Population structure and stock identification of British Columbia coho salmon, *Oncorhynchus kisutch*, based on microsatellite DNA variation

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Abstract.—We used genetic variation at three microsatellite DNA loci to describe population structure in 34 coho salmon populations from British Columbia and to perform stock composition analysis on simulated mixed-stock fishery samples. Each microsatellite locus was highly polymorphic, with 31 alleles at *Ots*101, 20 alleles at *Ots*3, and 38 alleles at *Ots*103. Average observed heterozygosities were 86.3%, 73.3% and 74.9%, respectively. Analysis of genetic distances revealed three relatively homogeneous, geographically based groups of coho salmon populations in the following regions: the upper Skeena and Nass River watersheds, the lower Fraser River drainage, and the upper Fraser River-Thompson River watersheds. Coastal populations from the mainland of British Columbia, Vancouver Island, and the Queen Charlotte Islands formed a more heterogeneous regional stock grouping. Significantly different allele frequencies were observed among populations within regions, and allele frequencies were generally temporally stable in multiyear samples. Phylogenetic lineages within British Columbia coho salmon likely reflect geographic patterns of recolonization from at least three separate glacial refugia after the last ice age. Local spawning populations within regions may form metapopulations, but current levels of gene flow among subpopulations are apparently insufficient to prevent differentiation at neutral genetic loci. Maximum-likelihood estimates of stock composition were accurate and precise, indicating great potential for management of coho salmon at the level of metapopulations or "evolutionarily significant units" in domestic and international mixed-stock fisheries. Individual fish were identified to stock by using a discriminant analysis with a high degree of accuracy in a few regions, but more generally with approximately 50% success.

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Of the five commercially important Pacific salmon (*Oncorhynchus*) species exploited in the commercial, recreational and aboriginal fisheries of British Columbia, coho salmon is the one that has shown the largest decline in abundance in both historical (the past 100 years) and recent (the past 40 years) times (Northcote and Atagi, 1997). Coho salmon abundance has also declined dramatically in Washington State, Oregon, and California, to the extent that a number of coho salmon populations, including all of those from the upper Columbia River system, are considered extinct and others are considered endangered (Nehlsen et al., 1991; Weitkamp et al., 1995). The list of factors that may have contributed to declining coho salmon abundance is long, and includes overfishing, loss of freshwater habitat, misguided enhancement efforts, limited marine carrying capacity, and climate changes resulting in altered oceanic conditions (Fraser et al., 1982; Beamish and Bouillon, 1993; Walters, 1993; Reisenbichler, 1997).

Because coho salmon tend to spawn in small streams and rivers that are especially vulnerable to degradation through human activities, freshwater habitat degradation has been considered a major factor in declining coho abundance (Fraser et al., 1982). Similarly, coho salmon commonly are believed to be overexploited because of the mixed-stock nature of most coho salmon fisheries and the frequent bycatch of coho salmon in fisheries directed toward other species (Fraser et al., 1982). Nevertheless, the consistent long-term decline in coho abundance, which has occurred over a broad geographic range in habitats both degraded and pristine and under a range of exploitation levels (Weitkamp et al., 1995; Northcote and Atagi, 1997), indicates that changes occurring in the marine environment are also having a major negative influence on coho salmon populations. This seems especially plausible because in some regions the recent decline in coho abundance coincides with a stable number or increase in abundance of other heavily freshwater-dependent salmonids, such as sockeye salmon and stream-type chinook salmon (Northcote and Atagi, 1997). Thus, coho salmon populations may be less amenable to rebuilding through local or regional habitat improvement and harvest management than populations of other species.

The increasing conservation concerns for coho salmon have led to substantial efforts to quantify

biodiversity in the species (Bartley et al., 1992; Forbes et al., 1993; Weitkamp et al., 1995; Miller and Withler, 1997), to define the appropriate geographic scale of management to conserve the observed biodiversity (Weitkamp et al., 1995; McPhail, 1997; Small et al., 1998), and to develop stock composition methods that would enable the geographically based management required for conservation efforts (Bartley et al., 1992; Beacham et al., 1996; Miller et al., 1996; Van Doornik et al., 1996; Small et al., 1998). Coho salmon populations of California, Oregon, Washington, and southern British Columbia have been categorized into evolutionarily significant units (ESUs), that is to say, reproductively isolated populations or groups of populations that represent the important phylogenetic components of genetic variability in the species (Waples, 1991; Weitkamp et al., 1995). The use of ESUs to delineate biodiversity in Pacific salmon is concordant with an emerging model of metapopulation structure that may supersede the stock concept that has long been applied to these species. Local spawning groups of salmon are no longer viewed as independent and persistent locally adapted "stocks" (Ricker, 1972), but rather as interrelated components, or subpopulations, of a geographically based cluster of such components (the metapopulation) that share a relatively recent evolutionary history and among which gene flow still occurs (McPhail, 1997). Although adaptive differences may arise among the subpopulations of a metapopulation as the result of an appropriate balance between migration and natural selection within subpopulations, they are unlikely to persist over evolutionary time scales as subpopulations go extinct or are swamped by gene flow from adjacent subpopulations. Given this model of salmonid population structure, it is individual metapopulations (ESUs), rather than individual stocks, that managers must conserve to provide the reservoirs of genetic diversity for future evolution within the species.

In coho salmon, and other Pacific salmonids, there is accumulating evidence that the dominant influence on population structure has been the pattern of dispersal from isolated glacial refugia after the last ice age (Gharrett et al., 1987; Wood et al., 1994; Bickham et al., 1995, Miller and Withler 1997; Small et al., 1998). The distinct phylogenetic lineages that can be traced with molecular markers reveal patterns of recolonization of freshwater habitat from refugia located in the Columbia River drainage (Cascadia), the Bering Sea-Yukon River (Beringia), and coastal refugia that likely existed in British Columbia, as well as in more southern waters. For coho, chinook and sockeye salmon, many of these genetically distinct intraspecific lineages converge in British Columbia, providing us with the opportunity and challenge of conserving biodiversity *in situ*.

