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Population Structure of Sockeye Salmon of the Central Coast of British Columbia: Implications for Recovery Planning

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Abstract.—The populations of sockeye salmon *Oncorhynchus nerka* of the south-central coast of British Columbia are in decline. To assist in recovery planning, we determined the population structure of sockeye salmon in the region by assaying the genetic variability of 10 microsatellite DNA loci in samples of sockeye salmon from 22 sites associated with 15 rearing lakes. Samples of sockeye salmon from the watersheds with the largest historical runs in the region were studied. Special emphasis was given to investigating genetic divergence among sockeye salmon spawning in seven rivers of the Owikeno Lake watershed, which once supported the largest sockeye salmon run in south-central British Columbia. Across the region, a mosaic of genetic divergence was evident. Reproductive isolation among watersheds was pronounced in all but one case, making transfer of fish between watersheds inadvisable. Genetic stock identification simulations demonstrated that fish from different watersheds could be accurately distinguished—which will allow for identification of threatened stocks in coastal mixed-stock fishery samples. Within the Owikeno Lake watershed we found little evidence of persistent genetic structure, which precludes the use of genetic stock identification to estimate escapements to its glacially turbid tributaries. Lack of persistent structure supports managing the majority of Owikeno Lake sockeye salmon as a single population.

The south-central coast of British Columbia supports a large number of sockeye salmon *Oncorhynchus nerka*, which are harvested in commercial, aboriginal, and sport fisheries. The number of fish returning to spawn in the rivers and lakes of this region declined dramatically until 2000 principally because of poor marine survival (Rutherford and Wood 2000; McKinnell et al. 2001). Historically, the largest run of sockeye salmon in the region consisted of fish bound for the Owikeno Lake watershed, of which annual harvests prior to 1979 averaged 808,000 fish (Wood et al. 1970; Rutherford 1997). In 1979, harvest restrictions were instituted to increase spawning escapement (Walters et al. 1993). Although escapements generally increased in the 1980s, they declined dramatically after 1993, reaching a record low of 5,000 fish in 1999 (Rutherford and Wood 2000). The second largest run in the region consisted of fish returning to the Long Lake watershed, of which an average of 200,000 fish had been harvested annually since 1951. Escapement to this watershed also dropped to its lowest level in 1999. Rutherford and Wood (2000) concluded that poor marine survival also affected smaller sockeye populations in the region. Small populations are of special concern because they are vulnerable to environmental and demographic stochasticity, as well as deleterious genetic effects, and thus are at a greater risk of extirpation (Lande 1993; Routledge and Irvine 1999).

Active management strategies can increase the likelihood of survival of vulnerable populations when environmental conditions are not ideal. The design and implementation of a recovery plan has been deemed necessary to aid in rebuilding sockeye salmon runs of Owikeno and Long lakes and to protect the smaller sockeye salmon runs of British Columbia's south-central coast (Holtby 2000).

In recovery planning, attention should be paid to genetic population structure to avoid losses of genetic diversity. A fundamental component of re-

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covery planning, therefore, is the delineation of conservation units, or stocks (Waples 1994). This delineation can be accomplished through analyzing discontinuities in habitat, differences in life histories or morphology, or straying rates (see Pawson and Jennings 1996). Also, surveys of molecular genetic variation can be used to delimit conservation units based on estimates of gene flow, which reflect the degree of reproductive isolation. Such measures of reproductive isolation provide a practical means of assessing the potential for local adaptation in the absence of habitat and life history information (Wood and Holtby 1998). Ideally, a combination of the above approaches should be used to delimit stocks.

If genetic divergence is sufficient, genetic stock identification (GSI) can be used to distinguish stocks in mixtures (Grant et al. 1980; Smouse et al. 1982). Identification of individual stocks in mixed stock samples can allow for protecting threatened populations in fisheries and aid in determining life history characters (e.g., run timing and migration route) so that fisheries may be conducted in a manner that minimizes the harvest of threatened populations (Waples et al. 1990). This capacity can also facilitate indirect estimates of spawning escapements in conditions that impede direct counts (Wood et al. 1987), as is the case for the glacially turbid rivers in the Owikeno Lake watershed.

Potential options for recovery efforts include supportive breeding and stock translocations; however, these tactics may be unproductive or harmful if local adaptation and population structure are not considered. Stock translocations may be ineffective if the transferred population is poorly adapted to the recipient habitat (Withler 1982; Altukhov and Salmenkova 1987; Burger et al. 2000). Pooling of different populations in hatcheries can result in the loss of local adaptations (Allendorf and Ryman 1987). Also, releasing large numbers of inappropriately bred hatchery fish can have deleterious genetic effects on populations targeted for recovery (Hindar et al. 1991; Waples 1991). Knowledge of local population structure can guide the development of an effective supportive breeding program and help avoid cross-hybridization of locally adapted populations.

A previous genetic study based on analysis of allozymes demonstrated that the nursery lake is a primary determinant of sockeye salmon population structure in British Columbia (Wood et al. 1994). This finding is concordant with studies of sockeye salmon from other regions (Grant et al. 1980; Wilmot and Burger 1985). Moreover, this work revealed that genetic similarity between Canadian sockeye salmon populations is only weakly correlated with geographic distance, showing a mosaic of divergent populations, as noted previously for sockeye salmon of other regions (Utter et al. 1984, 1989; Guthrie et al. 1994; Winans et al. 1996).

In this paper we present results of a genetic survey of sockeye salmon associated with 15 lakes of the south-central coast of British Columbia. Our objective was to determine the sockeye salmon population structure of the region in support of recovery planning efforts. We assessed (1) whether significant population structure exists across the Central Coast and within the Owikeno Lake watershed and how this knowledge should guide enhancement activities; (2) whether GSI based on the observed population structure could be used to identify threatened stocks in mixed-stock coastal fisheries; and (3) whether GSI could facilitate indirect enumeration of the sockeye salmon that spawn in the turbid tributaries to Owikeno Lake.

Methods

Sample collection.—Tissue biopsy samples or operculum punches were obtained from 1,324 sockeye salmon from 22 sites in south-central British Columbia (Table 1; Figure 1). Except for the samples from Woss Lake, which were taken from juvenile fish in a midwater trawl, samples were taken from spawning or spawned-out fish captured with either a gaff (Long Lake), dip net (Lagoon Creek), or tangle net of 110-mm mesh (all others) on historically known spawning grounds at or around peak spawning time (Wood et al. 1970; Rutherford et al. 1992). Sample sizes ranged from 12 to 130 fish (Table 1). Samples were collected in multiple years for some sites within the Atnarko River and Owikeno Lake watersheds and for Heydon and Sakinaw lakes.

Extraction of DNA, polymerase chain reaction, and electrophoretic conditions.—Crude DNA extracts were prepared according to the methods of Nelson et al. (1998). Each 25-μL polymerase chain reaction (PCR) required 0.1–1.0 μL of crude extract. We collected genotypic data for 10 microsatellite DNA loci, of which 8 had been previously published and 2 are being reported for the first time in this work. Novel loci were isolated as described in Smith et al. (1998). All loci are listed along with the PCR conditions in Appendix 1. An MJ PTC-100 thermal cycler (MJ Research, Watertown, Massachusetts) was used to carry out PCR

TABLE 1.—Sockeye salmon samples collected from south-central British Columbia. Sample codes refer to Figure 1 and contain the last two digits of the year in which the samples were collected. All samples were collected from spawning fish except those for Woss Lake, which were from juvenile fish. The number of loci for each sample that deviated from Hardy–Weinberg proportions is shown in the last column.

