Pacific Rim Population Structure of Sockeye Salmon as Determined from Microsatellite Analysis

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Abstract.—The Pacific Rim population structure of sockeye salmon *Oncorhynchus nerka* was examined with a survey of microsatellite variation. Variation at 14 microsatellite loci was surveyed for over 48,000 sockeye salmon sampled from 299 localities ranging from the Columbia River to Japan. The value of the genetic differentiation index *F*<sub>ST</sub> over all populations and loci was 0.097; individual locus values ranged from 0.038 to 0.154. Sockeye salmon from the Queen Charlotte Islands and the Columbia River displayed the least number of alleles relative to sockeye salmon from other regions in the Pacific Rim distribution of the species. Conversely, sockeye salmon displaying the greatest allelic diversity were observed in Southeast Alaska and the central coast of British Columbia. Sockeye salmon from these two regions displayed approximately 30% more alleles than did sockeye salmon from the Queen Charlotte Islands and the Columbia River. Sockeye salmon from Russia and western Alaska were, on average, less diverse than sockeye salmon from Southeast Alaska and more southerly locations in North America. A regional structuring of populations was generally observed among the sockeye salmon populations sampled, and populations were clustered within lakes and river drainages. At the Pacific Rim scale of population structure, there were two major groups of populations. The first group included populations from Russia, Bristol Bay, Kodiak Island, the Alsek River, and the Queen Charlotte Islands. The second group generally included populations from Southeast Alaska, British Columbia, and Washington. The distribution of microsatellite variation of sockeye salmon on a Pacific Rim basis reflected the origins of sockeye salmon radiating from refuges after the last glaciation period.

In North America, sockeye salmon *Oncorhynchus nerka* are widely distributed from the Columbia River to northwestern Alaska. In Asia, however, the distribution is more restricted, and most spawning occurs mainly on the Kamchatka Peninsula and the western coast of the Bering Sea. Sockeye salmon typically spawn in tributaries to lakes or along the lake shore, and the juveniles rear in these nursery lakes for at least 1 year before migrating to the ocean (Burgher 1991). Where lake-rearing habitat is inaccessible or unavailable, sockeye salmon spawn in river tributaries or main-stem side channels, and the juveniles rear for up to 1 year in a river environment before migrating to the ocean (Wood et al. 1987; Wood 1995). Given such a broad geographic distribution and considerable variation in life history, there is potential for substantial genetic differentiation among sockeye salmon populations in the geographic range of the species.

Genetic variation in sockeye salmon was initially evaluated with surveys of variation at allozymes. These studies indicated that there was considerable differentiation among sockeye salmon spawning in different lakes, and genetic differentiation among sockeye populations in different lakes is a key level of genetic differentiation (Varnavskaya et al. 1994b; Wood et al. 1994; Wood 1995). Within a large river drainage containing a number of lakes, there can be significant differentiation among sockeye salmon populations in the different lakes (Wood et al. 1994; Wood 1995). Although some degree of genetic similarity can occur among populations within large rivers, regional structuring of the populations is less apparent, as the nearest geographic populations are not necessarily the most similar genetically (Wood et al. 1994; Wood 1995; Winans et al. 1996). For example, in a study examining allozyme variation for over 70 sockeye salmon populations with a range of distribution from Kamchatka to Washington, genetic differentiation was typically greater among populations within regions than among regions (Varnavskaya et al. 1994a). However, the low level of polymorphism observed at...
most allozyme loci may not allow for adequate resolution of population structure.

Markers at the DNA level, particularly microsatellites, have substantially increased the number of highly polymorphic loci that are available for inclusion in a survey of population genetic variation. Surveys of microsatellite variation have been demonstrated to be effective in determining population structure of sockeye salmon in major river drainages (Beacham and Wood 1999; Beacham et al. 2000, 2004a, 2004b; Withler et al. 2000) and in small coastal lakes in localized geographic regions (Beacham et al. 2005b). A survey of microsatellite variation over the broad geographic range of sockeye salmon distribution would probably be very instructive in evaluating population structure.

