

**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.

a Allozyme -

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

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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 anal-

ysis 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  $-20^{\circ}\text{C}$  or to liquid nitrogen dewars at  $-196^{\circ}\text{C}$ . Long-term storage was maintained at  $-85^{\circ}\text{C}$ . 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://www.wabl.afsc.noaa.gov> in file *SIDA/pink\_salmon/evensia*.

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 ( $P < \text{about } 0.15$ ) has little influence on the analysis (Gharrett and Thomson, 1987). The genotypic frequencies observed at each

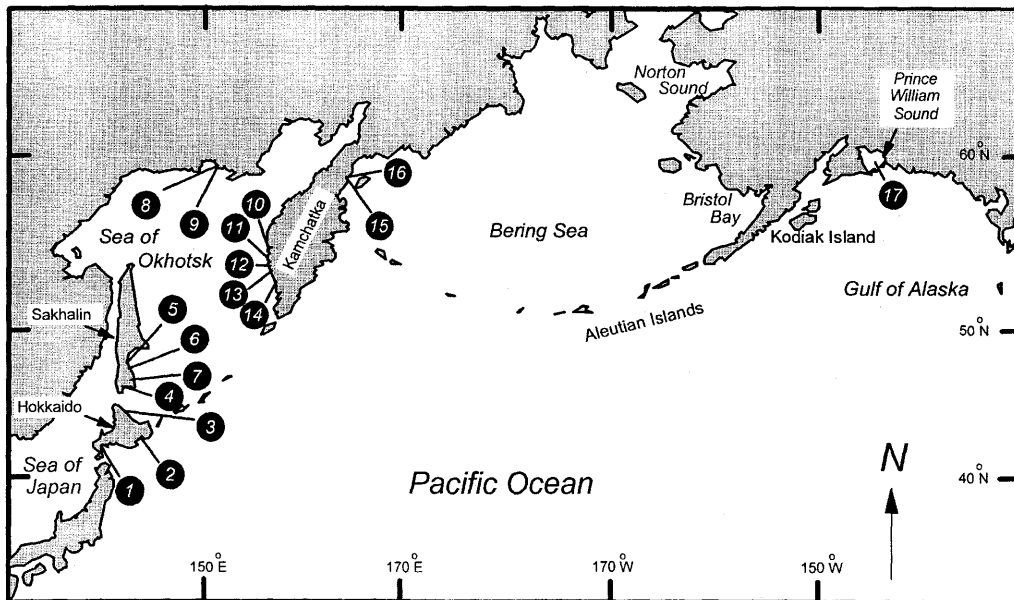


Figure 1

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 = Utkha 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  $\chi^2$ -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  $\chi^2$  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 <sup>1</sup>	Buffer <sup>2</sup>	Level of variability <sup>3</sup>
Aconitate hydratase	4.2.1.3	<i>sAH</i> *	L	8	2
		<i>mAH-1</i> *	H	4,5,6	2
		<i>mAH-2</i> *	H	4,5,6	3
		<i>mAH-3</i> * <sup>4,5</sup>	H,M	4,5,6	2
		<i>mAH-4</i> * <sup>4,5</sup>	H,M	4,5,6	3
Alanine aminotransferase	2.6.1.2	<i>ALAT</i> * <sup>4</sup>	M	2	2
Aspartate aminotransferase	2.6.1.1	<i>sAAT-1,2</i> * <sup>4</sup>	M,H	4,6	2
		<i>sAAT-3</i> * <sup>4,5</sup>	E	7	3
		<i>sAAT-4</i> *	L	8	3
		<i>mAAT-1</i> * <sup>4</sup>	M,H	4,6	1
		<i>mAAT-2</i> *	L	8	1
Creatine kinase	2.7.3.2	<i>CK-A1</i> * <sup>4,5</sup>	M	1	2
		<i>CK-A2</i> * <sup>4,5</sup>	M	1	2
		<i>CK-B</i> *	E	7	2
		<i>CK-C1</i> *	E	7	3
		<i>CK-C2</i> *	E	7	2
Formaldehyde dehydrogenase	1.2.1.1	<i>FDHG</i> * <sup>4</sup>	H	2	2
Fumarate hydratase	4.2.1.2	<i>FH</i> *	M	4	3
Glucose-6-phosphate isomerase	5.3.1.9	<i>GPI-A</i> * <sup>4,5</sup>	M	1	2
		<i>GPI-B1,2</i> * <sup>4,5</sup>	M	1	2
Glutathione reductase	1.6.4.2	<i>GR</i> * <sup>4</sup>	E	4,5	3
Glycerol-3-phosphate dehydrogenase	1.1.1.8	<i>G3PDH-1</i> * <sup>4,5</sup>	M	2,3	3
Guanine deaminase	3.5.4.3	<i>GDA</i> *	L	7,8	3
L-Iditol dehydrogenase	1.1.1.14	<i>IDDH</i> *	L	7	2
Isocitrate dehydrogenase	1.1.1.42	<i>mIDHP-1</i> * <sup>4</sup>	M,H	4	1