Sample code	Watershed	Site	Year	Sample size	Deviations
ALL96	Atnarko River	Atnarko River, 2 km above Lonesome Lake	1996	28	1
ALL97	Atnarko River	Atnarko River, 2 km above Lonesome Lake	1997	52	0
AR96	Atnarko River	Atnarko River, 5 km below Lonesome Lake	1996	20	0
AR97	Atnarko River	Atnarko River, 5 km below Lonesome Lake	1997	42	1
ATL85	Atnarko River	Tenas Lake, outlet of lake	1985	48	3
CAN86	Canoona Lake	Canoona River (inlet tributary), <1 km from lake	1986	79	2
DEV99	Devon Lake	Inlet tributary, <1 km from lake	1999	100	1
HEY00	Heydon Lake	Outlet tributary, <1 km from lake	2000	16	0
HEY01	Heydon Lake	Outlet tributary, <1 km from lake	2001	18	0
KOY86	Koeye Lake	Inlet tributary, <1 km from lake	1986	80	2
KSQ86	Kimsquit Lake	Kimsquit lakeshore	1986	62	0
KTL86	Kitlope Lake	Tezwa River (inlet tributary), 2 km from lake	1986	41	0
LAG99	Lagoon Lake	Inlet tributary, <1 km from lake	1999	50	0
LOL84	Long Lake	Canoe Creek (inlet tributary), <1 km from lake	1984	51	0
MIK99	Mikado Lake	Inlet tributary, <1 km from lake	1999	62	1
OAM97	Owikeno Lake	Amback River (inlet tributary), <1 km from lake	1997	48	2
OAS98	Owikeno Lake	Ashlum River (inlet tributary), <1 km from lake	1998	50	2
OIZ97	Owikeno Lake	Inziana River (inlet tributary), <1 km from lake	1997	47	1
OIZ98	Owikeno Lake	Inziana River (inlet tributary), <1 km from lake	1998	47	1
ONE98	Owikeno Lake	Neechanz River (inlet tributary), 2 km from lake	1998	50	2
OSH96	Owikeno Lake	Sheemahant River (inlet tributary), 6 km from lake	1996	38	3
OSH98	Owikeno Lake	Sheemahant River (inlet tributary), 7 km from lake	1998	48	2
OWN96	Owikeno Lake	Wannock River, outlet of lake	1996	27	1
OWN97	Owikeno Lake	Wannock River, outlet of lake	1997	69	1
OWN99	Owikeno Lake	Wannock River, outlet of lake	1999	34	1
OWW97	Owikeno Lake	Washwash River (inlet tributary), <1 km from lake	1997	56	3
OWW98	Owikeno Lake	Washwash River (inlet tributary), <1 km from lake	1998	48	0
SAK88	Sakinaw Lake	Sakinaw lakeshore	1988	81	0
SAK00	Sakinaw Lake	Sakinaw lakeshore	2000	20	0
SAK01	Sakinaw Lake	Sakinaw lakeshore	2001	12	1
TNK86	Tankeeah River	Tributary[a]	1986	78	2
WOS01	Woss Lake	Woss Lake (midwater trawl)	2001	50	2

[a] Samples taken from a spawning site less than 1 km from two small rearing lakes.

in 96-well microtiter plates; each reaction mixture of 25 μL contained 10 pmol (0.4 μM) of each primer, 80 μM of each nucleotide, 20 mM Tris (pH 8.8), 2 mM $MgSO_4$, 10 mM KCl, 0.1% Triton X-100, 10 mM $(NH_4)SO_4$, and 0.1 mg/mL bovine serum albumin. After a 3-min incubation at 94°C, PCR mixtures were held at 80°C while 1 unit of Taq DNA polymerase was added, after which temperature cycling was initiated. After the amplification reaction, 3 μL of 10× loading dye (50 mM EDTA [pH 8.0], 30% glycerol, 0.25% bromphenol blue) was added to each reaction, and 10 μL of this solution was loaded per gel electrophoresis lane.

Gel electrophoresis.—Microsatellite alleles were size-fractionated on nondenaturing polyacrylamide gels that were 17 cm wide × 14.5 cm long and contained acrylamide and bisacrylamide in a 19:1 ratio. Gels contained 2× TAE buffer (Sambrook et al. 1989), as did the running buffer. Each gel included three 20-basepair marker (GenSura Laboratories Inc., Del Mar, California) lanes to create a molecular size grid and 24 individual fish samples. In addition, each gel contained a PCR from an individual fish that was analyzed repeatedly to estimate the precision of band size determination. The precision of band size determination was taken into consideration when identifying alleles. Gels were stained with 0.5 μg/mL ethidium bromide in water and viewed in ultraviolet light. Digital images of gels were obtained with an Eagle-Eye system (Stratagene Corp., San Diego, California). Gels were manually scored using INTELLIGENT QUANTIFIER version 2.1.2a software (Millipore Corp., Bedford, Massachusetts). Allele frequencies for each sample are shown in Appendix 2.

Data analysis.—Each sample was tested for departures from Hardy–Weinberg genotypic proportions (HWP) with the exact test of Guo and

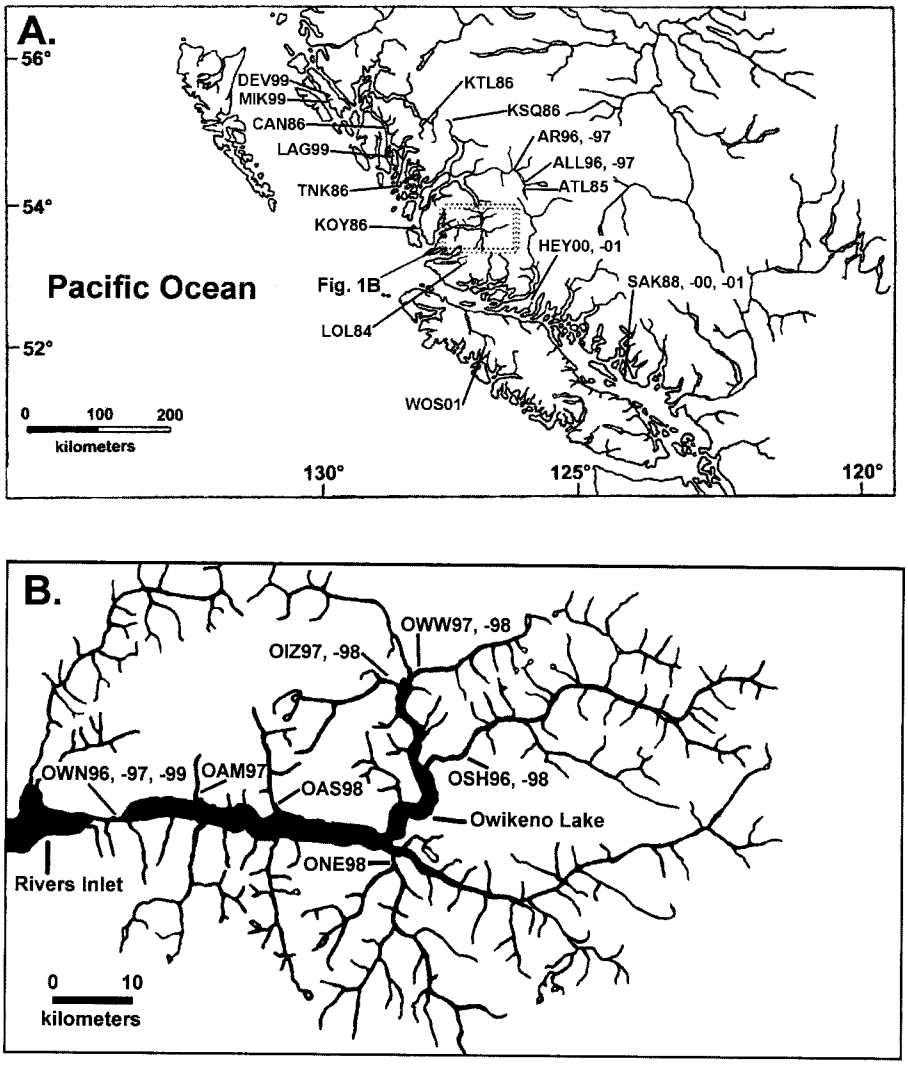

FIGURE 1.—Locations of sockeye salmon sampling in the south-central coast of British Columbia. Codes correspond to the samples listed in Table 1. The area within the stippled box in panel **A** is the Owikeno Lake watershed, which is shown in greater detail in panel **B.**

Thompson (1992) by using GENEPOP version 3.1 (Raymond and Rousset 1997); probability values were corrected with the sequential Bonferroni technique (Holm 1979; Rice 1989) with the initial significance level taken to be 0.05/number of loci (10).

