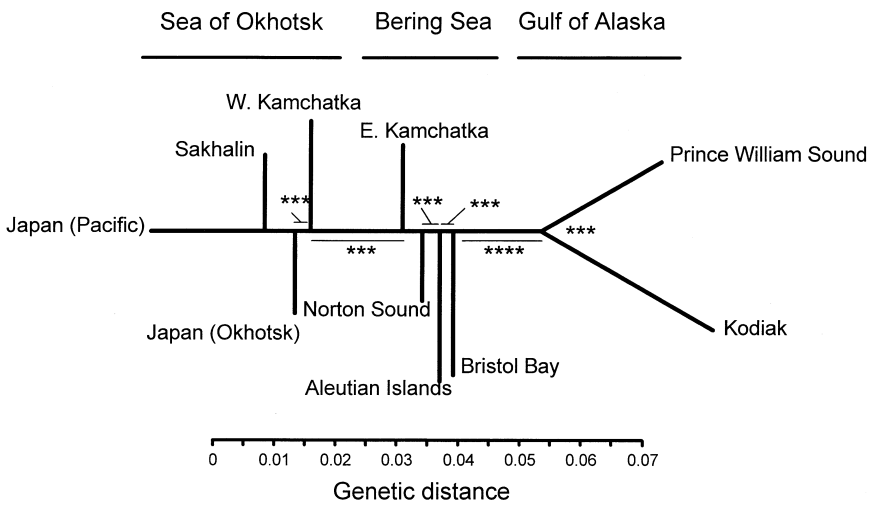

Figure 3

Neighbor-joining tree based on allele frequencies at 21 loci, showing Cavalli-Sforza and Edwards (1967) chord distances among pink salmon from Japan, Russia, and Alaska. Significance between nodes or of collections joined at nodes were tested within basins by using log-likelihood ratios (*G*-tests; Sokal and Rohlf, 1995) of the 21 loci to test homogeneity of branches joined at a node, and between basins by tests of homogeneity of the two adjacent branches. Jack-knifing populations to test the stability of the tree produced two local rearrangements that involved only the Aleutian Islands and Bristol Bay collections. The eastern Pacific Ocean and Bering Sea collections had the following sample sizes: Bristol Bay, n = 146; Aleutian Islands, n = 642; Norton Sound, n = 201; and Kodiak Island, n = 66 (Gharrett et al., 1988).

Table 5

Gene diversity analysis of even-year pink salmon broodlines. Relative gene diversities are estimated from the 21-locus set common to collections of this study and that of Gharrett et al. (1988). Estimates and standard deviations are jackknife estimates based on the total expected heterozygosity at each level of hierarchy.

Source	Number of regions	G_{ST}	G_{SG}	G_{GT}
Sea of Okhotsk	3	0.0031 ±0.0006		
Bering Sea	4	0.0079 ±0.0003		
Gulf of Alaska	2	0.0043 ±0.0006		
Total	9	0.0230 ±0.0025	0.0055 ±0.0002	0.0175 ±0.0025

ences among regions (G_{ST}) as well as to the average variation among regions within a basin (G_{SG}) and among basins (G_{GT}) (Table 5). The diversity within areas was low, ranging from 0.31 to 0.79%, and averaging 0.55%. The diversity among areas was 1.75%, and the average within each stream was 98.25%.

We also analyzed genetic variability by comparing average expected heterozygosities (Nei, 1978). Eastern Pacific pink salmon populations appeared to have higher heterozygosities than western populations. With the 36-locus data set, the average heterozygosity of the five Alaska collections was 0.074 ±0.004 (mean ±SE) compared with 0.056 ±0.004 for 13 Asian collections. Using the 21 loci common to the three geographic regions shown by Figure 3, we estimated heterozygosities of 0.061 ±0.002 for three regions within the Sea of Okhotsk, 0.073 ±0.004 for four regions in the Bering Sea, and 0.099 ±0.003 for the two regions in the Gulf of Alaska. Heterozygosities for these samples of allozyme loci increased from west to east.

Discussion

Heterogeneity among even-year pink salmon populations in Asian regions contrasted strongly with the relative homogeneity we observed within regions. For example,

western Kamchatka and eastern Sakhalin Island face each other across the Sea of Okhotsk but have different allele frequencies at *PEPD-2*100* [0.71 ±0.02 (SE) for western Kamchatka versus 0.61 ±0.01 for eastern Sakhalin), *GR*100* (0.90 ±0.01 versus 0.97 ±0.005), *PEPB*100* (0.91 ±0.01 versus 0.79 ±0.01), and *PGDH*100* (0.76 0.02 versus 0.82 ±0.01). Therefore, it is unlikely that there is substantial gene flow between these regions. If large movements of spawning pink salmon occur (fluctuating stock hypothesis; e.g. Zhivotovsky and Glubokovsky, 1989; Shuntov et al. 1994), our results suggest that they are restricted to within-region movements for even-year pink salmon. Moreover, the relative homogeneity observed within regions does not necessarily indicate large numbers of strays. Relatively small exchanges between drainages (say 10 fish or so per generation) can arrest genetic divergence (e.g. Gharrett, 1994). This level of straying does not, however, provide demographic insurance against overfishing or environmental catastrophes in the short run (Hop and Gharrett, 1989).