It has been suggested that the Pacific Rim structure of sockeye salmon populations is almost certainly associated with colonization events that occurred after the last glaciation (Wood 1995). Allozyme variation had suggested that modern sockeye salmon populations were derived principally from a northern race that survived glaciation in the Bering Sea area and a southern race that survived in the Columbia River area. Local refuges may also have been present in an inland mountain area in Kamchatka (Varnavskaya et al. 1994a), Kodiak Island in the Gulf of Alaska (Karlstrom and Ball 1969), and on coastal islands in British Columbia (Warner et al. 1982; Wood et al. 1994). Varnavskaya et al. (1994a) suggested that existing sockeye salmon populations in Kamchatka and adjacent regions were derived from two colonizing races, one originating from the inland mountain refuge and the other originating from the Bering Sea refuge. The latter race was suggested to have founded the Columbia River refuge. The specific populations, collection years, and sample sizes included in the survey have been outlined by Beacham et al. (2005a) in their Appendix Table 1. A summary of the number of populations surveyed by local geographic area is outlined in Table 1. Polymerase chain reaction products at 14 microsatellite loci—Ots2, Ots3 (Banks et al. 1999), Ots100, Ots103, Ots107, Ots108 (Beacham et al. 1998; Nelson and Beacham 1999), Oki1a, Oki1b, Oki6, Oki10, Oki16, Oki29 (Smith et al. 1998; Nelson et al. 2003), One8 (Scribner et al. 1996), and Omy77 (Morris et al. 1996)—were size fractionated on denaturing polyacrylamide gels, and allele sizes were determined with an ABI 377 automated DNA sequencer. Allele sizes were determined with Genescan 3.1 and Genotyper 2.5 software (Applied Biosystems 2000, 2001).

Data analysis.—All annual samples available for a location were combined to estimate population allele frequencies, as was recommended by Waples (1990). Weir and Cockerham’s (1984) genetic differentiation index ($F_{ST}$) estimates for each locus over all populations were calculated with FSTAT version 2.9.3.2 (Goudet 1995). The significance of the multi-locus $F_{ST}$ value over all samples was determined by jackknifing over loci. Cavalli-Sforza and Edwards’ (CSE) (1967) chord distances were used to estimate genetic distances among all populations. An unrooted neighbor-joining tree based upon CSE chord distances was generated with NJPLOT (Perriere and Gouy 1996). Bootstrap support for the major nodes in the tree was evaluated with the CONSENSE program from PHYLIP based upon 200 replicate trees (Felsenstein 1993). FSTAT was used to measure the allelic richness (allelic diversity standardized to a sample size of 146 fish) for each group of populations evaluated. Computation of the number of alleles observed per locus was carried out with Genetic Data Analysis (GDA) software (Lewis and Zaykin 2001). We evaluated the distribution of genetic variation in sockeye salmon among river drainages, among

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populations within drainages, and among sampling years within populations. River drainages or regions and lakes within drainages or regions were as follows (specific populations are given in parentheses): Fraser River (Stellako River, Birkenhead River, Weaver Creek), Somass River (Sproat, Great Central, and Henderson lakes), central coast (Inziana River, Devon Lake, Long Lake), Skeena River (Swan River, Pinkut Creek), Nass River (Damodchax Lake, Bowser Lake, Bonney River), Stikine River (Tahltan Lake, Scud River, Verrett River), Taku River (Kuthai and Little Tatsamenie lakes), Alsek River (Kluksu and Upper Tatshenshini rivers), Southeast Alaska (Hugh Smith, Heckman, and McDonald lakes), Kvichak River (Knutsen Bay, Copper River), Olutorsky Bay (Ilir Lake, Vatit Lake), and Bolshaya River (Bolshaya and Plotnikova rivers). Estimation of variance components of river drainage differentiation (among populations within drainages or regions; among years within populations) was determined with GDA software. Allele frequencies for all location samples surveyed in this study are available at the Molecular Genetics Laboratory web site (http://www-sci.pac.dfo-mpo.gc.ca/mgl/default_e.htm).