Because deviations from HWP were observed, we tested genetic homogeneity between replicate samples collected in different years by using a *G*-based exact test with genotype frequencies rather than allele frequencies (Goudet et al. 1996); again, we used GENEPOP for this, and adjusted probability values with the sequential Bonferroni technique, taking the initial significance level to be 0.05/number of loci (10). This test was not corrected for bias towards a ''significant'' result attributable to genetic drift alone, according to Waples (1989), because the size of the samples studied was unlikely to be more that 10% of the effective population size of the populations sampled (Williams et al. 1994). Gametic disequilibrium of the two loci amplified by the *Oki1* primer set was tested by carrying out *G*-based exact tests (Goudet et al. 1996) with GENEPOP.

Across watersheds, correlation between pairwise Cavalli-Sforza and Edwards (1967) genetic

distance (D_{CSE}) generated with PHYLIP (Felsenstein 1995) and geographic distance was calculated and tested by using a permutation procedure (Mantel 1967) implemented by ARLEQUIN, version 1.1 (Schneider et al. 1999); for this analysis we used a single sample from each watershed. D_{CSE} was used in this analysis because it models divergence based on genetic drift—an appropriate model for sockeye salmon in British Columbia, which colonized the region 10,000–15,000 years ago after the Fraser glacial period. Divergence of sockeye salmon in the region is probably a result of genetic drift caused by fluctuations in population size or bottlenecks associated with colonization of newly ice-free areas (Wood et al. 1994). Hierarchical analysis of *F*-statistics carried out with BIOSYS-1, release 1.7 (Swofford and Selander 1981) was used to examine the distribution of genetic variation between replicate samples from the same spawning site collected in different years, between spawning sites within watersheds, and between watersheds. To explore population structuring over the entire sample set, we carried out principal component analysis (PCA) with SPSS (SPSS 2001) based on pairwise D_{CSE} between all samples. Also using ARLEQUIN, we analyzed molecular variance (AMOVA; Excoffier et al. 1992) to examine partitioning of genetic variation between replicate samples from the same site, and between spawning sites within the Owikeno Lake and Atnarko River watersheds. To gain insight into the biological basis for the pattern of divergence observed, we computed *F*-statistics (Wright 1951) according to Weir and Cockerham (1984), using GENETIX version 4.02; the significance of F_{ST} values was tested by performing 500 permutations.

The program SPAM, version 3.5 (Debevec et al. 2000) was used to test the potential for GSI of sockeye salmon of south-central British Columbia. We determined the proportion of fish from each watershed estimated to compose hypothetical mixture samples of 100 fish, each drawn randomly with replacement from a single sample in the baseline. To generate confidence intervals, each estimation was repeated 100 times, and the baseline was bootstrap-resampled for each of these estimations. In this context, contributions from the Atnarko River watershed were considered together, as were contributions from the Owikeno Lake watershed. In each case the correct estimate was 100% of the corresponding watershed; deviations reflect the maximum bias expected under ideal conditions.

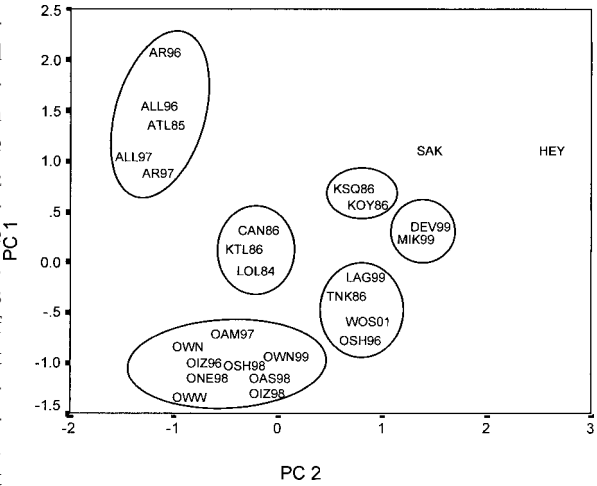

FIGURE 2.—Principal components analysis of Cavalli-Sforza and Edwards genetic distance between populations. Sample codes are listed in Table 1. The first two principal components are plotted.

Results

Hardy–Weinberg Equilibrium and Pooling of Samples from Different Years

We tested each of the 32 samples for departures from HWP (Table 1). Out of the 32 samples, 20 showed at least one deviation from HWP. The maximum number of deviations observed for any sample was three each for Tenas Lake, Sheemahant River-1996, and Washwash River-1997.

Analysis of the genetic homogeneity of temporal replicate samples indicated that the replicate samples Washwash River-1997, -1998, Wannock River-1996, -1997, Heydon Lake-2000, -2001, and Sakinaw Lake-1988, -2000, -2001 were not significantly different and therefore were pooled for further analysis. Genotypic frequencies, however, were significantly different between all other replicate samples for at least one locus; therefore, these samples were not pooled in subsequent analyses.

Population Structure

Several groupings were evident when principal components 1 (PC1; 46% of variation) and 2 (PC 2; 26% of variation) were plotted for each sample (Figure 2). The Atnarko River watershed samples clustered together, as did the Owikeno Lake watershed samples, whereas the Sheemahant River 1996 sample (Owikeno Lake watershed) was separated from the other Owikeno Lake watershed samples by PC2. Two clusters contained more than two samples and had a mixture of geographically

TABLE 2.—Pairwise F_{ST} values for all samples. Sample codes are explained in Table 1. Pooled samples are indicated by the absence of a date suffix. All values are significant ($P < 0.05$) except those in brackets.

	Sample											
Sample	ALL96	ALL97	AR96	AR97	ATL85	CAN86	DEV99	HEY99	KOY86	KSQ86	KTL86	LAG99
ALL97	0.011											
AR96	{0.003}	0.024										
AR97	{0.009}	{0.005}	{0.015}									
ATL85	{0.005}	0.027	{0.001}	0.013								
CAN86	0.114	0.089	0.140	0.094	0.112							
DEV99	0.145	0.112	0.168	0.094	0.145	0.147						
HEY99	0.199	0.173	0.220	0.150	0.190	0.161	0.116					
KOY86	0.110	0.087	0.146	0.079	0.119	0.099	0.081	0.131				
KSQ86	0.185	0.153	0.215	0.136	0.184	0.117	0.142	0.145	0.090			
KTL86	0.104	0.080	0.122	0.069	0.110	0.077	0.108	0.112	0.074	0.071		
LAG99	0.096	0.082	0.112	0.061	0.093	0.086	0.088	0.093	0.075	0.083	0.068	
LOL84	0.090	0.075	0.111	0.055	0.091	0.099	0.083	0.111	0.063	0.061	0.054	0.047
MIK99	0.152	0.117	0.178	0.099	0.152	0.142	{0.004}	0.114	0.079	0.122	0.099	0.082
OAM97	0.082	0.091	0.097	0.067	0.069	0.079	0.103	0.147	0.089	0.134	0.074	0.058
OAS98	0.103	0.085	0.124	0.070	0.105	0.084	0.089	0.127	0.064	0.092	0.033	0.042
OIZ97	0.094	0.082	0.123	0.066	0.092	0.053	0.111	0.140	0.056	0.101	0.043	0.053
OIZ98	0.108	0.098	0.133	0.079	0.101	0.079	0.107	0.150	0.066	0.109	0.056	0.058
ONE98	0.086	0.072	0.110	0.058	0.085	0.056	0.098	0.127	0.056	0.092	0.035	0.050
OSH96	0.105	0.095	0.127	0.075	0.109	0.097	0.107	0.134	0.091	0.137	0.052	0.056
OSH98	0.097	0.080	0.118	0.064	0.095	0.063	0.101	0.120	0.058	0.086	0.033	0.045
OWN	0.088	0.078	0.112	0.070	0.086	0.043	0.114	0.125	0.070	0.108	0.049	0.053
OWN99	0.097	0.083	0.122	0.074	0.100	0.067	0.103	0.128	0.075	0.104	0.045	0.036
OWW	0.093	0.081	0.116	0.065	0.094	0.061	0.091	0.124	0.055	0.090	0.035	0.048
SAK	0.162	0.124	0.193	0.107	0.162	0.127	0.094	0.133	0.061	0.091	0.108	0.102
TNK86	0.118	0.106	0.144	0.097	0.113	0.122	0.097	0.148	0.074	0.150	0.121	0.064
WOS	0.117	0.099	0.149	0.091	0.130	0.112	0.102	0.140	0.082	0.110	0.037	0.076