		<i>mIDHP-2</i> * <sup>4</sup>	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*\*<sub>95</sub> 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 \*<sub>100</sub> 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 Znamenska 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 <sup>1</sup>	Buffer <sup>2</sup>	Level of variability <sup>3</sup>
Lactate dehydrogenase	1.1.1.27	<i>LDH-A1</i> <sup>*4,5</sup>	M	1	3
		<i>LDH-A2</i> <sup>*4,5</sup>	M	1	1
		<i>LDH-B1</i> <sup>*4</sup>	H	1	2
		<i>LDH-B2</i> <sup>*</sup>	L	1	2
		<i>LDH-C</i> <sup>*4,5</sup>	E	7	1
Malate dehydrogenase	1.1.1.37	<i>sMDH-A1,2</i> <sup>*</sup>	L	6	3
		<i>sMDH-B1,2</i> <sup>*4,5</sup>	M	2,3	3
Malic enzyme	1.1.1.40	<i>mMEP-1</i> <sup>*4,5</sup>	M	3,4	3
Mannose-6-phosphate isomerase	5.3.1.8	<i>MPI</i> <sup>*4,5</sup>	H	2	2
Peptidase:					
Cytosol non-specific dipeptidase (glycyl-leucine)	3.4.--	<i>PEPA</i> <sup>*4</sup>	M	2	1
Tripeptide aminopeptidase (zinc enzyme) (leucyl-glycyl-glycine)	3.4.--	<i>PEPB</i> <sup>*4</sup>	M	1	3
Leucyl-tyrosine peptidase	3.4.--	<i>PEP-LT</i> <sup>*</sup>	M	2,4	3
Phosphoglucomutase	5.4.2.2	<i>PGM-2</i> <sup>*4,5</sup>	M	3	2
Phogluconate dehydrogenase	1.1.1.44	<i>PGDH</i> <sup>*4,5</sup>	E	3	3
Phosphoglycerate kinase	2.7.2.3	<i>PGK-1</i> <sup>*</sup>	L	8	1
		<i>PGK-2</i> <sup>*</sup>	L	8	1
X-proline dipeptidase	3.4.13.9	<i>PEPD-1</i> <sup>*4,5</sup>	M	2	2
		<i>PEPD-2</i> <sup>*4,5</sup>	M	2	3
Superoxide dismutase	1.15.1.1	<i>sSOD-1</i> <sup>*4,5</sup>	L	7	1
		<i>mSOD</i> <sup>*</sup>	H	1,2	1
Triose-phosphate isomerase	5.3.1.1	<i>TPI-1</i> <sup>*4</sup>	E	7	1
		<i>TPI-2</i> <sup>*4</sup>	E	7	2
		<i>TPI-3</i> <sup>*4</sup>	E	7	1
		<i>TPI-4</i> <sup>*4</sup>	E	7	2

<sup>1</sup> E = eye; H = heart; L = liver; M = muscle; preferred tissue listed first.  
<sup>2</sup> 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).  
<sup>3</sup> 1 = monomorphic;  
2 = low (frequency of most prevalent allele >0.95);  
3 = high (frequency of most prevalent allele ≤0.95).  
<sup>4</sup> Loci included in 36-locus version of neighbor-joining tree and gene diversity analysis.  
<sup>5</sup> 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 de-

rived 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*<sup>\*</sup> ( $P=0.018$ , 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.