Results

Variation within Populations

There was substantial variation in the number of alleles observed for the 14 microsatellite loci surveyed in the study. The fewest number of alleles was observed at Oki1a (eight alleles), and the greatest number of alleles was observed at Oki10 (83 alleles) (Table 2). Lower heterozygosity was observed at loci with 15 or fewer alleles. The genotypic frequencies at each locus generally conformed to those expected under Hardy–Weinberg equilibrium (HWE), except Oki10. At this locus, populations in southern British Columbia were in HWE. Populations in more distant areas, such as Russia and Alaska, displayed increased occurrence of non-HWE genotypic frequencies that probably resulted from the wide range in allele size and reduced amplification of larger-sized alleles.

Genetic diversity in terms of the number of alleles observed varied considerably among regional groups of sockeye salmon populations. Sockeye salmon from the Queen Charlotte Islands off the northern coast of British Columbia displayed the least number of alleles relative to sockeye salmon from other regions in the Pacific Rim distribution of the species (Table 3). Sockeye salmon from the Columbia River also displayed reduced allelic diversity. Conversely, sockeye salmon displaying the greatest allelic diversity were observed in Southeast Alaska and the central coast of British Columbia. Sockeye salmon from these two regions displayed approximately 30% more alleles than did sockeye salmon from the Queen Charlotte Islands and the Columbia River. Not surprisingly, the greatest differentiation in terms of allelic diversity...
among regions was observed at those loci with larger numbers of total observed alleles. Sockeye salmon from Russia and western Alaska were, on average, less diverse than sockeye salmon from Southeast Alaska and more southerly locations in North America.

**Distribution of Genetic Variation**

Gene diversity analysis of the 14 loci surveyed was used to evaluate the distribution of genetic variation among years within populations, among populations within river drainages or regions, and among river drainages or regions. For 12 river drainages or regions with a Pacific Rim geographic distribution, the amount of variation within populations ranged from 83% (Oki16) to 97% (Oki10); the average for an individual locus was 91.1% (Table 4). The variation among sampling years within populations was the smallest source of variation observed, accounting for 0.4% of all variation. Variation among populations within river drainages or geographic regions accounted for 4.4% of observed variation. Variation among the 12 river drainages or regions accounted for 4.0% of total observed variation. Differentiation among river drainages and populations within river drainages was approximately 19 times greater than that of annual variation within populations. For the time intervals surveyed in our study, annual variation in microsatellite allele frequencies was minor relative to differences among populations within river drainages and among river drainages on a Pacific scale of distribution.

**Population Structure**

Genetic differentiation was clearly evident among the sockeye salmon populations sampled in our survey. The $F_{ST}$ value over all populations and loci was 0.097, and individual locus values ranged from 0.038 (Oki10) to 0.154 (Ots100) (Table 2). The most distinctive regional group of sockeye salmon, although it was comprised of only a single population, was that from Hokkaido Island in Japan (Table 5). This population (Abira River) displayed substantially reduced genetic diversity relative to other populations in Russia or in North America. Sockeye salmon from Washington were also quite distinct, but this differentiation was
accentuated by the inclusion of the distinctive Ozette Lake population in the survey. Populations from the Queen Charlotte Islands were also distinct (\(F_{ST} = 0.09–0.16\)) from other regions in the Pacific Rim distribution of the species.