In this study, we examine variation among and within major river systems and coastal regions in British Columbia at three coho salmon microsatellite loci: *Ots*101, *Ots*3, and *Ots*103. Microsatellite DNA loci consist of highly variable single locus markers containing tandemly repeated arrays of noncoding 1–6 basepair core sequences (Tautz, 1989). For each locus, variation in the number of core sequences creates alleles differing in size by multiples of core-unit length. The rapid rate of mutation and high heterozygosity that characterize microsatellite loci have made them the molecular tool of choice in studies of population structure in vertebrates, including salmonid fish (Angers et al., 1995; McConnell et al., 1995; Scribner et al., 1996; Beacham et al., 1998; Small et al., 1998). In our study, we demonstrate the dual utility of microsatellite variation in defining the regionally based phylogenetic lineages of coho salmon and in accurately detecting their presence in mixed-stock fisheries for management purposes.

Methods

DNA samples and PCR

Adult coho salmon tissue samples were collected from 34 coho salmon populations in British Columbia (Fig. 1). Several populations were sampled in multiple years. See Miller et al., (1996) for descriptions of purified genomic DNA extractions from tissues collected up to 1993. Genomic DNA samples from 1994 and 1995 were extracted by using a chelex resin protocol (Small et al., 1998). Microsatellite alleles at three loci were polymerase chain reaction (PCR)-amplified (Sakai et al., 1985) from DNA samples by using primers for the tetranucleotide microsatellites *Ots*101 and *Ots*103 (Small et al., 1998) and the dinucleotide microsatellite, *Ots*3 (Banks[1]). Primer sequences, the PCR conditions, and size-fractionation of the PCR products are described in Small et al. (1998). PCR products from standard test fish were included on each gel to estimate the precision of allele sizing among gels.

DNA band analysis

Gels were scanned with a Kodak charge-coupled device camera and the images were analyzed as outlined in Small et al. (1998) with BioImage Whole

[1] Banks, M. 1995. Bodega Marine Laboratory, POB 247, Bodega Bay, CA 94923. Personal commun.

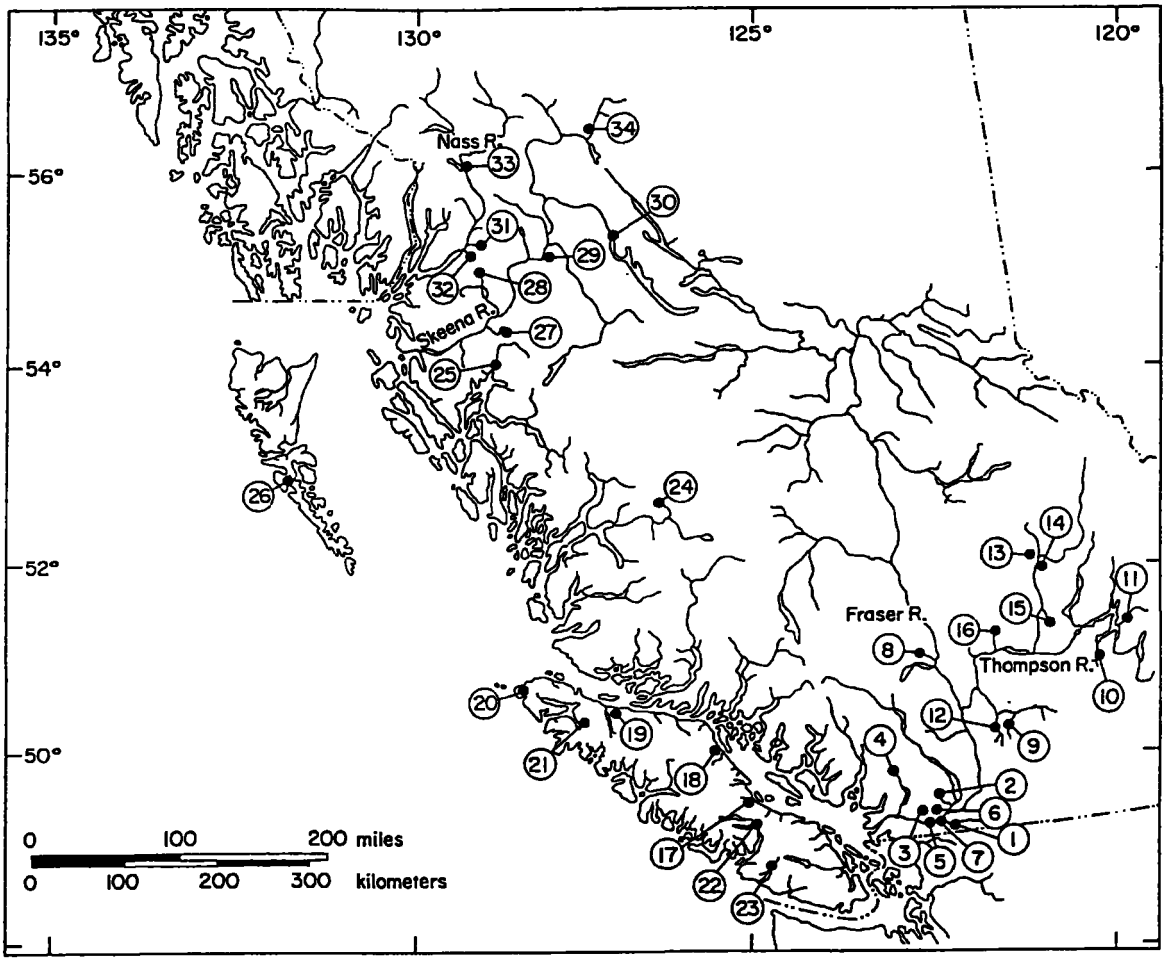

Figure 1

Map of British Columbia showing locations of coho salmon samples. Population numbers are placed near the waterway (region or river system name in bold type precedes population names) : **lower Fraser River** 1) Chilliwack River; 2) Chehalis River; 3) Stave River; 4) Upper Pitt River; 5) Nicomen Slough; 6) Norrish Creek; 7) Inch Creek; **upper Fraser River** 8) Bridge River; **Thompson River** 9) Coldwater River; 10) Salmon River; 11) Eagle River; 12) Spius Creek; 13) Lemieux Creek; 14) Dunn Creek; 15) Louis River; 16) Deadman River; **East Coast Vancouver Island** 17) Big Qualicum River; 18) Quinsam River; **North Coast Vancouver Island** 19) Cluxewe River; 20) Stephens Creek; 21) Waukwaas Creek; **West Coast Vancouver Island** 22) Robertson Creek; 23) Nitinat River; **Central Coast** 24) Atnarko River; 25) Kitimat River; **Queen Charlotte Island** 26) Pallant Creek; **Skeena River** 27) Clearwater River; 28) Cedar River; 29) Toboggan Creek; 30) Babine River; 34) Sustut River; **Nass River** 31) Tseax River; 32) Zolzap River; 33) Meziadin River.