proximate and disparate populations. Samples from Canoona and Long lakes clustered together, but the cluster did not include any samples from the five watersheds between Long Lake and Canoona Lake. Tankeeha River clustered with Woss Lake, but the sample from Koeye Lake, which is between Tankeeha River and Woss Lake, was not in this cluster. The samples from Devon and Mikado lakes, which empty into the same estuary, clustered together. Sakinaw and Heydon lakes did not cluster with any other sample. The correlation between geographic distance and D_{CSE} between watersheds was weak but positive ($r^2 = 0.13$, $P < 0.05$).

We used AMOVA to examine the genetic relationship between samples, sample sites, and watersheds. The majority of the genetic variance available for examining population structure, 6.3% of the total, was partitioned among watersheds. The remainder of the available variance (2.0% of total) was distributed among temporal replicate samples; no variance was attributed to sites within watersheds. Based on the approximation that $N_e m = (1 - F_{ST})/4F_{ST}$ (Wright 1969), the between-watershed F_{ST} value of 0.063 suggests that, across the region, approximately four migrants are exchanged between each watershed per generation.

Insight into the biological basis for the pattern of divergence between watersheds was gained by computing pairwise *F*-statistics (Table 2). With two exceptions, all pairwise F_{ST} values between samples from different watersheds were significant and greater than the maximum F_{ST} value observed between temporal replicate samples. The first exception was Devon and Mikado lakes, which empty into the same estuary; the second exception was Woss Lake and the single deviant sample from the Owikeno Lake watershed (OSH96; see Figure 2).

Consistent with the AMOVA across all watersheds, separate AMOVAs for the Atnarko River or Owikeno Lake watersheds showed that more than 98% ($P < 0.05$) of the genetic variance was within samples, the balance of the variance being distributed between temporal replicate samples ($P < 0.05$). This was true regardless of whether or not temporal replicate samples from the Owikeno Lake watershed were pooled before analysis.

Of the eight combinations of Atnarko River watershed samples, only the pairwise F_{ST} between the 1997 sample from Lonesome Lake and the 1996 sample from Atnarko River ($F_{ST} = 0.024$) and between the 1997 sample from Lonesome Lake and the sample from Tenas Lake ($F_{ST} = 0.027$) were significant ($P < 0.05$) and exceeded

TABLE 2.—Extended.

Sample													
LOL84	MIK99	OAM97	OAS98	OIZ97	OIZ98	ONE98	OSH96	OSH98	OWN	OWN99	OWW	SAK	TNK86
0.081													
0.062	0.108												
0.046	0.088	0.033											
0.053	0.117	0.018	0.013										
0.056	0.108	0.018	0.005	{0.006}									
0.045	0.099	0.028	0.005	{0.007}	{0.001}								
0.058	0.117	0.035	0.015	0.015	0.025	0.022							
0.041	0.097	0.034	0.005	0.010	0.009	{0.001}	0.025						
0.059	0.114	0.023	0.033	0.012	0.025	0.023	0.036	0.031					
0.063	0.092	0.041	0.015	0.032	{0.021}	0.012	{0.042}	0.016	0.025				
0.039	0.092	0.022	0.005	0.006	0.005	0.001	0.019	0.001	0.016	0.014			
0.079	0.102	0.125	0.092	0.082	0.096	0.082	0.114	0.085	0.117	0.127	0.090		
0.068	0.106	0.073	0.066	0.069	0.068	0.072	0.065	0.080	0.065	0.090	0.064	0.111	
0.064	0.098	0.066	0.023	0.044	0.039	0.034	0.041	0.037	0.051	0.030	0.029	0.125	0.107

the F_{ST} value observed between replicate samples from within the watershed (Table 2). The 1996 Lonesome Lake sample had low and nonsignificant F_{ST} values with these same samples, casting doubt on the biological significance of this observation. Of the 33 pairwise F_{ST} values between different sites within the Owikeno Lake watershed, only those involving the Amback and Wannock river samples exceeded 0.025 ($P < 0.05$), which is the F_{ST} value observed between temporal replicate samples from the Sheemahant and Wannock rivers.

Genetic Stock Identification

Genetic stock identification estimates of the composition of hypothetical single-stock mixture samples drawn from watersheds represented by a single sample site had bias that ranged from −23% (SD, 11%) for Lagoon Lake to −2% (SD, 2%) for Sakinaw Lake (Table 3). For assignment of any of the Atnarko River watershed samples to the Atnarko River watershed, bias did not exceed −7% (SD, 5%). For assignment of any of the Owikeno Lake watershed samples to the Owikeno Lake watershed, bias ranged from −5% (SD, 3%) to −1% (SD, 1%).

Discussion

Our results reveal substantial population structure in sockeye salmon of British Columbia's south-central coast. The clustering of samples from geographically proximate and disparate sites by PCA shows the overall pattern of genetic heterogeneity across the range of sampling to be a mosaic, similar to the pattern of population divergence noted by Utter et al. (1984, 1989), Wood et al. (1994), Winans et al. (1996), and Guthrie et al. (1994). The general similarity of our results with those of previous studies that used allozyme markers provides additional support for a general concordance of genetic inferences based on allozyme and nuclear DNA markers (Scribner et al. 1998; Allendorf and Seeb 2000). As judged by AMOVA, our results suggest that the watershed is a fundamental unit of population structuring of sockeye salmon in British Columbia. Analysis of gene flow as estimated from F_{ST} indicates that sockeye salmon inhabiting different watersheds are somewhat reproductively isolated, across the region exchanging four individuals per generation. Although this is only an approximation of gene flow based on ideal assumptions, these estimates

TABLE 3.—Results of mixed stock analysis simulations. Shown are the regional stock compositions of hypothetical samples of 100 fish containing 100% of each of the samples listed in the first column, as estimated with SPAM (Debevec et al. 2000). The sum of allocations (%) to the Atnarko River and Owikeno Lake watersheds is listed; standard deviations are given in parentheses.