A regional structuring of populations was generally observed among the sockeye salmon populations sampled, and populations clustered within lakes and river drainages. Similarities among sampling sites or populations within lakes received strong bootstrap support. For example, the 12 populations from Kurilskoye Lake on the Kamchatka Peninsula clustered together in 94% of dendrograms evaluated, and the seven populations from Azabachie Lake in the Kamchatka River drainage clustered together in 96% of dendrograms (Figure 2). In North America, 6 populations from Iliamna Lake in Bristol Bay clustered together in 89% of dendrograms, 9 populations from Fraser Lake on Kodiak Island clustered together in 99% of dendrograms, 10 populations from Owikeno Lake in the central coast of British Columbia clustered together in 97% of dendrograms, and 6 populations from Great Central Lake on Vancouver Island clustered together in 100% of dendrograms evaluated.

Sockeye salmon in different lakes or spawning areas within a given river drainage were generally more similar to each other than they were to populations in different regions or river drainages. For example, the 16 sampling locations from the Alsek River drainage in northern British Columbia clustered together in 73% of dendrograms evaluated, the 10 sampling locations in the Somass River drainage on Vancouver Island clustered together in 84% of dendrograms evaluated, and 52 of 53 Fraser River populations in southern British Columbia clustered together in 33% of dendrograms evaluated. In more northerly areas, four Wood River populations in Bristol Bay clustered together in 100% of dendrograms evaluated, and in Kamchatka 12 populations from the Kamchatka River clustered together in 58% of dendrograms evaluated. However, there were some exceptions to a strict clustering of populations with river drainages. For example, populations from Lakelse Lake in the lower Skeena River in northern British Columbia were quite unlike any other populations in the Skeena River drainage, as was the Sustut River population in the upper portion of the drainage (Figure 2). The Widgeon Slough population in the lower Fraser River was also unlike any other Fraser River population. Although there were certain exceptions, there was a general clustering of populations based upon river drainage and geographical location.

At the Pacific Rim scale of population structure, there were two major groups of populations. The first group included populations from Russia, Bristol Bay, Kodiak Island, the Alsek River, and the Queen Charlotte Islands (Figure 2). Within this group, distinct groups of populations were observed in the Alsek River, the Queen Charlotte Islands, and Kodiak Island. Bristol Bay and adjacent Alaska Peninsula populations were distinct from but most similar to those from the Kamchatka Peninsula and were less similar to Russian populations on the western Bering Sea coast (Chukotka, Olotorsky Bay, Karaginsky Bay). The Lake Andrew population, located on the Aleutian Islands, was more similar to Russian western Bering Sea coast populations than to those in Bristol Bay. The second group generally included populations from Southeast Alaska, British Columbia, and Washington (Figure 2). Although a regional population structure generally existed, there was not a perfect split in central coastal populations of British Columbia. Seven of the 16 surveyed populations were more similar to Asian, northern Alaskan, and Queen Charlotte Islands populations than to other mainland British Columbia populations. These seven populations were all located in the north and central regions of the central coast, across Hecate Strait from the Queen Charlotte Islands. They were more closely related to the Queen Charlotte Islands populations than they were to Asian or Bristol Bay populations. Within the second group, there were two general subgroups. The more northerly subgroup was composed of populations from the major northern rivers (Taku, Stikine, Nass, and Skeena) as well as Owikeno Lake populations, and the southern subgroup was composed of central coast British Columbia, southern British Columbia, Fraser River, Vancouver Island, Washington, and Columbia River populations.