Band software (Millipore Corp. Imaging systems, Ann Arbor, MI). The software estimated allele sizes to the nearest basepair with a molecular weight-size-grid created with a 20-bp DNA ladder. Alleles were identified by using a binning procedure (Gill et al., 1990; Galbraith et al., 1991). Allelic bin intervals were created from peaks in allele frequency histograms and precision estimates from standard test fish (Small et al., 1998). Bin intervals for *Ots*101 and *Ots*3 alleles are presented in Table 1 and bin intervals for *Ots*103 alleles are presented in Table 2. The mean bin width was four or more standard deviations from allele sizes of test fish. Allele size was generally four bp for *Ots*101, two bp for *Ots*3, and four bp for *Ots*103. When alleles became infrequent at the extremes of the size ranges and the precision of sizing alleles decreased, alleles were grouped into larger bins (Small et al., 1998). Thirty-one alleles were defined for *Ots*101, 20 alleles were defined for *Ots*3, and 37 alleles (as well as a null allele) were defined for *Ots*103.

Data analysis

Linkage tests confirmed that the three loci are unlinked and pedigree analysis confirmed Mendelian

Table 1

Allele frequencies, observed heterozygosity (Hobs) and expected heterozygosity (Hexp) at *Ots*101 and *Ots*3 loci for coho salmon populations region with region names abbreviated as follows: Central Coast (C Coast), North Coast Vancouver Island (NCVI), West Coast Vancouver Island Populations out of Hardy-Weinberg equilibrium are indicated by * next to the observed heterozygosity. The allele number (in basepairs) is the al. (1998), Table 3. Sample sizes for *Ots*101 are given underneath the population names and for *Ots*3 are indicated by *N*.

Alleles	**Pallant** 93	Atnarko 87	Kitimat 148	**C Coast** 235	Cluxewe 38	Stephens 65	Waukwaas 30	**NCVI** 133	Nitinat 39	Robertson 84	**WCVI** 123	Quinsam 160
*Ots*101												
96	**0**	0	0	**0**	0	0	0	**0**	0	0.065	**0.045**	0
100	**0.016**	0.034	0.014	**0.021**	0.053	0.031	0.017	**0.034**	0	0.030	**0.021**	0.003
104	**0.005**	0.011	0.051	**0.036**	0.053	0.077	0.067	**0.068**	0	0	**0**	0.003
108	**0.016**	0.011	0.014	**0.013**	0.039	0.031	0.083	**0.045**	0	0	**0**	0.019
112	**0.054**	0.011	0.037	**0.028**	0.013	0.008	0.017	**0.011**	0.103	0.036	**0.057**	0.072
116	**0.022**	0.029	0.064	**0.051**	0	0.023	0	**0.011**	0	0.071	**0.049**	0.051
120	**0.065**	0.138	0.081	**0.098**	0.092	0.023	0.017	**0.041**	0.051	0	**0.016**	0.081
124	**0.141**	0.092	0.088	**0.088**	0.171	0.131	0.101	**0.135**	0	0.042	**0.028**	0.084
127	**0.091**	0.075	0.057	**0.064**	0.066	0.008	0.051	**0.034**	0	0.054	**0.037**	0.097
131	**0.124**	0.098	0.095	**0.094**	0.145	0.108	0.101	**0.117**	0.141	0.024	**0.061**	0.151
135	**0.027**	0.006	0.031	**0.021**	0.013	0.038	0.017	**0.026**	0.091	0.071	**0.077**	0.019
139	**0.081**	0.011	0.031	**0.024**	0.013	0.054	0.067	**0.045**	0.051	0.054	**0.053**	0.041
143	**0.032**	0.011	0.024	**0.019**	0.039	0.069	0.033	**0.053**	0.013	0.083	**0.061**	0.063
147	**0.011**	0.017	0.041	**0.032**	0.079	0.123	0	**0.083**	0.205	0.149	**0.167**	0.022
151	**0.022**	0.011	0.010	**0.011**	0	0.054	0.017	**0.030**	0.051	0.054	**0.053**	0.009
154	**0.011**	0.006	0.027	**0.019**	0.039	0.015	0.017	**0.023**	0.013	0	**0.004**	0.003
158	**0.011**	0.029	0.047	**0.041**	0.013	0	0.017	**0.008**	0.077	0.012	**0.033**	0.019
161	**0.027**	0.034	0.027	**0.031**	0	0.008	0.051	**0.015**	0.064	0.125	**0.106**	0.041
165	**0**	0.069	0.021	**0.038**	0	0.023	0.051	**0.023**	0.026	0.048	**0.041**	0.059
169	**0**	0.046	0.047	**0.047**	0.053	0	0	**0.015**	0.038	0.048	**0.045**	0.069
173	**0.048**	0.040	0.057	**0.051**	0.026	0.008	0.101	**0.034**	0.013	0	**0.004**	0.031
177	**0.043**	0.057	0.017	**0.031**	0.013	0.046	0.117	**0.053**	0.038	0.012	**0.021**	0.022
181	**0.038**	0.052	0.041	**0.045**	0.039	0.054	0	**0.038**	0	0.006	**0.004**	0.009
185	**0**	0.034	0.037	**0.036**	0.026	0.038	0	**0.026**	0	0.012	**0.008**	0.019
189	**0**	0.040	0.021	**0.028**	0.013	0	0	**0.004**	0	0.006	**0.004**	0
193	**0.005**	0.006	0.021	**0.015**	0	0.015	0.017	**0.011**	0	0	**0**	0
197	**0.027**	0	0	**0**	0	0	0.017	**0.004**	0	0	**0**	0
201	**0.016**	0.011	0	**0.004**	0	0	0.017	**0.004**	0	0	**0**	0.009
205	**0.032**	0.011	0.003	**0.006**	0	0	0.017	**0.004**	0.013	0	**0.004**	0.003
210	**0.016**	0.006	0.003	**0.004**	0	0.015	0	**0.008**	0	0	**0**	0
215	**0.032**	0.011	0	**0.004**	0	0	0	**0**	0.013	0	**0.004**	0.003
Hobs	**0.861**	*0.862	0.909	**0.885**	0.921	0.877	0.967	**0.909**	0.718	0.869	**0.821**	0.900
Hexp	**0.935**	0.943	0.946	**0.945**	0.921	0.938	0.933	**0.939**	0.897	0.940	**0.927**	0.931
*Ots*3												
N	93	86	145	231	38	68	32	138	40	84	124	160
66	**0.129**	0.052	0.045	**0.048**	0	0.029	0.109	**0.040**	0.013	0.012	**0.012**	0
68	**0.005**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
70	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
72	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
74	**0.011**	0	0.007	**0.004**	0	0	0	**0**	0	0	**0**	0
76	**0**	0	0.003	**0.002**	0.013	0	0	**0.004**	0	0	**0**	0
78	**0**	0.035	0.003	**0.015**	0	0	0	**0**	0	0	**0**	0
82	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
84	**0**	0	0.014	**0.009**	0	0	0	**0**	0	0	**0**	0.025
86	**0.027**	0.285	0.124	**0.184**	0.079	0.051	0.063	**0.062**	0.112	0.024	**0.052**	0.125
88	**0.258**	0.215	0.328	**0.286**	0.316	0.191	0.234	**0.236**	0.275	0.179	**0.211**	0.281
90	**0.071**	0.017	0.003	**0.009**	0.013	0.059	0.047	**0.043**	0	0.221	**0.149**	0.034
92	**0.011**	0.012	0.066	**0.045**	0.092	0.141	0.078	**0.112**	0.151	0.101	**0.117**	0.019
94	**0.323**	0.251	0.238	**0.242**	0.368	0.419	0.234	**0.362**	0.138	0.292	**0.242**	0.338
96	**0**	0.017	0.024	**0.022**	0.039	0.007	0.047	**0.025**	0	0.006	**0.004**	0.003
98	**0.145**	0.116	0.124	**0.121**	0.066	0.051	0.094	**0.065**	0.313	0.161	**0.211**	0.166
100	**0.016**	0	0.003	**0.002**	0	0.029	0.016	**0.018**	0	0.006	**0.004**	0.006
102	**0.005**	0	0.017	**0.011**	0.005	0.078	0.013	**0.033**	0	0	**0**	0.003
104	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
106	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
Hobs	**0.699**	0.698	*0.752	**0.732**	0.816	0.765	0.751	**0.775**	0.751	0.786	**0.774**	0.712
Hexp	**0.785**	0.790	0.800	**0.809**	0.763	0.765	0.875	**0.789**	0.775	0.798	**0.814**	0.762