Source	Atnarko	Owikeno	CAN86	DEV99	HEY99	KOY86	KSQ86	KTL86	LAG99	LOL84	MIK99	SAK	TNK86	WOS
ALL96	93 (4)	3 (3)	0	0	0	0	0	1 (2)	0	0	0	0	0	0
ALL97	93 (5)	5 (4)	0	0	0	0	0	1 (2)	0	0	0	0	0	0
AR96	96 (3)	2 (2)	0	0	0	0	0	1 (1)	0	0	0	0	0	0
AR97	89 (7)	7 (5)	0	1 (1)	0	0	0	1 (2)	0	1 (1)	0	0	0	0
ATL85	97 (3)	2 (2)	0	0	0	0	0	0	0	0	0	0	0	0
CAN86	1 (2)	4 (4)	92 (6)	0	0	0	0	1 (2)	0	0	0	0	0	0
DEV99	0	1 (1)	0	87 (6)	0	0	0	0	0	0	10 (5)	0	0	0
HEY99	0	5 (4)	0	1 (2)	89 (7)	0	0	2 (2)	0	0	0	0	0	1 (1)
KOY86	0	3 (2)	0	1 (1)	0	94 (4)	0	1 (1)	0	0	0	0	0	0
KSQ86	0	2 (2)	1 (1)	0	0	1 (1)	90 (6)	1 (1)	1 (1)	3 (3)	0	1 (1)	0	0
KTL86	3 (3)	11 (6)	1 (1)	0	0	2 (2)	0	81 (9)	0	1 (1)	0	0	0	0
LAG99	2 (2)	14 (8)	0	0	0	0	1 (2)	0	77 (11)	1 (1)	0	0	4 (3)	0
LOL84	1 (1)	6 (5)	0	0	0	0	2 (2)	0	0	90 (7)	0	0	0	0
MIK99	0	2 (2)	0	15 (8)	0	0	0	0	0	0	81 (8)	0	0	0
OAM97	1 (1)	95 (3)	0	0	0	1 (1)	0	0	0	2 (2)	0	1 (1)	0	0
OAS98	0	98 (2)	0	0	0	0	0	0	0	0	0	0	0	0
OIZ97	1 (1)	97 (3)	0	0	0	1 (1)	0	0	0	0	0	0	0	0
OIZ98	0	99 (1)	0	0	0	0	0	0	0	0	0	0	0	0
ONE98	0	98 (2)	0	0	0	0	0	0	0	0	0	0	0	0
OSH96	0	98 (2)	0	0	0	0	0	0	0	0	0	0	0	0
OSH98	0	98 (2)	0	0	0	0	0	0	0	0	0	0	0	0
OWN	1 (1)	97 (2)	1 (1)	0	0	0	0	0	0	0	0	0	0	0
OWN99	0	99 (1)	0	0	0	0	0	0	0	0	0	0	0	0
OWW	0	97 (2)	1 (1)	0	0	0	0	1 (1)	0	0	0	0	0	0
SAK	0	1 (1)	0	0	0	0	0	0	0	0	0	98 (2)	0	0
TNK86	0	4 (3)	0	0	0	1 (1)	0	0	0	0	0	0	94 (5)	0
WOS	0	6 (4)	0	0	0	1 (1)	0	0	0	0	0	0	0	91 (5)

of gene flow are within the range that allows for population divergence in the absence of selection (Allendorf and Phelps 1981; Adkison 1995). Homing and genetic drift have probably largely shaped the observed distribution of genetic variation. This explanation seems reasonable, given that in general, sockeye salmon may home more precisely than do other Pacific salmon (Quinn 1993; see also Gustafson and Winans 1999), which tend to have a more graded distribution of genetic heterogeneity (Utter et al. 1984, 1989).

This pattern of sockeye salmon population structuring implies that physical discontinuities of habitat are more important than distance in determining gene flow. Even so, we observed a weak positive relationship between geographic and genetic distance. However, the weak correlation between these two parameters indicates that geographic distance is not a reliable predictor of genetic relationships in sockeye salmon over this spatial scale.

In this study, we used temporal variation estimated by computing pairwise F_{ST} values between replicate samples as a benchmark measure from which to interpret the biological relevance of genetic differences among samples collected from different sites. As such, this rationale gauges the amount of variation attributable to genetic drift and sample collection (Waples 1989). Spatial population structuring cannot be persistent or biologically meaningful if it is generally less than temporal variation. The F_{ST} between watersheds observed here was greater (0.063) than the maximum F_{ST} value between temporal replicate samples (0.025).

The only case of watersheds being strongly reproductively connected was Devon and Mikado lakes, which share an estuary. Other than this, fish spawning at sites separated by marine habitat were highly differentiated. Under rates of natural selection proposed for salmon (Mork 1994; Adkison 1995), spawning sites separated by more than 40 ocean kilometers are probably sufficiently isolated to allow adaptation to local conditions (Wood and Holtby 1998). This suggests that transfer of fish to an area more than 40 km away from their natal system may be ineffective. Investigating the amount of gene flow between sockeye spawning at sites less than 40 km apart should be useful.

People have long relied on the sockeye salmon populations of British Columbia, so any recovery plan may have to allow for harvest even in the

face of declining abundance. We found that sockeye salmon could be traced to their natal watershed with high accuracy, demonstrating that genetic stock identification could be used to monitor catch composition of mixed-stock fishery samples at the regional level. Within the Owikeno Lake system, glacial turbidity in the Sheemahant, Wannock, and Neechanz rivers thwarts accurate visual estimation of escapement. The use of GSI could increase the accuracy of escapement estimates by providing information on the stock composition of samples of fish entering the watershed. Because GSI is predicated on previously obtained baseline information, genetic differentiation between spawning sites must be persistent and exceed year-to-year variation. This was not generally true within the Owikeno Lake watershed, thus precluding indirect enumeration of escapement to the glacially turbid tributaries with GSI.

The seven different spawning sites we surveyed within the Owikeno Lake basin together encompass 83% of the estimated escapement to the system from 1950 to 1989 (Walters et al. 1993). We found no evidence for decidedly isolated populations within the drainage, although the Wannock and Amback rivers gave some indication of being partially isolated from the other sites. The Wannock River is the sole outlet for Owikeno Lake. Fry emerging in the Wannock River must swim upstream to gain access to the rearing lake, whereas fry emerging in the inlets swim downstream. Local adaptation in rheotactic behavior of sockeye salmon fry has been demonstrated in lakes with inflow and outflow spawning (Brannon 1967; Raleigh 1967; Hensleigh and Hendry 1998). At least partial reproductive isolation is presumed to be necessary for this to evolve, which supports our speculation that Wannock River fish may be partially isolated from fish that spawn in inlets. Consistent with this hypothesis, restricted gene flow has been noted between the outlet-spawning subpopulations and the spatially proximate tributary and beach-spawning subpopulations of sockeye salmon in Tustumena Lake (Burger et al. 1997) and elsewhere (summarized by Wood 1995). Fish from the most seaward tributary to Owikeno Lake, the Amback River, also appear to be partially isolated, but this conclusion is based on sampling in a single year. Until additional data are gathered, fish spawning in the Wannock and Amback rivers should be regarded as potentially distinct subpopulations. Overall, however, a general lack of differentiation among the tributaries to Owikeno Lake suggests that gene flow is high enough to greatly constrain opportunities for local adaptation. This finding supports management of the majority of Owikeno Lake sockeye salmon as a single population.

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Appendix 1: Polymerase Chain Reaction Conditions

TABLE A.1.—Polymerase chain reaction (PCR) conditions for microsatellite DNA loci examined.

Locus	Temperature (°C)	PCR cycles (s)	Reference
Omy 77	47	30/20/20	McConnell et al. 1995
Ots3	47	30/30/30	Banks et al. 1999
Ots100	54	30/30/30	Nelson and Beacham 1999
Ots103	58	30/30/30	Small et al. 1998
Ots107	48	30/30/30	Nelson and Beacham 1999
Oki1a[a]	55	30/30/30	Smith et al. 1998
Oki1b[a]	55	30/30/30	Smith et al. 1998
Oki6[b]	56	30/30/30	This work
Oki23	55	30/30/30	Smith et al. 1998
Oki29[b]	52	30/30/30	This work

[a] Two unlinked loci were amplified with a single PCR primer set.

[b] The primer sequences and GenBank accession numbers for *Oki6* and *Oki29* are as follows: *Oki6* (AF055431): `TCAACAGATAGACAGGTGACACA` (forward), `AACAGACAGCTAATGCAGAACG` (reverse); *Oki29* (AF055453): `CAACTAGACCCAGCCTCACAG` (forward); `GGCCTTCCAGCAGAGAGTTA` (reverse).

Appendix 2: Allele Frequencies for Sockeye Salmon

TABLE A.2.—Allele frequencies for all loci in sockeye salmon samples from south-central British Columbia. The symbol *N* refers to the number of fish successfully analysed for each locus.