### Table 2

<table>
<thead>
<tr>
<th>Locus</th>
<th>Number of alleles</th>
<th>Number of alleles</th>
<th>Hs</th>
<th>Ho</th>
<th>FST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oki1a</td>
<td>8</td>
<td>0.46</td>
<td>0.46</td>
<td>0.105 (0.011)</td>
<td></td>
</tr>
<tr>
<td>Oki1b</td>
<td>10</td>
<td>0.51</td>
<td>0.51</td>
<td>0.090 (0.007)</td>
<td></td>
</tr>
<tr>
<td>Oki6</td>
<td>37</td>
<td>0.63</td>
<td>0.62</td>
<td>0.140 (0.009)</td>
<td></td>
</tr>
<tr>
<td>Oki10</td>
<td>83</td>
<td>0.91</td>
<td>0.80</td>
<td>0.036 (0.003)</td>
<td></td>
</tr>
<tr>
<td>Oki16</td>
<td>26</td>
<td>0.65</td>
<td>0.65</td>
<td>0.134 (0.011)</td>
<td></td>
</tr>
<tr>
<td>Oki29</td>
<td>39</td>
<td>0.79</td>
<td>0.78</td>
<td>0.073 (0.004)</td>
<td></td>
</tr>
<tr>
<td>Omv77</td>
<td>20</td>
<td>0.67</td>
<td>0.67</td>
<td>0.142 (0.007)</td>
<td></td>
</tr>
<tr>
<td>Ome8</td>
<td>32</td>
<td>0.67</td>
<td>0.69</td>
<td>0.105 (0.007)</td>
<td></td>
</tr>
<tr>
<td>Ots2</td>
<td>26</td>
<td>0.75</td>
<td>0.75</td>
<td>0.118 (0.008)</td>
<td></td>
</tr>
<tr>
<td>Ots3</td>
<td>26</td>
<td>0.55</td>
<td>0.54</td>
<td>0.124 (0.009)</td>
<td></td>
</tr>
<tr>
<td>Ots100</td>
<td>33</td>
<td>0.80</td>
<td>0.77</td>
<td>0.154 (0.008)</td>
<td></td>
</tr>
<tr>
<td>Ots103</td>
<td>30</td>
<td>0.88</td>
<td>0.86</td>
<td>0.067 (0.005)</td>
<td></td>
</tr>
<tr>
<td>Ots107</td>
<td>15</td>
<td>0.40</td>
<td>0.40</td>
<td>0.077 (0.007)</td>
<td></td>
</tr>
<tr>
<td>Ots108</td>
<td>29</td>
<td>0.86</td>
<td>0.83</td>
<td>0.110 (0.006)</td>
<td></td>
</tr>
<tr>
<td>All loci</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.097 (0.010)</td>
</tr>
</tbody>
</table>
likely that the close genetic relationship among these populations was falsely inferred. Similar clustering of samples or populations within lakes was observed for other lakes surveyed in the study, but sample sizes were considerably larger than those available for Azabachie Lake populations.

The survey of microsatellite variation in sockeye salmon examined the variation at 14 loci, resulting in identification of over 410 alleles. This variation provided the power to determine population structure of sockeye salmon on a Pacific Rim basis while at the same time yielding details of structure on a local basis. Kalinowski (2002) suggested that the total number of alleles was correlated with the precision of estimated genetic differences among populations. Similar results could be achieved by examining a limited number of loci with larger numbers of alleles or more loci with restricted numbers of alleles. Approximately 30 alleles per locus were observed in our study, which is well in excess of the 6–10 microsatellite alleles recommended by Bernatchez and Duchesne (2000) for population assignment studies and well above the number of alleles observed at allozyme or single nucleotide polymorphism loci. If loci with restricted numbers of alleles are employed in surveys of salmon population structure, it is quite likely that the number of loci required for determining the precision of the level of structure observed will be substantially greater than the 14 loci employed in the current study.
All samples available for a specific sampling site or population were combined in our study in order to estimate allele frequencies, regardless of the year of sample collection. Annual stability of allele frequencies relative to population differentiation has been repeatedly observed for sockeye salmon populations (Beacham and Wood 1999; Beacham et al. 2000, 2004b, 2005b). The current study has again demonstrated that annual variation in allele frequencies is minor relative to population differentiation, even for populations not evaluated previously. Annual stability of allele frequencies is an attractive feature of microsatellite variation, as samples can be collected over a period of time to evaluate population structure. Annual stability of allele frequencies is also a key attribute of microsatellites for stock identification applications. The utility of the baseline for stock identification applications on a Pacific Rim basis has been outlined by Beacham et al. (2005a).