The contemporary genetic structure of even-year pink salmon has practical implications for fishery scientists. Genetic differences among populations can be used as markers for stock identification. It is often necessary to manage a species that has as many small populations as pink salmon as a regional assemblage. The regional basis for genetic structure observed in Asian pink salmon lends itself to stock separation analyses (Hawkins et al., 1998).

Most of the genetic variability observed in even-year pink salmon is attributable to within-population variability (e.g. Gharrett et al., 1988; Beacham et al., 1988). However, low levels of divergence among populations do not preclude hierarchical population structure. In our study we saw little or no temporal structure among Sakhalin Island populations. This finding does not necessarily conflict with observations of temporal structure observed by Altukhov et al. (1983) who used much larger numbers of fish (but fewer alleles), by McGregor et al. (1998) who used multiple years of data and numerous loci, and by Brykov et al. (1999) who used highly variable mitochondrial DNA haplotypes, because their tests had much greater statistical power. In addition, allozymes may not be appropriate for detecting some kinds of population structure because a very low level of gene flow can "homogenize" frequencies of neutral or nearly neutral loci. Note, for example, the genetic component observed for time of return within a spawning season (Smoker et al., 1998) and the persistence of a genetic marker for time of spawning (Lane et al., 1990).

The strong regional structure we observed in Asian even-year pink salmon populations is a stark contrast to the nearly complete absence of structure reported for odd-year Kamchatka pink salmon (Varnavskaya and Beacham, 1992; Shaklee and Varnavskaya, 1994). However, the latter surveys covered smaller geographic ranges and included neither Sakhalin Island nor Japanese pink salmon populations. These combined studies involving numerous allozyme loci confirm the work of Zhivotovsky et al. (1989) who, using four allozyme loci, also recognized the brood-year differences; and who estimated that 1.6% (we estimated 1.75%) and 0.6% of the total genetic variability were attributable to interregional divergence for even- and odd-year broods, respectively.

The differences observed between Asian and North American even-year pink salmon are not surprising; they have been reported previously for both even-year (Zhivotovsky et al., 1989) and odd-year broodlines (Varnavskaya and Beacham, 1992; Shaklee and Varnavskaya, 1994). However, the strong coherence of populations within each of the major North Pacific basins (Sea of Okhotsk, Bering Sea, and Gulf of Alaska) is striking. Each basin includes a range of habitats and climates that suggests that the genetic similarity among populations within a geographic region does not result from convergent or homogeneous selection. The differences among populations of different basins are also reflected by the different average heterozygosities. The apparent directional change in heterozygosities could be interpreted in terms of differences in effective population size, age of the populations, or the extent of environmental variation. However, speculation is probably not warranted because three different variables can be arranged in a monotonic pattern in two of six different possible orders.

A more evocative explanation of the genetic structure combines geographic and oceanographic influences, as well as recent geologic history. Populations in the contemporary Sea of Okhotsk, Bering Sea, and Gulf of Alaska are separated geographically by land masses and oceanographically by the different currents that flow into or between the oceanic basins and that influence migration routes of the fish (Royce et al., 1968). The geographic separation was greatly exacerbated by the limits and effects of late Pleistocene glaciation. In their northern range, pink salmon populations experienced increased isolation between the marine basins as a result of lower sea level, loss of freshwater habitat to increased ice cover, and more extensive sea ice. Just as recent fluctuations in salmon productivity have resulted from relatively minor climate changes (Mantua et al., 1997), less favorable freshwater and marine environmental conditions undoubtedly decreased the sizes and numbers of populations dramatically, further isolating the remaining populations in this region.

During the past several 100,000 years, there have been periodic changes in climate, sea level, glacial extent, and oceanographic conditions. It is important to realize that our modern, interglacial conditions are an extreme (Sancetta and Silvestri, 1986) and that the oceanic record of global ice volumes (from the $\delta^{18}O$ record in marine sediments) and geologic evidence (Mann and Hamilton, 1995) from the north Pacific realm during that period indicate that lower sea levels, more extensive glaciation, colder sea surface temperatures, and more extensive and southerly sea ice were typical (Bartlein et al., 1991; Rohling et al., 1998). The relative proportion of the ^{18}O isotope ($\delta^{18}O$) in a stratum of a core is related to the portion of the earth's water tied up in ice at the time corresponding to the stratum, and consequently the sea level in relation to the modern sea level.