from British Columbia. The weighted mean of allele frequencies for regions (in bold type) follow allele frequencies for individual populations in the (WCVI), East Coast Vancouver Island (ECVI), Skeena River (Skeena), Nass River (Nass), Thompson River (TR), and lower Fraser River (L Fr). lower limit of the allele bin. Allele frequencies for individual populations in the lower Fraser River and the Thompson River are given in Small et

Big Qualicum 200	**ECVI** 260	Toboggan 164	Cedar 47	Babine 139	Clear-water 48	Sustut 36	**Skeena** 434	Tseax 40	Zolzap 47	Mexiadin 64	**Nass** 151	**TR** 1015	**L Fr** 1043
0	**0**	0	0	0	0	0	**0**	0	0	0	**0**	**0**	**0**
0.011	**0.007**	0	0	0	0	0	**0**	0.013	0	0	**0.004**	**0**	**0.018**
0.023	**0.014**	0.018	0	0.029	0.010	0.028	**0.020**	0.013	0.011	0.063	**0.022**	**0**	**0.009**
0.025	**0.022**	0.015	0.053	0.068	0.063	0.056	**0.045**	0.025	0.096	0.078	**0.059**	**0.001**	**0.037**
0	**0.032**	0.003	0.021	0.004	0.021	0.042	**0.010**	0.025	0.021	0.031	**0.026**	**0.001**	**0.011**
0.011	**0.028**	0.165	0.149	0.032	0.042	0.125	**0.104**	0.162	0.138	0.078	**0.114**	**0.077**	**0.034**
0.085	**0.084**	0.186	0.138	0.273	0.302	0.181	**0.220**	0.151	0.074	0.172	**0.129**	**0.015**	**0.122**
0.081	**0.082**	0.049	0.138	0.137	0.031	0.056	**0.084**	0.101	0.096	0.078	**0.088**	**0.001**	**0.082**
0.081	**0.088**	0.003	0.043	0.011	0.073	0	**0.017**	0.051	0.011	0.078	**0.037**	**0.007**	**0.112**
0.131	**0.139**	0.076	0.074	0.007	0.115	0.014	**0.052**	0.025	0.064	0.023	**0.037**	**0.071**	**0.119**
0.055	**0.039**	0.031	0.085	0.094	0.011	0.028	**0.054**	0.151	0.117	0.016	**0.088**	**0.011**	**0.121**
0.063	**0.053**	0.006	0.043	0.011	0.031	0	**0.014**	0.025	0.021	0.023	**0.022**	**0.014**	**0.073**
0.025	**0.042**	0	0.053	0	0.031	0	**0.009**	0.013	0.021	0.016	**0.011**	**0**	**0.042**
0.018	**0.019**	0.003	0.043	0	0.021	0.028	**0.010**	0.075	0.043	0.031	**0.051**	**0.002**	**0.048**
0.027	**0.019**	0.006	0.011	0.004	0.031	0	**0.008**	0.013	0.032	0	**0.015**	**0.019**	**0.027**
0.035	**0.021**	0.006	0	0	0.011	0	**0.003**	0	0.106	0	**0.037**	**0.051**	**0.021**
0.013	**0.015**	0	0	0.004	0	0.014	**0.002**	0	0.011	0.008	**0.007**	**0.011**	**0.011**
0.018	**0.028**	0	0.011	0	0.042	0.028	**0.008**	0.013	0.021	0	**0.011**	**0.081**	**0.033**
0.058	**0.058**	0	0.043	0	0.021	0.014	**0.008**	0	0	0.039	**0.015**	**0.056**	**0.011**
0.045	**0.054**	0.031	0	0.022	0.011	0	**0.020**	0.050	0.021	0.016	**0.029**	**0.159**	**0.005**
0.051	**0.041**	0.064	0.021	0.141	0.063	0.014	**0.075**	0	0.064	0.055	**0.048**	**0.111**	**0.011**
0.005	**0.013**	0.046	0.011	0.051	0.021	0.069	**0.041**	0	0	0.086	**0.040**	**0.086**	**0.005**
0.005	**0.007**	0.031	0.011	0.018	0.031	0.111	**0.030**	0.013	0.011	0.047	**0.029**	**0.091**	**0.006**
0.013	**0.015**	0.052	0.032	0.058	0.052	0.097	**0.055**	0.038	0	0	**0.011**	**0.076**	**0.009**
0.013	**0.007**	0.119	0.011	0.029	0	0.056	**0.060**	0.038	0.011	0.055	**0.040**	**0.026**	**0.013**
0.027	**0.015**	0.082	0	0.011	0	0.042	**0.038**	0.025	0.011	0.008	**0.015**	**0.017**	**0.008**
0.035	**0.019**	0.009	0	0	0.021	0	**0.006**	0	0	0	**0**	**0.006**	**0.011**
0.011	**0.011**	0.003	0.011	0	0	0	**0.002**	0.013	0.011	0.016	**0.015**	**0.007**	**0.003**
0.045	**0.026**	0	0	0.004	0.011	0	**0.002**	0	0	0	**0**	**0.001**	**0.001**
0	**0**	0.003	0	0	0	0	**0.001**	0	0	0	**0**	**0.001**	**0.001**
0	**0.001**	0	0	0	0	0	**0**	0	0	0	**0**	**0.001**	**0**
0.885	**0.889**	0.835	0.809	0.853	0.813	0.806	**0.822**	0.851	0.883	0.844	**0.821**	**0.881**	**0.874**
0.935	**0.936**	0.902	0.915	0.871	0.915	0.892	**0.902**	0.925	0.936	0.718	**0.914**	**0.915**	**0.915**
191	351	161	48	139	47	37	432	39	46	52	137	1016	1048
0.065	**0.036**	0.012	0.021	0.108	0	0.068	**0.047**	0.013	0.033	0.048	**0.033**	**0**	**0.034**
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**	**0.001**
0.003	**0.001**	0	0	0	0	0	**0**	0	0	0	**0**	**0**	**0**
0	**0**	0.003	0	0	0	0	**0.001**	0	0	0	**0**	**0**	**0**
0.011	**0.006**	0.003	0	0	0	0	**0.001**	0	0	0	**0**	**0**	**0**
0	**0**	0	0	0	0.011	0	**0.002**	0	0.022	0	**0.007**	**0**	**0**
0.005	**0.003**	0	0.011	0	0	0	**0.002**	0	0	0	**0**	**0**	**0.001**
0.016	**0.021**	0.006	0.031	0	0	0.054	**0.010**	0.051	0.011	0.011	**0.022**	**0**	**0.004**
0.102	**0.113**	0.065	0.229	0.111	0.128	0.271	**0.132**	0.154	0.272	0.125	**0.182**	**0.011**	**0.082**
0.209	**0.241**	0.181	0.156	0.227	0.181	0.054	**0.182**	0.103	0.174	0.163	**0.150**	**0.125**	**0.249**
0.045	**0.041**	0.102	0	0.065	0.053	0.041	**0.068**	0.077	0.076	0.067	**0.073**	**0.078**	**0.051**
0.071	**0.047**	0.009	0.021	0.007	0.011	0.108	**0.019**	0.167	0.011	0.115	**0.095**	**0.235**	**0.114**
0.262	**0.296**	0.363	0.292	0.223	0.319	0.203	**0.292**	0.218	0.185	0.115	**0.168**	**0.444**	**0.282**
0.063	**0.036**	0.006	0.011	0.014	0.021	0.027	**0.013**	0.128	0.033	0.106	**0.088**	**0.047**	**0.028**
0.136	**0.151**	0.127	0.198	0.108	0.149	0.054	**0.125**	0.038	0.152	0.154	**0.120**	**0.026**	**0.106**
0.013	**0.011**	0	0	0	0.021	0	**0.002**	0.051	0.011	0	**0.018**	**0.006**	**0.018**
0.003	**0.003**	0	0	0	0	0	**0**	0	0	0	**0**	**0.029**	**0.031**
0	**0**	0.051	0.041	0	0	0.014	**0.037**	0.011	0.058	0.032	**0.026**	**0**	**0**
0	**0**	0.071	0.068	0	0	0.095	**0.064**	0	0.038	0.064	**0.015**	**0**	**0**
*0.757	**0.735**	0.714	0.792	0.763	0.723	*0.703	**0.728**	0.744	0.696	0.788	**0.729**	**0.657**	**0.772**
0.848	**0.815**	0.801	0.812	0.849	0.796	0.865	**0.826**	0.850	0.812	0.885	**0.864**	**0.722**	**0.822**

Table 2

Uncorrected and corrected (bold type) allele frequencies, observed heterozygosity (Hobs) and expected heterozygosity (Hexp) at *Ots*103 locus frequencies of the populations in the region, with region names abbreviated as in Table 1. Populations out of Hardy-Weinberg equilibrium cies for individual populations in the lower Fraser River and the Thompson River are given in Table 3 of Small et al. (1998). Sample sizes