Sockeye salmon juveniles that do not rear in lakes for at least a year, but rather rear in streams or migrate directly to the ocean upon emergence (riverine type), have been suggested as the principal colonists of new habitat (Wood 1995). The lack of differentiation at allozyme loci for this life history type was thought to be indicative of higher rates of straying (Gustafson and Winans 1999). In British Columbia, riverine populations are more common in the Alsek, Taku, and Stikine rivers than in more southerly locations. In the Stikine and Taku rivers, there is a lack of differentiation between riverine populations from these two drainages at both allozyme (Wood 1995) and microsatellite loci (Beacham et al. 2004a). This result is consistent with the concept that riverine sockeye salmon are more prone to stray, as lake-type populations in these two drainages are distinct. However, riverine populations from the Alsek River were distinct from those in the Taku and Stikine river drainages. On the Kamchatka Peninsula, riverine populations are fairly common, and there was clear differentiation among populations from different regions. In the Kamchatka River drainage, riverine populations were more similar to each other and distinct from other riverine populations along the east coast of the Kamchatka Peninsula. Lack of differentiation among riverine populations is largely confined to comparisons between Taku River and Stikine River populations. Interestingly, the one Fraser River population that did not cluster with the other 52 populations surveyed was Widgeon Slough in the lower Fraser River, a riverine population. The other known riverine population in the drainage, Harrison River, did cluster with other lake-type populations in the Harrison River drainage. Outside of the Stikine and Taku river drainages, riverine populations do not display reduced differentiation. Based upon the survey of microsatellite variation, it is unclear whether riverine populations are the principal source of colonists for new habitats.

### Table 4

Hierarchical gene diversity analysis of 30 sockeye salmon populations within 12 river drainages or regions in terms of 14 microsatellite loci. River drainages or regions and lakes within drainages or regions had a Pacific Rim distribution and they were (specific populations in parentheses): Fraser River (Stellako River, Birkenhead River, Weaver Creek), Somass River (Sproat, Great Central, and Henderson lakes), central coast (Inziana River, Devon Lake, Long Lake), Skeena River (Swan River, Pinkut Creek), Nass River (Damodchax Lake, Bowser Lake, Bonney River), Stikine River (Tahitian Lake, Scud River, Verrett River), Taku River (Kuthai and Little Tatsamenie Lakes), Alsek River (Klukshu and Upper Tatshenshini rivers), Southeast Alaska (Hugh Smith, Heckman, and McDonald lakes), Kvichak River (Knutsen Bay, Copper River), Olutorsky Bay (Ilir Lake, Vatit Lake), and Bolshaya River (Bolshaya and Plotnikova rivers). Sampling years within populations were outlined by Beacham et al. (2005a). The last column shows the ratio of the sum of the variance components among populations within drainages and among drainages divided by the variance component among years within populations; $P < 0.05$, $P < 0.01$.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Within populations</th>
<th>Among years within populations</th>
<th>Among populations within drainages</th>
<th>Among drainages</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oki1a</td>
<td>0.9152</td>
<td>0.0020</td>
<td>0.0461**</td>
<td>0.0367*</td>
<td>41.4</td>
</tr>
<tr>
<td>Oki1b</td>
<td>0.9386</td>
<td>0.0000</td>
<td>0.0171**</td>
<td>0.0443**</td>
<td></td>
</tr>
<tr>
<td>Oki6</td>
<td>0.9178</td>
<td>0.0061*</td>
<td>0.0423**</td>
<td>0.0338*</td>
<td>12.5</td>
</tr>
<tr>
<td>Oki10</td>
<td>0.9655</td>
<td>0.0023</td>
<td>0.0209**</td>
<td>0.0062</td>
<td>14.0</td>
</tr>
<tr>
<td>Oki16</td>
<td>0.8257</td>
<td>0.0252**</td>
<td>0.0489**</td>
<td>0.1002**</td>
<td>5.9</td>
</tr>
<tr>
<td>Oki29</td>
<td>0.9381</td>
<td>0.0038*</td>
<td>0.0328**</td>
<td>0.0253*</td>
<td>15.3</td>
</tr>
<tr>
<td>Omy77</td>
<td>0.8889</td>
<td>0.0026*</td>
<td>0.0694**</td>
<td>0.0391*</td>
<td>41.7</td>
</tr>
<tr>
<td>One8</td>
<td>0.9219</td>
<td>0.0034*</td>
<td>0.0350**</td>
<td>0.0397*</td>
<td>22.0</td>
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<tr>
<td>Ots2</td>
<td>0.8971</td>
<td>0.0007</td>
<td>0.0607**</td>
<td>0.0415*</td>
<td>146.0</td>
</tr>
<tr>
<td>Ots3</td>
<td>0.8655</td>
<td>0.0044*</td>
<td>0.0907**</td>
<td>0.0394</td>
<td>29.6</td>
</tr>
<tr>
<td>Ots100</td>
<td>0.8701</td>
<td>0.0023</td>
<td>0.0451**</td>
<td>0.0825**</td>
<td>55.5</td>
</tr>
<tr>
<td>Ots103</td>
<td>0.9400</td>
<td>0.0011</td>
<td>0.0283**</td>
<td>0.0306*</td>
<td>53.5</td>
</tr>
<tr>
<td>Ots107</td>
<td>0.9404</td>
<td>0.0048*</td>
<td>0.0358**</td>
<td>0.0490</td>
<td>11.4</td>
</tr>
<tr>
<td>Ots108</td>
<td>0.9311</td>
<td>0.0036*</td>
<td>0.0449**</td>
<td>0.0204</td>
<td>30.6</td>
</tr>
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<td>All</td>
<td>0.9112</td>
<td>0.0044*</td>
<td>0.0443**</td>
<td>0.0401*</td>
<td>19.2</td>
</tr>
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</table>