At the last glacial maximum (LGM: ca. 14,000–20,000 years before the present [BP]), the paleogeography of the

North Pacific coast line was severely altered, reducing the sizes of the enclosed basins as well as the circulation among them. $\delta^{18}O$ records (e.g. Bartlein et al., 1991; Rohling, 1998), and limited data from Beringia (Hopkins, 1982) suggest that during most of the mid-Wisconsin glaciation, sea level was 50 m lower than at present and that at the LGM, the level was 120 to 130 m lower in areas not affected by ice loading or tectonic activity (Fairbanks, 1989). Sakhalin Island was connected to the mainland and Hokkaido Island, blocking the northern outflow of the Sea of Japan; and the connection of a smaller Sea of Okhotsk with the Pacific Ocean through the Kurile islands was restricted. In the Bering Sea, the extensive continental shelf was exposed, blocking circulation through the Bering Strait. To the south, the Aleutian Islands and the Alaska Peninsula were joined to about 170°W, and many of the islands to the west were also connected, thus limiting the connections between the Gulf of Alaska and the Bering Sea. In Cook Inlet, glaciers may have remained advanced throughout the middle Wisconsin glaciation (Reger and Updike, 1983).

Pink salmon spawning habitat along the Gulf of Alaska was nearly completely eliminated at the LGM and much of the Beringian coastline was probably ice bound much of the year, minimizing available freshwater habitat. Coastal areas of the Gulf of Alaska, including most of the continental shelf, were extensively glaciated during the Quaternary Period, although a few isolated areas of the outer coast may have been ice free (Hamilton, 1986); and the ice cover of the eastern Aleutians coalesced with the Alaska Peninsula and ice caps covered all the major islands (Thorson and Hamilton, 1986). In these areas there may have been ephemeral streams from melted snow or ice at the southern margin, near the present shelf break. Although the rivers draining the Yukon-Kuskokwim region flowed over the exposed shelf and probably served as a refugium, the Bering Sea appears to have had sea ice cover much of the year (Sancetta, 1983; Sancetta and Robinson, 1983); and seasonal sea ice may have persisted as far south as 54°N for 6–8 months a year during the LGM (de Vernal and Pedersen, 1997). On the Asian side, glaciation was much less extensive and included some alpine glaciation; but few glaciers extended to tidewater, except possibly on the southeast side of the Kamchatka Peninsula (Bespalyy, 1984; Velichko, 1984; Anderson, 1981). Freshwater habitat was probably not reduced to the extent of the Gulf of Alaska coast. Nevertheless, the Sea of Okhotsk, like the Bering Sea, probably had sea ice cover much of the year (Sancetta, 1983; Sancetta and Robinson, 1983).

Harsh conditions greatly reduced marine surface water productivity over the entire region (Morley et al., 1991; Keigwin et al., 1992; deVernal and Pederson, 1997). Microfossils indicate that the subarctic Pacific Ocean was similar to the present day Sea of Okhotsk, with cold fresh surface water and a highly stratified water column. Sea surface temperatures estimated by CLIMAP were 2° to 4°C colder than present throughout the year over most of the area (Moore et al., 1980). Off Japan, temperatures were even colder (>6°C) at the LGM, indicating that the cold Oyashio Current penetrated farther south than it does at present (Moore et al., 1980).

Most of the description above considered the LGM, but $\delta^{18}O$ records indicate that periodically other major glacial advances occurred at about 135,000 BP (^{18}O stage 6), about 225,000 BP (^{18}O stage 8), and so forth (Bartlein et al., 1991). Another less extensive advance may have occurred in the North Pacific region about 75 ka BP (Hopkins, 1982). It is likely that those events also influenced the distribution and demographics of salmon species including pink salmon.

Many of the streams populated by pink salmon are short coastal streams that are transient. Consequently, in maximizing productivity opportunities, pink salmon may exhibit a higher level of gene flow (straying) than other Pacific salmon (Quinn, 1984). Geologic evidence suggests that the LGM did not affect Asian streams as broadly or severely as Alaskan streams. However, the freshwater environments were less favorable than at present, and it would be expected that the harsh marine environment severely reduced productivity, probably creating a situation in which many local populations repeatedly went extinct. The ability to exploit spawning habitat rapidly would have been an advantage during the LGM and many local extinctions were probably followed by recolonization. As a consequence, it is likely that a few systems provided the source for stock colonization following deglaciation. In the eastern range where habitat was ice-covered, re-establishment of pink salmon probably depended on colonization from the Bering or more southerly refugia, or possibly from the "off-year" broodline, if the rigid two year life cycle relaxes in marginal environments, such as appears to have happened in the Laurentian Great Lakes (e.g., Kwain and Chappel, 1978).

Overall, the geological events should have accentuated geographic boundaries and increased the importance of random drift. Divergence between Asian and North American populations suggests colonization from different refugia, and significant, but lesser, regional divergence supports homing in pink salmon, at least regionally. However, the low overall divergence observed among both Asian and North American populations (G_{ST}=0.023) suggests that the populations studied are either recently diverged and derived from a single population or from genetically similar ancestral populations, or that there is sufficient gene flow to arrest divergence. One of the advantages of studying pink salmon is that there are two broodlines occupying much of the same range. It will be interesting to examine the genetic structure of odd-broodline pink salmon in the same range, which will represent a second natural experiment with which to examine the influences of geography, oceanography, and geologic history on the genetic structure of pink salmon populations.

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