Locus	Allele and *N*	Sample							
		ALL96	ALL97	AR96	AR97	ATL	CAN	DEV	HEY
Ots107	1	0	0	0.05	0.038	0	0.132	0.253	0
	2	0	0	0	0	0	0.007	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0.02	0	0	0.01	0	0	0
	6	0	0.01	0	0	0	0	0	0
	7	0.339	0.26	0.35	0.313	0.375	0.176	0.024	0.033
	8	0.589	0.65	0.575	0.613	0.552	0.632	0.688	0.783
	9	0.071	0.06	0.025	0.038	0.063	0.046	0.035	0.167
	10	0	0	0	0	0	0.007	0	0
	11	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0.017
	N	28	50	20	40	48	76	85	30
Oki23	1	0.315	0.279	0.3	0.298	0.228	0.105	0.156	0
	2	0.667	0.702	0.65	0.56	0.652	0.855	0.558	0.471
	3	0.019	0.019	0.05	0.143	0.098	0.039	0.286	0.529
	4	0	0	0	0	0.022	0	0	0
	N	27	52	20	42	46	76	77	34
Oki1a	1	0.268	0.319	0.25	0.3	0.205	0.629	0.241	0.493
	2	0.089	0.053	0.125	0.033	0.17	0.026	0.118	0.313
	3	0.625	0.628	0.625	0.65	0.625	0.344	0.629	0.164
	4	0.018	0	0	0.017	0	0	0.012	0.03
	N	28	47	20	30	44	75	85	33
Oki1b	1	0	0	0	0	0	0	0.011	0
	2	0	0.122	0	0.145	0.011	0	0.178	0
	3	0.357	0.551	0.275	0.435	0.278	0.576	0.626	0.897
	4	0.643	0.316	0.725	0.419	0.711	0.418	0.132	0.103
	5	0	0.01	0	0	0	0.006	0.052	0
	N	28	49	20	31	45	79	87	34
Oki29	1	0	0	0	0	0	0.006	0	0
	2	0.554	0.577	0.684	0.632	0.716	0.636	0.777	0.853
	3	0.161	0.144	0.211	0.118	0.108	0.091	0.054	0
	4	0.232	0.26	0.079	0.176	0.068	0.265	0.12	0.088
	5	0.054	0.019	0.026	0.074	0.108	0	0.048	0.059
	N	28	52	19	34	37	66	83	34
Oki6	1	0.074	0.061	0.026	0.145	0.119	0.162	0.073	0.117
	2	0	0.02	0	0	0.06	0.058	0.024	0.217
	3	0.833	0.867	0.895	0.697	0.738	0.571	0.207	0.033
	4	0.093	0.051	0.079	0.158	0.083	0.195	0.323	0.633
	5	0	0	0	0	0	0	0.018	0
	6	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0.006	0
	9	0	0	0	0	0	0	0.012	0
	10	0	0	0	0	0	0.013	0.335	0
	11	0	0	0	0	0	0	0	0
	N	27	49	19	38	42	77	82	30
Omy77	1	0	0	0	0.038	0	0.026	0.046	0
	2	0.071	0.117	0.125	0.05	0.093	0.072	0.015	0.103
	3	0.214	0.277	0.175	0.138	0.267	0.697	0.162	0.309
	4	0.411	0.277	0.275	0.313	0.407	0.184	0.146	0.088
	5	0.071	0.16	0.15	0.275	0.128	0.013	0.469	0.206
	6	0.054	0.021	0.075	0	0	0	0.138	0.279
	7	0.179	0.149	0.2	0.188	0.105	0.007	0.023	0.015
	8	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0
	N	28	47	20	40	43	76	65	34

TABLE A.2.—Extended (1).

Locus	Sample									
	KOY	KSQ	KTL	LAG	LOL	MIK	OAM97	OAS98	OIZ97	OIZ98
Ots107	0.03	0	0.092	0.103	0.069	0.21	0.24	0.16	0.133	0.244
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0.138	0.01	0	0	0	0	0
	0	0	0.026	0	0	0.008	0	0.02	0	0
	0.083	0.036	0.066	0	0.029	0.024	0.031	0.04	0.022	0.122
	0.652	0.911	0.75	0.759	0.814	0.742	0.5	0.69	0.7	0.544
	0.212	0.045	0.053	0	0.049	0	0.208	0.09	0.144	0.089
	0	0.009	0	0	0.01	0	0.021	0	0	0
	0.023	0	0	0	0	0.016	0	0	0	0
	0	0	0.013	0	0.02	0	0	0	0	0
	66	56	38	29	51	62	48	50	45	45
Oki23	0.301	0.033	0.212	0.086	0.198	0.177	0.244	0.26	0.226	0.25
	0.596	0.9	0.727	0.621	0.771	0.661	0.622	0.65	0.581	0.674
	0.103	0.067	0.061	0.293	0.031	0.161	0.133	0.09	0.194	0.076
	0	0	0	0	0	0	0	0	0	0
	73	45	33	29	48	62	45	50	31	46
Oki1a	0.214	0.524	0.595	0.5	0.25	0.347	0.34	0.33	0.337	0.205
	0.019	0.073	0.076	0.054	0.057	0.116	0.138	0.14	0.12	0.205
	0.767	0.403	0.329	0.429	0.659	0.529	0.489	0.53	0.543	0.545
	0	0	0	0.018	0.034	0.008	0.032	0	0	0.045
	79	62	39	28	44	60	47	50	46	44
Oki1b	0	0	0	0.017	0	0.008	0	0.02	0.011	0.011
	0.05	0	0.037	0.034	0	0.23	0	0.16	0.011	0.098
	0.587	0.79	0.707	0.448	0.667	0.639	0.266	0.49	0.468	0.457
	0.125	0.202	0.195	0.328	0.333	0.107	0.734	0.33	0.457	0.435
	0.237	0.008	0.061	0.172	0	0.016	0	0	0.053	0
	80	62	41	29	48	61	47	50	47	46
Oki29	0	0	0	0	0	0	0	0	0	0
	0.551	0.481	0.371	0.696	0.531	0.844	0.641	0.388	0.4	0.447
	0.147	0.358	0.419	0.214	0.302	0.082	0.231	0.408	0.26	0.298
	0.288	0.075	0.097	0.089	0.104	0.074	0.115	0.163	0.3	0.213
	0.013	0.085	0.113	0	0.063	0	0.013	0.041	0.04	0.043
	78	53	31	28	48	61	39	49	25	47
Oki6	0.071	0.025	0.3	0.135	0.24	0.093	0.354	0.31	0.429	0.36
	0.007	0	0.075	0.077	0	0.068	0.021	0.08	0	0.128
	0.236	0.221	0.262	0.327	0.229	0.127	0.302	0.21	0.357	0.174
	0.536	0.754	0.262	0.385	0.448	0.432	0.219	0.19	0.186	0.174
	0.021	0	0	0.019	0.063	0	0.094	0.1	0.029	0.116
	0	0	0	0	0.021	0	0.01	0	0	0
	0	0	0	0	0	0	0	0.01	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0.012
	0.121	0	0.013	0	0	0.028	0	0	0	0
	0.007	0	0.087	0.058	0	0	0	0.1	0	0.035
	70	61	40	26	48	59	48	50	35	43
Omy77	0.008	0.122	0.014	0.043	0.01	0.1	0.098	0.122	0.1	0.075
	0.077	0.044	0.029	0.346	0	0.044	0.076	0.265	0.083	0.138
	0.408	0.144	0.186	0.261	0.219	0.176	0.359	0.235	0.45	0.363
	0.231	0.344	0.229	0.217	0.354	0.178	0.174	0.041	0.183	0.188
	0.038	0.311	0.243	0.13	0.271	0.433	0.261	0.276	0.117	0.225
	0.085	0.011	0.1	0	0.135	0.033	0.022	0.061	0.033	0.013
	0.154	0.022	0.2	0	0.01	0.022	0.011	0	0.033	0
	0	0	0	0	0	0.011	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	65	45	35	23	48	45	46	49	30	40

TABLE A.2.—Extended (2).