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Table 5.—Mean pairwise F_{ST} values averaged over 14 microsatellite loci from 22 regional groups of sockeye salmon that were sampled at 299 locations across the Pacific Rim. Comparisons were conducted between individual populations in each region. Values on the diagonal are in bold italics and represent comparisons among populations within each region. The F_{ST} values are listed below the diagonal, and SDs are given above the diagonal. Some of the regions listed in Table 1 were either combined or omitted to facilitate the analysis. Region codes (RC) are as follows: (1) Fraser River, (2) Washington, (3) southern British Columbia, (4) Vancouver Island, (5) Columbia River, (6) Nass River, (7) Skeena River, (8) Stikine River, (9) central coast British Columbia, (10) Taku River, (11) Alsek River, (12) Otiwakeno Lake, (13) Queen Charlotte Islands, (14) Southeast Alaska, (15) Bristol Bay, (16) Kodiak Island, (17) Alaska Peninsula, (18) Kurilskoye Lake, (19) West Kamchatka (includes southwest Kamchatka and the Bolshaya, Tigil, and Palana rivers), (20) East Kamchatka (includes Karaginsky Bay, Kamchatka River, Kronotsky Bay, and southeast Kamchatka), (21) Bering Sea and coast (includes Chukotka, Otulotary Bay, and the Navarin region), and (22) Hokkaido Island.