Collection site	<i>sAAT-4*</i>		<i>sAH*</i>		<i>GDA*</i>		<i>FDHG*</i>		<i>sAAT-3*</i>		<i>CK-C1*</i>		<i>PGDH*</i>		<i>TPI-2*</i>																																																																																																																																																																																																																																																																														
	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>																																																																																																																																																																																																																																																																													
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Hokkaido	0.96	1	1.46	1	0.66	4	1.8	2	0.48	1	1.36	1	8.79 <sup>a</sup>	3	0	1																																																																																																																																																																																																																																																																													
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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 <sup>a</sup>	3	0	1																																																																																																																																																																																																																																																																													
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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 <sup>a</sup>	1	1.01	4	4.74 <sup>a</sup>	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 <sup>a</sup>	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 <sup>b</sup>	1	3.04	3	39.75 <sup>d</sup>	12	19.89 <sup>a</sup>	8	56.59 <sup>d</sup>	3	3.00	3	65.95 <sup>d</sup>	12	0	4																																																																																																																																																																																																																																																																													
Total Asia	7.60 <sup>a</sup>	2	13.84	14	80.75 <sup>a</sup>	56	42.93	36	69.99 <sup>d</sup>	16	13.84	12	151.11 <sup>d</sup>	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 <sup>a</sup>	12	3.38	4																																																																																																																																																																																																																																																																													
Total within	15.40 <sup>a</sup>	6	16.29	18	90.77	72	46.13	44	73.95 <sup>d</sup>	20	18.74	16	169.69 <sup>d</sup>	111	3.38	22																																																																																																																																																																																																																																																																													
Between Alaska and Asia	0.95	1	0	1	107.53 <sup>d</sup>	4	23.51 <sup>d</sup>	2	269.38 <sup>d</sup>	1	8.83 <sup>b</sup>	1	43.12 <sup>d</sup>	3	39.30 <sup>d</sup>	1																																																																																																																																																																																																																																																																													
Total for collections	16.34 <sup>a</sup>	7	16.29	19	198.30 <sup>d</sup>	76	69.64 <sup>a</sup>	46	343.33 <sup>d</sup>	21	27.57	17	212.81 <sup>d</sup>	114	42.68 <sup>b</sup>	23																																																																																																																																																																																																																																																																													