	Sample								
Locus	ONE	OSH96	OSH98	OWN	OWN99	OWW	SAK	TNK	WOS
Ots107	0.18	0.217	0.149	0.234	0.279	0.188	0	0.042	0.233
	0	0	0	0	0	0.012	0	0	0
	0	0	0	0	0	0	0	0	0.011
	0	0	0	0	0	0	0	0	0.033
	0	0	0	0	0	0.006	0	0	0
	0.03	0	0.011	0	0.029	0.018	0.099	0	0
	0.2	0.033	0.117	0.057	0.147	0.094	0.038	0.117	0.022
	0.49	0.667	0.585	0.538	0.485	0.512	0.764	0.8	0.567
	0.07	0.05	0.106	0.158	0.029	0.153	0.099	0.025	0.133
	0.03	0.033	0.032	0.006	0	0.018	0	0	0
	0	0	0	0	0.029	0	0	0.017	0
	0	0	0	0.006	0	0	0	0	0
	50	30	47	79	34	85	106	60	45
Oki23	0.25	0.359	0.26	0.131	0.088	0.191	0.252	0.238	0.174
	0.68	0.391	0.677	0.731	0.868	0.698	0.376	0.54	0.707
	0.07	0.188	0.063	0.138	0.044	0.111	0.372	0.222	0.098
	0	0.063	0	0	0	0	0	0	0.022
	50	32	48	80	34	81	113	63	46
Oki1a	0.31	0.394	0.344	0.464	0.438	0.352	0.109	0.092	0.449
	0.13	0.061	0.094	0.042	0.141	0.045	0.218	0.086	0.143
	0.55	0.53	0.552	0.479	0.406	0.591	0.673	0.809	0.408
	0.01	0.015	0.01	0.016	0.016	0.011	0	0.013	0
	50	33	48	96	32	88	110	76	24
Oki1b	0.03	0.132	0.021	0.005	0.015	0	0	0	0
	0.06	0.053	0.073	0.06	0.147	0.117	0.004	0.063	0.121
	0.55	0.487	0.573	0.456	0.5	0.5	0.888	0.507	0.652
	0.35	0.329	0.333	0.462	0.338	0.377	0.107	0.389	0.227
	0.01	0	0	0.016	0	0.006	0	0.042	0
	50	38	48	91	34	81	112	72	33
Oki29	0	0	0	0	0	0	0	0	0
	0.46	0.406	0.511	0.492	0.5	0.448	0.575	0.646	0.271
	0.29	0.438	0.34	0.282	0.309	0.381	0.084	0.326	0.583
	0.22	0.156	0.149	0.202	0.191	0.164	0.332	0.014	0.115
	0.03	0	0	0.024	0	0.007	0.009	0.014	0.031
	50	32	47	62	34	67	113	72	48
Oki6	0.311	0.446	0.365	0.349	0.324	0.375	0.116	0.096	0.394
	0.1	0.041	0.094	0.027	0.118	0.042	0	0.083	0.181
	0.267	0.264	0.219	0.355	0.235	0.215	0.37	0.321	0.255
	0.189	0.068	0.25	0.263	0.221	0.271	0.514	0.359	0.096
	0.022	0.041	0.063	0.005	0.059	0.056	0	0.036	0.011
	0	0	0	0	0	0.007	0	0	0
	0	0.041	0	0	0	0	0	0	0
	0	0.041	0	0	0	0	0	0	0
	0	0.027	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0.064	0.064
	0.111	0.014	0.01	0	0.044	0.035	0	0.038	0
	45	37	48	93	34	72	108	78	47
Omy77	0.065	0.086	0.13	0.012	0.048	0.053	0	0.033	0.053
	0.185	0.086	0.261	0.025	0.403	0.127	0.054	0.08	0.074
	0.304	0.314	0.228	0.648	0.306	0.353	0.277	0.707	0.234
	0.163	0.071	0.196	0.142	0.129	0.167	0.321	0.06	0.191
	0.185	0.186	0.087	0.148	0.097	0.187	0.348	0.12	0.234
	0.098	0.071	0.098	0	0.016	0.093	0	0	0.202
	0	0	0	0.025	0	0.02	0	0	0.011
	0	0	0	0	0	0	0	0	0
	0	0.157	0	0	0	0	0	0	0
	0	0.029	0	0	0	0	0	0	0
	48	35	46	81	31	75	112	75	47

TABLE A.2.—Continued.

Locus	Allele and *N*	Sample							
		ALL96	ALL97	AR96	AR97	ATL	CAN	DEV	HEY
Ots100	1	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0.018	0	0.024	0.026	0	0.008	0
	5	0	0	0	0.071	0	0	0.016	0
	6	0.34	0.321	0.294	0.262	0.263	0.058	0.398	0.176
	7	0.16	0.089	0.029	0.095	0.053	0.106	0.039	0.074
	8	0.04	0.036	0.029	0.071	0.092	0.192	0.008	0.044
	9	0	0.036	0	0	0.013	0.067	0	0.147
	10	0.02	0.054	0.059	0.048	0.026	0.048	0.023	0.029
	11	0.06	0.071	0.059	0.119	0.026	0.308	0.273	0.221
	12	0.08	0.069	0.029	0.024	0.118	0.144	0.211	0.221
	13	0.08	0.018	0	0.071	0.026	0	0.016	0.074
	14	0.1	0.089	0.147	0	0.079	0.029	0	0.015
	15	0.06	0.161	0.353	0.143	0.25	0.038	0	0
	16	0.06	0.018	0	0.071	0.026	0.01	0.008	0
	17	0	0	0	0	0	0	0	0
	N	25	28	17	21	38	52	64	34
Ots103	1	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0.023	0.025	0	0.013	0	0	0
	6	0.054	0.091	0.1	0.077	0.092	0	0.026	0
	7	0.161	0.125	0.1	0.058	0.092	0.059	0.072	0
	8	0.018	0.08	0.05	0.038	0	0.044	0.02	0
	9	0.036	0.023	0.075	0.019	0.013	0.118	0.039	0
	10	0.036	0.08	0.075	0.096	0.066	0.022	0.033	0.015
	11	0.089	0.159	0.125	0.096	0.118	0.044	0.151	0.103
	12	0.161	0.057	0.025	0.077	0.105	0.059	0.138	0.088
	13	0.054	0.034	0.05	0.019	0.079	0.162	0.243	0.25
	14	0.054	0.023	0	0.038	0	0.037	0.059	0.206
	15	0.018	0.011	0	0.038	0.013	0.029	0.079	0.206
	16	0.071	0.125	0.05	0.135	0.158	0.007	0.059	0.074
	17	0.179	0.102	0.15	0.096	0.079	0.088	0.046	0.044
	18	0.036	0.045	0.125	0.154	0.079	0.066	0	0
	19	0	0.023	0.05	0.058	0.053	0.199	0.033	0
	20	0.036	0	0	0	0.039	0.015	0	0
	21	0	0	0	0	0	0.051	0	0.015
	22	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	N	28	44	20	26	38	68	76	34
Ots3	1	0.071	0.18	0.05	0.141	0.064	0.125	0.601	0.088
	2	0.036	0	0	0	0.064	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0.013	0	0	0	0
	6	0	0	0	0	0	0.013	0.006	0
	7	0	0	0	0	0	0	0.012	0
	8	0.089	0.18	0.125	0.244	0.202	0.638	0.119	0.221
	9	0.089	0	0	0	0	0.02	0.036	0.029
	10	0.607	0.52	0.775	0.551	0.606	0.197	0.143	0.662
	11	0	0.01	0	0	0.011	0.007	0	0
	12	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0
	15	0	0.02	0.025	0	0.011	0	0.06	0
	16	0.071	0.08	0.025	0.051	0.021	0	0.024	0
	17	0.036	0.01	0	0	0.021	0	0	0
	N	28	50	20	39	47	76	84	34

TABLE A.2.—Continued Extended (1).