If the concordance of genetic differences between allozymes and microsatellites in sockeye salmon reported by Allendorf and Seeb (2000) is generally applicable, then one should expect concordant patterns of population structure between the two techniques. Winans and Urawa (2000), in a survey of incorporating variation at five allozymes in sockeye salmon, reported that the 14 surveyed populations grouped into two sets of samples: (1) Skeena River sockeye salmon in northern British Columbia grouping with Asian and Columbia River populations, and (2) Fraser River, Washington, and Columbia River populations. This was similar to a previous study of mitochondrial DNA variation, in which Russian, Alaskan, and northern British Columbia populations were distinct from those in Babine and Meziadin lakes. Fraser River populations were also described as not forming a tight regional cluster. In the analysis of microsatellite variation, Lliamia Lake populations clustered with other Bristol Bay populations, and Kuril Lake populations were very distinct from those in Babine and Meziadin lakes. Fraser River populations except the Widgeon Slough population formed a single cluster. Our analysis supported the broad concept of two major groups of sockeye salmon populations but did not support the concept of concordant patterns of population differentiation within groups when derived from analysis of allozyme and microsatellite variation.

The distribution of microsatellite variation in sockeye salmon on a Pacific Rim basis is expected to reflect the origins of sockeye salmon radiating from refuges after the last glaciation period ended some 10,000 years ago. For populations in the Gulf of
FIGURE 2.—Neighbor-joining dendrogram of Cavalli-Sforza and Edwards (1967) chord distances for 299 populations of sockeye salmon surveyed at 14 microsatellite loci. Bootstrap values at major tree nodes indicate the percentages of 200 trees for which populations beyond the node clustered together. Note that the dendrogram proceeds vertically from one page to the next.
FIGURE 2.—Continued

PACIFIC RIM SOCKEYE SALMON POPULATION STRUCTURE

Fraser River

Columbia River

Stikine River

Skeena River

Taku River

Skeena River

Nass River

Owikon Lake

Quatse Lake

Mckey

SE Alaska

Central Coast

QCI
FIGURE 2.—Continued
Alaska, western Alaska, and Russia, our analysis of microsatellite variation is consistent with the proposal that Kodiak Island may have been a glacial refuge (Karlstrom 1969). All Kodiak Island populations clustered together in the dendrogram analysis and were distinct from populations in other areas. It is likely that existing western Alaska and Russian populations were derived from a single northern refuge. If additional refuges did contribute to existing populations (Var-navskaya et al. 1994a), it would probably have been on a limited local basis. The distinctiveness of the Alsek River populations suggests that they may have been derived from a different northern refuge than the western Alaska and Russian populations and very likely originated from a refuge differing from that of other populations in Southeast Alaska or British Columbia. Kluane Lake, situated in the southwest Yukon Territory in Canada, is now part of the Yukon River drainage. However, it has been suggested that Kluane Lake used to be part of the Alsek River drainage until the advance of the Kaskawulsh glacier some 400 years ago (Bostock 1969). Given the distinctiveness of the Alsek River populations, it is possible that these populations, and perhaps those bordering the eastern Gulf of Alaska, were derived from a different northern refuge than the one from which western Alaska and Russian populations originated. For populations in Southeast Alaska, British Columbia, and Washington, our analysis is consistent with a glacial refuge present on the Queen Charlotte Islands (Warner et al. 1982). Queen Charlotte Islands populations were quite distinct but displayed reduced genetic variation, perhaps a result of a recent bottleneck in population size. The analysis is also consistent with a southern glacial refuge, probably in the Columbia River, from which a northward movement of sockeye salmon occurred after the glacial retreat. The central coast of British Columbia probably represents an area in which colonization occurred with sockeye salmon originating from two glacial refuges. This may also account for a reported mosaic pattern of population structure (Nelson et al. 2003). There may have been local refuges on coastal islands (Wood 1995), but it is also possible that the northern part of the central coast was colonized by sockeye salmon originating from the Queen Charlotte Islands refuge, while the southern portion of the central coast was colonized by sockeye salmon that originated from a southern refuge.

Microsatellites have been effective in facilitating an evaluation of the population structure of sockeye salmon on a Pacific Rim basis. The ease of processing and analyzing large numbers of fish in the laboratory provides a method that is powerful in elucidating population structure and accurate in stock identification applications. It is likely that microsatellites will become increasingly applied in the assessment of population structure, the determination of management units, and the management of mixed-stock fisheries.

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References