Alleles	**Pallant** 93	Atnarko 87	**Kitimat** 148	**C Coast** 235	Cluxewe 38	Stephens 65	Waukwaas 30	**NCVI** 133	Nitinat 39	Robertson 84	**WCVI** 123	Quinsam 160
61	**0**	0	0.007	**0.004**	0	0.037	0	**0.018**	0.105	0	**0.031**	0
	0	**0**	**0.006**	**0.004**	**0**	**0.037**	**0**	**0.018**	**0.080**	**0**	**0.024**	**0**
71	**0**	0	0	**0**	0.013	0.022	0	**0.014**	0	0	**0**	0
	0	**0**	**0**	**0**	**0.013**	**0.022**	**0**	**0.014**	**0**	**0**	**0**	**0**
75	**0.218**	0.039	0.081	**0.064**	0.184	0.265	0.156	**0.217**	0	0.018	**0.012**	0.147
	0.223	**0.041**	**0.077**	**0.064**	**0.162**	**0.257**	**0.152**	**0.205**	**0**	**0.017**	**0.012**	**0.139**
79	**0.048**	0.006	0.017	**0.012**	0	0	0.016	**0.004**	0.053	0.185	**0.138**	0.038
	0.048	**0.006**	**0.016**	**0.012**	**0**	**0**	**0.016**	**0.004**	**0.050**	**0.161**	**0.124**	**0.035**
83	**0.021**	0	0	**0**	0.026	0	0	**0.007**	0	0	**0**	0
	0.021	**0**	**0**	**0**	**0.026**	**0**	**0**	**0.007**	**0**	**0**	**0**	**0**
86	**0.005**	0	0.003	**0.002**	0.013	0.088	0.047	**0.058**	0.026	0.012	**0.016**	0
	0.005	**0**	**0.003**	**0.002**	**0.013**	**0.089**	**0.033**	**0.053**	**0.025**	**0.011**	**0.016**	**0**
90	**0**	0.006	0.003	**0.004**	0	0.007	0.016	**0.007**	0	0.030	**0.020**	0.034
	0	**0.006**	**0.003**	**0.004**	**0**	**0.007**	**0.016**	**0.007**	**0**	**0.023**	**0.016**	**0.033**
94	**0**	0.079	0.013	**0.037**	0.013	0	0	**0.004**	0.053	0	**0.016**	0.053
	0	**0.075**	**0.013**	**0.035**	**0.013**	**0**	**0**	**0.004**	**0.039**	**0**	**0.012**	**0.051**
98	**0.005**	0.067	0.010	**0.031**	0.026	0.059	0.031	**0.043**	0	0.024	**0.016**	0
	0.005	**0.064**	**0.010**	**0.029**	**0.014**	**0.059**	**0.017**	**0.038**	**0**	**0.023**	**0.016**	**0**
102	**0.117**	0.028	0.037	**0.033**	0.105	0	0	**0.029**	0.039	0	**0.012**	0.016
	0.117	**0.028**	**0.033**	**0.031**	**0.096**	**0**	**0**	**0.026**	**0.038**	**0**	**0.012**	**0.016**
106	**0.165**	0.017	0.047	**0.035**	0.026	0.051	0.016	**0.036**	0.276	0.042	**0.110**	0.003
	0.163	**0.017**	**0.043**	**0.033**	**0.026**	**0.051**	**0.016**	**0.036**	**0.224**	**0.040**	**0.095**	**0.003**
110	**0.069**	0.073	0.044	**0.053**	0	0.015	0.047	**0.018**	0.039	0.054	**0.047**	0.034
	0.063	**0.073**	**0.037**	**0.050**	**0**	**0.015**	**0.033**	**0.015**	**0.026**	**0.037**	**0.033**	**0.029**
114	**0.027**	0.051	0.034	**0.037**	0.013	0.044	0.125	**0.054**	0.026	0.060	**0.043**	0.009
	0.027	**0.042**	**0.029**	**0.034**	**0.013**	**0.039**	**0.125**	**0.052**	**0.025**	**0.047**	**0.040**	**0.009**
117	**0.005**	0.006	0.060	**0.039**	0	0.015	0.156	**0.043**	0	0	**0**	0
	0.005	**0.006**	**0.056**	**0.037**	**0**	**0.015**	**0.124**	**0.034**	**0**	**0**	**0**	**0**
121	**0.011**	0	0.013	**0.008**	0.079	0.007	0.047	**0.036**	0.053	0.048	**0.047**	0
	0.011	**0**	**0.013**	**0.008**	**0.073**	**0.007**	**0.033**	**0.030**	**0.039**	**0.046**	**0.044**	**0**
125	**0.005**	0.006	0.007	**0.006**	0.092	0.037	0.219	**0.094**	0.013	0.036	**0.028**	0.013
	0.005	**0.006**	**0.006**	**0.006**	**0.092**	**0.037**	**0.191**	**0.087**	**0.013**	**0.034**	**0.028**	**0.010**
129	**0.011**	0	0.020	**0.012**	0.066	0	0	**0.018**	0	0	**0**	0.025
	0.011	**0**	**0.017**	**0.010**	**0.054**	**0**	**0**	**0.015**	**0**	**0**	**0**	**0.022**
133	**0.053**	0.056	0.007	**0.025**	0	0	0	**0**	0	0	**0**	0.022
	0.053	**0.052**	**0.006**	**0.023**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.022**
136	**0.011**	0.011	0.003	**0.006**	0	0	0	**0**	0.039	0.006	**0.016**	0.041
	0.011	**0.011**	**0.003**	**0.006**	**0**	**0**	**0**	**0**	**0.038**	**0.006**	**0.016**	**0.038**