<table border="1"> <thead> <tr> <th rowspan="2">Collection site</th> <th colspan="2"><i>TPI-4*</i></th> <th colspan="2"><i>mAH-4*</i></th> <th colspan="2"><i>G3PDH-1*</i></th> <th colspan="2"><i>GPI-B2*</i></th> <th colspan="2"><i>GPI-A*</i></th> <th colspan="2"><i>LDH-A1*</i></th> <th colspan="2"><i>LDH-B1*</i></th> </tr> <tr> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> <th><i>G</i></th> <th><i>df</i></th> </tr> </thead> <tbody> <tr> <td colspan="15">Asia</td> </tr> <tr> <td>Hokkaido</td> <td>5.30<sup>a</sup></td> <td>1</td> <td>0</td> <td>2</td> <td>0.14</td> <td>3</td> <td>1.33</td> <td>3</td> <td>2.9</td> <td>2</td> <td>0</td> <td>3</td> <td>1.45</td> <td>2</td> </tr> <tr> <td colspan="15">Sakhalin</td> </tr> <tr> <td>Dolinka</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>0.02</td> <td>3</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> </tr> <tr> <td>Lutoga</td> <td>0.07</td> <td>1</td> <td>2.76</td> <td>2</td> <td>1.69</td> <td>9</td> <td>0</td> <td>3</td> <td>1.01</td> <td>2</td> <td>1.05</td> <td>3</td> <td>1.05</td> <td>2</td> </tr> <tr> <td>Monetka</td> <td>1.39</td> <td>1</td> <td>1.73</td> <td>2</td> <td>0.47</td> <td>3</td> <td>1.45</td> <td>3</td> <td>0</td> <td>2</td> <td>0</td> <td>3</td> <td>0</td> <td>2</td> </tr> <tr> <td colspan="15">Ochepukha</td> </tr> <tr> <td>Other</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>3.16</td> <td>15</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> <td>—</td> </tr> <tr> <td>Znamenka</td> <td>1.39</td> <td>1</td> <td>0.76</td> <td>2</td> <td>12.71</td> <td>24</td> <td>0</td> <td>3</td> <td>1.39</td> <td>2</td> <td>1.43</td> <td>3</td> <td>0</td> <td>2</td> </tr> <tr> <td>Within Ochepukha</td> <td>1.39</td> <td>1</td> <td>0.76</td> <td>2</td> <td>15.88</td> <td>39</td> <td>0</td> <td>3</td> <td>1.39</td> <td>2</td> <td>1.43</td> <td>3</td> <td>0</td> <td>2</td> </tr> <tr> <td>Between Ochepukha</td> <td>0.81</td> <td>1</td> <td>0.20</td> <td>2</td> <td>0.01</td> <td>3</td> <td>0</td> <td>3</td> <td>0.83</td> <td>2</td> <td>0.22</td> <td>3</td> <td>2.20</td> <td>2</td> </tr> <tr> <td>Total Ochepukha</td> <td>2.20</td> <td>2</td> <td>0.97</td> <td>4</td> <td>15.89</td> <td>42</td> <td>0</td> <td>6</td> <td>2.22</td> <td>4</td> <td>1.65</td> <td>6</td> <td>2.20</td> <td>4</td> </tr> <tr> <td>Within Sakhalin</td> <td>3.66</td> <td>4</td> <td>5.45</td> <td>8</td> <td>18.06</td> <td>57</td> <td>1.45</td> <td>12</td> <td>3.23</td> <td>8</td> <td>2.70</td> <td>12</td> <td>3.25</td> <td>8</td> </tr> <tr> <td>Among Sakhalin</td> <td>1.41</td> <td>3</td> <td>5.41</td> <td>6</td> <td>4.54</td> <td>9</td> <td>3.93</td> <td>9</td> <td>2.22</td> <td>6</td> <td>6.76</td> <td>9</td> <td>2.14</td> <td>6</td> </tr> <tr> <td>Total Sakhalin</td> <td>5.06</td> <td>7</td> <td>10.86</td> <td>14</td> <td>22.60</td> <td>66</td> <td>5.38</td> <td>21</td> <td>5.45</td> <td>14</td> <td>9.47</td> <td>21</td> <td>5.39</td> <td>14</td> </tr> <tr> <td>Northern Sea of Okhotsk</td> <td>0.19</td> <td>1</td> <td>0.64</td> <td>2</td> <td>0.33</td> <td>3</td> <td>0.19</td> <td>3</td> <td>0.19</td> <td>2</td> <td>—</td> <td>—</td> <td>0</td> <td>2</td> </tr> </tbody> </table>																	Collection site	<i>TPI-4*</i>		<i>mAH-4*</i>		<i>G3PDH-1*</i>		<i>GPI-B2*</i>		<i>GPI-A*</i>		<i>LDH-A1*</i>		<i>LDH-B1*</i>		<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	Asia															Hokkaido	5.30 <sup>a</sup>	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
Collection site	<i>TPI-4*</i>		<i>mAH-4*</i>		<i>G3PDH-1*</i>		<i>GPI-B2*</i>		<i>GPI-A*</i>		<i>LDH-A1*</i>		<i>LDH-B1*</i>																																																																																																																																																																																																																																																																																
	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>																																																																																																																																																																																																																																																																															