	Sample									
Locus	KOY	KSQ	KTL	LAG	LOL	MIK	OAM97	OAS98	OIZ97	OIZ98
Ots100	0	0	0	0	0	0	0	0	0	0
	0.009	0	0	0	0	0	0	0.01	0	0
	0.009	0	0	0	0	0	0.031	0	0	0
	0.017	0	0	0	0	0	0	0	0.016	0
	0.034	0	0.017	0.109	0	0.07	0	0.051	0.063	0.087
	0.302	0.026	0.241	0	0.053	0.45	0.188	0.071	0.094	0.054
	0.121	0.053	0.052	0.043	0.043	0.06	0	0.031	0	0.022
	0.129	0.395	0.017	0.065	0.213	0.02	0.031	0	0.078	0
	0.034	0	0.017	0	0	0	0.031	0.051	0.016	0.043
	0.017	0.013	0.069	0.043	0.128	0.03	0.063	0.133	0.125	0.12
	0	0.066	0.086	0.109	0.149	0.22	0.063	0.112	0.141	0.054
	0.112	0.132	0.138	0.261	0.277	0.12	0.5	0.347	0.344	0.457
	0.078	0.184	0	0.304	0.117	0.02	0.063	0.133	0.094	0.141
	0.086	0.079	0.034	0.043	0.011	0	0.031	0.031	0.031	0.022
	0.034	0.053	0.276	0.022	0.011	0	0	0.031	0	0
	0.009	0	0.052	0	0	0.01	0	0	0	0
	0.009	0	0	0	0	0	0	0	0	0
	58	38	29	23	47	50	16	49	32	46
Ots103	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0.007	0	0	0	0	0	0	0	0	0.011
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0.096	0	0	0.052	0.04	0.08	0.033
	0	0	0	0	0	0.056	0.034	0.05	0.02	0.043
	0	0.01	0.1	0.019	0	0.081	0.069	0.03	0.02	0.043
	0	0.019	0.043	0	0.063	0	0.034	0.08	0.08	0.065
	0.007	0.01	0.114	0	0.063	0.008	0.069	0.05	0	0
	0.065	0.154	0.029	0.308	0.052	0.048	0.017	0.09	0.06	0.163
	0.196	0.173	0.114	0.038	0.094	0.081	0.052	0.08	0.1	0.065
	0.109	0.038	0.129	0.115	0.042	0.145	0.069	0.15	0.16	0.109
	0	0	0.2	0.019	0.052	0.194	0.103	0.12	0.08	0.054
	0.043	0.106	0.086	0.019	0.01	0.065	0.103	0	0.08	0.065
	0.196	0.067	0.029	0.058	0.073	0.089	0.034	0.13	0.08	0.065
	0.094	0.067	0.029	0.019	0.156	0.113	0.138	0.07	0.14	0.087
	0.007	0.221	0.029	0.173	0.135	0.056	0.103	0.04	0.04	0.054
	0.036	0.096	0.014	0.038	0.188	0.016	0.034	0.04	0.04	0.076
	0.065	0.019	0.029	0.038	0.063	0.04	0.017	0.02	0.02	0.043
	0.036	0.019	0.014	0.058	0.01	0.008	0.069	0.01	0	0
	0.138	0	0.043	0	0	0	0	0	0	0.022
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	69	52	35	26	48	62	29	50	25	46
Ots3	0.204	0.18	0.014	0.28	0.235	0.576	0.196	0.12	0.083	0.096
	0	0	0	0	0	0.008	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0.008	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0.025	0	0	0	0
	0.013	0	0	0	0	0.034	0	0.02	0	0
	0.447	0.631	0.528	0.26	0.245	0.119	0.478	0.48	0.667	0.617
	0.132	0.033	0.097	0.04	0	0.034	0.022	0.15	0.033	0.128
	0.092	0.148	0.333	0.42	0.51	0.102	0.283	0.19	0.183	0.128
	0.059	0	0.028	0	0	0	0.022	0.01	0.017	0
	0.053	0	0	0	0.01	0	0	0.02	0	0.021
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0.085	0	0	0.017	0.011
	0	0	0	0	0	0.017	0	0.01	0	0
	0	0	0	0	0	0	0	0	0	0
	76	61	36	25	49	59	46	50	30	47

TABLE A.2.—Continued Extended (2).

	Sample								
Locus	ONE	OSH96	OSH98	OWN	OWN99	OWW	SAK	TNK	WOS
Ots100	0	0	0	0	0	0	0.004	0	0
	0	0	0.01	0	0	0	0.022	0	0
	0	0	0	0	0	0	0.159	0	0
	0	0	0	0.008	0	0	0	0	0
	0.076	0.04	0.042	0.083	0.227	0.064	0.013	0.042	0.012
	0.033	0	0.042	0.142	0.136	0.071	0.009	0.008	0.31
	0.043	0	0.042	0.017	0.015	0.026	0.146	0	0.024
	0.098	0.08	0.01	0.042	0	0	0.235	0.033	0
	0.011	0	0.104	0.042	0	0.032	0.018	0	0
	0.163	0.06	0.208	0.075	0.045	0.147	0.124	0.025	0.083
	0.152	0.2	0.208	0.042	0.106	0.218	0.119	0.058	0.083
	0.326	0.52	0.24	0.325	0.273	0.333	0.102	0.5	0.25
	0.087	0.08	0.063	0.167	0.182	0.077	0.035	0.158	0.226
	0.011	0.02	0	0.05	0.015	0.019	0	0.017	0.012
	0	0	0.01	0.008	0	0.006	0.013	0	0
	0	0	0.021	0	0	0.006	0	0.125	0
	0	0	0	0	0	0	0	0.033	0
	46	25	48	60	33	78	113	60	42
Ots103	0	0.03	0	0	0	0	0	0	0
	0	0.03	0	0	0	0	0	0	0
	0	0	0.021	0.014	0	0	0	0	0
	0.021	0	0.021	0.007	0	0.014	0	0	0
	0	0.045	0.043	0.014	0.044	0.068	0	0.007	0
	0.042	0	0.043	0.041	0.029	0.034	0.009	0	0
	0.104	0.015	0.043	0.061	0.015	0.068	0.062	0.112	0
	0.042	0.106	0.117	0.054	0.044	0.074	0.071	0.022	0
	0.031	0	0.053	0.014	0.015	0.054	0.164	0	0
	0.083	0.045	0.085	0.068	0.044	0.041	0.049	0.119	0.063
	0.125	0.045	0.074	0.101	0.118	0.081	0.173	0.06	0.094
	0.104	0.212	0.096	0.108	0.103	0.122	0	0.246	0.083
	0.083	0.121	0.074	0.176	0.132	0.074	0.013	0.022	0.063
	0.063	0.106	0.043	0.135	0.118	0.047	0.009	0.112	0.042
	0.042	0.061	0.074	0.068	0.088	0.095	0.115	0.179	0.229
	0.125	0.076	0.085	0.068	0.118	0.074	0.049	0.03	0.271
	0.01	0.045	0.043	0.027	0.059	0.074	0.124	0.03	0.104
	0.01	0.015	0.021	0.041	0.029	0.027	0.071	0.007	0.052
	0.083	0.045	0.021	0.007	0	0.041	0	0.037	0
	0.031	0	0.043	0	0.044	0.007	0	0.015	0
	0	0	0	0	0	0.007	0	0	0
	0	0	0	0	0	0	0.088	0	0
	0	0	0	0	0	0	0.004	0	0
	48	33	47	74	34	74	113	67	48
Ots3	0.051	0.088	0.064	0.038	0.103	0.071	0.315	0.36	0.118
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0.032	0	0.013
	0	0	0	0	0	0	0.032	0	0.039
	0	0	0.011	0	0	0.006	0	0	0
	0	0	0	0	0	0.012	0	0	0.013
	0	0	0.011	0.006	0	0	0	0	0
	0.582	0.368	0.606	0.462	0.368	0.506	0.563	0.16	0.303
	0.133	0.074	0.043	0.025	0.162	0.095	0.045	0.073	0.211
	0.214	0.353	0.245	0.342	0.235	0.214	0.014	0.313	0.145
	0	0	0	0.019	0.015	0.03	0	0.04	0.079
	0	0.044	0.021	0	0	0.012	0	0.033	0.053
	0	0	0	0	0	0	0	0.007	0.026
	0	0	0	0.013	0.015	0.006	0	0	0
	0.01	0.044	0	0.013	0.015	0.03	0	0	0
	0.01	0.029	0	0.038	0.059	0.018	0	0.013	0
	0	0	0	0.044	0.029	0	0	0	0
	49	34	47	79	34	84	111	75	38