140	**0**	0	0.003	**0.002**	0	0.022	0	**0.011**	0.066	0.006	**0.024**	0.056
	0	**0**	**0.003**	**0.002**	**0**	**0.022**	**0**	**0.011**	**0.052**	**0.006**	**0.020**	**0.054**
144	**0**	0.017	0.010	**0.012**	0	0.088	0.016	**0.047**	0.079	0	**0.024**	0.022
	0	**0.017**	**0.007**	**0.010**	**0**	**0.088**	**0.016**	**0.047**	**0.064**	**0**	**0.020**	**0.022**
148	**0**	0.034	0.010	**0.019**	0.039	0.066	0	**0.043**	0	0	**0**	0.019
	0	**0.034**	**0.010**	**0.019**	**0.039**	**0.066**	**0**	**0.043**	**0**	**0**	**0**	**0.019**
152	**0**	0.051	0.010	**0.025**	0.053	0	0	**0.014**	0	0.024	**0.016**	0.009
	0	**0.039**	**0.010**	**0.019**	**0.053**	**0**	**0**	**0.014**	**0**	**0.023**	**0.016**	**0.009**
156	**0**	0.062	0.040	**0.047**	0.053	0.029	0.016	**0.033**	0	0	**0**	0.025
	0	**0.062**	**0.039**	**0.047**	**0.042**	**0.029**	**0.016**	**0.030**	**0**	**0**	**0**	**0.025**
160	**0.021**	0.079	0.084	**0.080**	0	0.015	0	**0.007**	0.013	0	**0.004**	0.041
	0.021	**0.079**	**0.071**	**0.075**	**0**	**0.015**	**0**	**0.007**	**0.013**	**0**	**0.004**	**0.036**
165	**0.021**	0.022	0.101	**0.070**	0.105	0.029	0.016	**0.047**	0	0.006	**0.004**	0.159
	0.021	**0.022**	**0.086**	**0.063**	**0.087**	**0.024**	**0.016**	**0.038**	**0**	**0.006**	**0.004**	**0.143**
170	**0.037**	0.017	0.104	**0.070**	0.013	0.051	0.031	**0.036**	0.026	0.018	**0.020**	0.056
	0.037	**0.017**	**0.096**	**0.067**	**0.013**	**0.047**	**0.031**	**0.033**	**0.025**	**0.017**	**0.020**	**0.056**
175	**0.106**	0.028	0.084	**0.062**	0.013	0	0	**0.004**	0	0.036	**0.024**	0.013
	0.105	**0.023**	**0.071**	**0.054**	**0.013**	**0**	**0**	**0.004**	**0**	**0.029**	**0.020**	**0.013**
180	**0.027**	0.067	0.027	**0.041**	0.013	0	0	**0.004**	0.013	0	**0.004**	0.022
	0.027	**0.060**	**0.026**	**0.038**	**0.013**	**0**	**0**	**0.004**	**0.013**	**0**	**0.004**	**0.022**
185	**0**	0.028	0.020	**0.023**	0	0	0.016	**0.004**	0	0.179	**0.118**	0.025
	0	**0.028**	**0.019**	**0.023**	**0**	**0**	**0.016**	**0.004**	**0**	**0.147**	**0.097**	**0.022**
190	**0**	0.039	0.027	**0.031**	0.013	0.015	0	**0.011**	0.026	0.208	**0.146**	0.047
	0	**0.039**	**0.026**	**0.031**	**0.013**	**0.015**	**0**	**0.011**	**0.025**	**0.185**	**0.132**	**0.045**
200	**0.005**	0.028	0.027	**0.027**	0.026	0.015	0	**0.014**	0.013	0.006	**0.008**	0.063
	0.005	**0.018**	**0.026**	**0.023**	**0.026**	**0.016**	**0**	**0.015**	**0.013**	**0.006**	**0.008**	**0.058**
210	**0.005**	0.062	0.030	**0.041**	0.013	0.007	0.016	**0.011**	0	0	**0**	0.003
	0.005	**0.058**	**0.029**	**0.040**	**0.013**	**0.007**	**0.016**	**0.011**	**0**	**0**	**0**	**0.003**
220	**0**	0.011	0.010	**0.010**	0	0.015	0.016	**0.011**	0	0.006	**0.004**	0.003
	0	**0.011**	**0.010**	**0.010**	**0**	**0.011**	**0.016**	**0.084**	**0**	**0.006**	**0.004**	**0.003**
230	**0**	0.011	0.007	**0.008**	0	0	0	**0**	0.039	0	**0.012**	0
	0	**0.005**	**0.006**	**0.008**	**0**	**0**	**0**	**0**	**0.026**	**0**	**0.008**	**0**
250	**0**	0	0	**0**	0	0	0	**0**	0	0	**0**	0
	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
270	**0.011**	0	0.003	**0.002**	0	0	0	**0**	0	0.006	**0.004**	0.003
	0.006	**0**	**0.003**	**0.002**	**0**	**0**	**0**	**0**	**0**	**0.006**	**0.004**	**0.001**
Null	**0**	0	0.032	**0.021**	0	**0**	0	**0**	0.050	0.034	**0.039**	0
	0.006	**0.069**	**0.092**	**0.079**	**0.104**	**0.035**	**0.136**	**0.154**	**0.176**	**0.124**	**0.154**	**0.062**
Hobs	**0.856**	0.764	*0.779	**0.849**	*0.697	0.831	*0.625	**0.885**	*0.632	*0.714	**0.705**	*0.747
Hexp	**0.777**	0.791	0.948	**0.979**	0.921	0.897	0.906	**0.920**	0.899	0.885	**0.959**	0.931