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Hokkaido	5.30 <sup>a</sup>	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																																																																																																																																																																																																																																																																															
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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	<i>TPI-4*</i>		<i>mAH-4*</i>		<i>G3PDH-1*</i>		<i>GPI-B2*</i>		<i>GPI-A*</i>		<i>LDH-A1*</i>		<i>LDH-B1*</i>	
	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	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 <sup>b</sup>	4	14.21	8	10.69	12	13.85	12	9.58	8	7.59	12	1.60	8
Total Asia	38.16 <sup>b</sup>	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 <sup>b</sup>	12	6.78	8
Total within	38.16 <sup>a</sup>	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 <sup>b</sup>	1	28.86 <sup>d</sup>	2	42.64 <sup>d</sup>	3	28.71 <sup>d</sup>	3	6.12 <sup>a</sup>	2	23.20 <sup>d</sup>	3	4.09	2
Total for collections	45.52 <sup>b</sup>	23	67.93 <sup>a</sup>	46	98.62	114	67.44	69	37.39	46	59.02	66	21.37	46
Collection site	<i>LDH-B2*</i>		<i>PEPLT*</i>		<i>PGM-2*</i>		<i>PEPD-1*</i>		<i>PEPD-2*</i>		<i>FH*</i>		<i>GR*</i>	
	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	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 <sup>a</sup>	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 <sup>a</sup>	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 <sup>d</sup>	16	79.18 <sup>d</sup>	8	76.78 <sup>d</sup>	8
Total Asia	21.79	48	18.95	16	16.73	36	24.69	20	139.99	120	103.18 <sup>d</sup>	32	96.98 <sup>d</sup>	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 <sup>d</sup>	40	100.24 <sup>d</sup>	42
Between Alaska and Asia	12.25 <sup>b</sup>	3	6.27 <sup>a</sup>	2	2.94	2	0.32	1	18.69 <sup>c</sup>	4	6.72 <sup>a</sup>	2	33.91 <sup>d</sup>	2
Total for collections	37.24	63	30.82	26	27.82	46	27.38	25	161.78	140	120.92 <sup>d</sup>	42	134.15 <sup>d</sup>	44
Collection site	<i>sMDH-A1,2*</i>		<i>sMDH-B1,2*</i>		<i>mMEP-1*</i>		<i>MPI*</i>		<i>PEPB*</i>		<i>mAH-2*</i>		Total for loci	
	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df	<i>G</i>	df
Asia														
Hokkaido	0.09	4	2.74	6	0.77	2	0.001	2	6.64 <sup>a</sup>	2	4.30 <sup>a</sup>	1	48.87 <sup>a</sup>	62
Sakhalin														
Dolinka	—		1.95	6	5.95 <sup>a</sup>	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	<i>sMDH-A1,2*</i>		<i>sMDH-B1,2*</i>		<i>mMEP-1*</i>		<i>MPI*</i>		<i>PEPB*</i>		<i>mAH-2*</i>		Total for loci	
	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>
Monetka	1.75	4	1.20	6	0.01	2	0.34	2	1.33	2	2.07	1	41.20	59
Ochepukha														
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 <sup>b</sup>	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 <sup>d</sup>	16	45.82 <sup>b</sup>	24	8.14	8	15.98 <sup>a</sup>	8	76.91 <sup>d</sup>	8	15.69 <sup>b</sup>	4	768.81 <sup>d</sup>	236
Total Asia	90.87 <sup>a</sup>	68	164.42	198	37.21	66	28.81	36	117.87 <sup>d</sup>	40	34.47 <sup>b</sup>	14	1492.22 <sup>d</sup>	1293
North America														
Prince William Sound	5.67	16	13.22	24	4.12	8	6.27	8	11.49	8	8.31 <sup>a</sup>	3	176.78 <sup>a</sup>	247
Total within	96.53	84	177.64	222	41.33	74	35.08	44	129.36 <sup>d</sup>	48	42.78	17	1669.01 <sup>d</sup>	1540
Between Alaska and Asia	9.40	4	12.09	6	4.06	2	1.73	2	12.88 <sup>b</sup>	2	2.33	1	717.87 <sup>d</sup>	62
Total for collections	105.93	88	189.73	228	45.39	76	36.81	46	142.24 <sup>d</sup>	50	45.11 <sup>c</sup>	18	2386.85 <sup>d</sup>	1602

<sup>a</sup>*P* < 0.05, <sup>b</sup>*P* < 0.01, <sup>c</sup>*P* < 0.001, <sup>d</sup>*P* < 0.0001.

## diversity -

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<sup>-4</sup>) (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<sup>-6</sup>) (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