for coho salmon populations from British Columbia. The weighted means of allele frequencies for regions are in bold and follow the are indicated by * next to the observed heterozygosity. The allele number (in basepairs) is the lower limit of the allele bin. Allele frequen- are given underneath the population names.

Big Qualicum	ECVI	Toboggan	Cedar	Babine	Clear-water	Sustut	Skeena	Tseax	Zolzap	Mexiadin	Nass	TR	L Fr
200	260	164	47	139	48	36	434	40	47	64	151	1015	1043
0	**0**	0.079	0.020	0.072	0.024	0	**0.056**	0.038	0.063	0.019	**0.039**	**0.002**	**0.001**
0	**0**	**0.076**	**0.019**	**0.065**	**0.010**	**0**	**0.052**	**0.038**	**0.055**	**0.015**	**0.037**	**0.001**	**0.001**
0	**0**	0	0	0.004	0.024	0	**0.003**	0	0	0	**0**	**0.024**	**0.027**
0	**0**	**0**	**0**	**0.004**	**0.010**	**0**	**0.002**	**0**	**0**	**0**	**0**	**0.016**	**0.025**
0.136	**0.136**	0.201	0.265	0.040	0.146	0.167	**0.144**	0.075	0.115	0.144	**0.114**	**0.016**	**0.086**
0.114	**0.125**	**0.176**	**0.208**	**0.037**	**0.076**	**0.132**	**0.121**	**0.075**	**0.103**	**0.093**	**0.105**	**0.011**	**0.082**
0.019	**0.026**	0.028	0.020	0.036	0.012	0	**0.025**	0.038	0.031	0.010	**0.025**	**0.002**	**0.010**
0.017	**0.025**	**0.027**	**0.009**	**0.036**	**0.010**	**0**	**0.024**	**0.038**	**0.031**	**0.007**	**0.025**	**0.001**	**0.009**
0	**0**	0.003	0	0.047	0.037	0	**0.019**	0	0	0	**0**	**0.001**	**0.023**
0	**0**	**0.003**	**0**	**0.046**	**0.021**	**0**	**0.018**	**0**	**0**	**0**	**0**	**0.001**	**0.022**
0.045	**0.024**	0.097	0.029	0.086	0	0.014	**0.067**	0.038	0.021	0.067	**0.043**	**0.003**	**0.018**
0.038	**0.021**	**0.091**	**0.028**	**0.080**	**0**	**0.014**	**0.063**	**0.038**	**0.021**	**0.045**	**0.040**	**0.002**	**0.017**
0.019	**0.025**	0.022	0	0.036	0.037	0.014	**0.024**	0.025	0.042	0.067	**0.046**	**0.001**	**0.056**
0.015	**0.022**	**0.021**	**0**	**0.036**	**0.021**	**0.014**	**0.023**	**0.014**	**0.042**	**0.045**	**0.043**	**0.001**	**0.053**
0.043	**0.046**	0	0	0	0.024	0	**0.002**	0	0	0	**0**	**0.029**	**0.011**
0.040	**0.045**	**0**	**0**	**0**	**0.010**	**0**	**0.001**	**0**	**0**	**0**	**0**	**0.020**	**0.010**
0.029	**0.015**	0	0	0.014	0	0	**0.005**	0.038	0	0	**0.011**	**0.003**	**0.014**
0.027	**0.015**	**0**	**0**	**0.014**	**0**	**0**	**0.005**	**0.038**	**0**	**0**	**0.011**	**0.003**	**0.014**
0	**0.007**	0.003	0.049	0.011	0.012	0	**0.011**	0.025	0.021	0	**0.014**	**0.002**	**0.038**
0	**0.007**	**0.003**	**0.038**	**0.011**	**0.010**	**0**	**0.010**	**0.025**	**0.021**	**0**	**0.014**	**0.001**	**0.036**
0.005	**0.004**	0.013	0.010	0.119	0.085	0.069	**0.057**	0.050	0.010	0.029	**0.029**	**0.049**	**0.034**
0.005	**0.004**	**0.012**	**0.009**	**0.111**	**0.042**	**0.056**	**0.049**	**0.050**	**0.010**	**0.022**	**0.029**	**0.034**	**0.033**
0.008	**0.019**	0.126	0.010	0.194	0.061	0.083	**0.121**	0.025	0.073	0.029	**0.043**	**0.302**	**0.031**
0.007	**0.017**	**0.109**	**0.009**	**0.181**	**0.051**	**0.070**	**0.107**	**0.014**	**0.066**	**0.022**	**0.037**	**0.209**	**0.028**
0.019	**0.014**	0.006	0.069	0.004	0.110	0.056	**0.026**	0.013	0.021	0.038	**0.025**	**0.123**	**0.036**
0.017	**0.014**	**0.006**	**0.057**	**0.004**	**0.063**	**0.029**	**0.020**	**0.014**	**0.021**	**0.030**	**0.025**	**0.080**	**0.035**
0.011	**0.006**	0.053	0.049	0	0	0	**0.025**	0.013	0.021	0.019	**0.018**	**0.025**	**0.069**
0.010	**0.006**	**0.047**	**0.038**	**0**	**0**	**0**	**0.022**	**0.013**	**0.021**	**0.015**	**0.018**	**0.018**	**0.065**
0.005	**0.003**	0.006	0	0	0.024	0	**0.005**	0.038	0.031	0.019	**0.029**	**0.012**	**0.019**
0.005	**0.003**	**0.006**	**0**	**0**	**0.010**	**0**	**0.003**	**0.038**	**0.031**	**0.015**	**0.029**	**0.009**	**0.018**
0.021	**0.015**	0	0	0	0.037	0	**0.003**	0.038	0.031	0	**0.021**	**0.035**	**0.033**
0.017	**0.014**	**0**	**0**	**0**	**0.031**	**0**	**0.003**	**0.038**	**0.031**	**0**	**0.021**	**0.027**	**0.033**
0.021	**0.021**	0	0	0.004	0	0	**0.001**	0	0	0	**0**	**0.008**	**0.019**
0.015	**0.018**	**0**	**0**	**0.004**	**0**	**0**	**0.001**	**0**	**0**	**0**	**0**	**0.005**	**0.018**
0.003	**0.011**	0	0	0	0	0	**0**	0	0	0	**0**	**0**	**0.006**
0.002	**0.011**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.006**
0.045	**0.042**	0	0.010	0.011	0	0	**0.005**	0	0.010	0.010	**0.007**	**0.002**	**0.037**
0.036	**0.037**	**0**	**0.009**	**0.011**	**0**	**0**	**0.005**	**0**	**0.010**	**0.007**	**0.007**	**0.002**	**0.036**
0.024	**0.038**	0.003	0.010	0.004	0.037	0.014	**0.008**	0.038	0.063	0.087	**0.064**	**0.001**	**0.059**
0.022	**0.036**	**0.003**	**0.009**	**0.004**	**0.031**	**0.014**	**0.008**	**0.038**	**0.066**	**0.060**	**0.062**	**0.001**	**0.056**
0.016	**0.018**	0.016	0.010	0.011	0	0	**0.010**	0	0.042	0.029	**0.025**	**0.006**	**0.058**
0.013	**0.017**	**0.015**	**0.009**	**0.007**	**0**	**0**	**0.009**	**0**	**0.042**	**0.022**	**0.025**	**0.003**	**0.056**
0.008	**0.013**	0.006	0.020	0.004	0.049	0	**0.010**	0.038	0.010	0.019	**0.021**	**0.019**	**0.039**
0.007	**0.013**	**0.006**	**0.019**	**0.004**	**0.021**	**0**	**0.008**	**0.038**	**0.011**	**0.008**	**0.018**	**0.014**	**0.037**
0.051	**0.031**	0.022	0	0.018	0.049	0.042	**0.022**	0.075	0.021	0.029	**0.039**	**0.017**	**0.038**
0.041	**0.027**	**0.021**	**0**	**0.018**	**0.031**	**0.028**	**0.020**	**0.067**	**0.022**	**0.022**	**0.037**	**0.015**	**0.037**
0.106	**0.067**	0.035	0.059	0.061	0.085	0.153	**0.059**	0.038	0.083	0.058	**0.061**	**0.004**	**0.036**
0.088	**0.060**	**0.031**	**0.056**	**0.058**	**0.042**	**0.117**	**0.052**	**0.038**	**0.077**	**0.038**	**0.056**	**0.011**	**0.036**
0.061	**0.050**	0.041	0.010	0.036	0.037	0	**0.031**	0.100	0.031	0.077	**0.068**	**0.008**	**0.026**
0.044	**0.041**	**0.037**	**0.009**	**0.036**	**0.031**	**0**	**0.030**	**0.093**	**0.031**	**0.046**	**0.061**	**0.003**	**0.025**
0.056	**0.100**	0.009	0.029	0.004	0	0.014	**0.009**	0.063	0.021	0.029	**0.036**	**0.020**	**0.035**
0.044	**0.085**	**0.009**	**0.028**	**0.004**	**0**	**0.014**	**0.009**	**0.063**	**0.021**	**0.022**	**0.036**	**0.006**	**0.033**
0.053	**0.053**	0.003	0.029	0.025	0.073	0.042	**0.023**	0.025	0.021	0.019	**0.021**	**0.065**	**0.036**
0.045	**0.051**	**0.003**	**0.028**	**0.025**	**0.042**	**0.041**	**0.021**	**0.025**	**0.021**	**0.008**	**0.018**	**0.045**	**0.035**
0.056	**0.035**	0.025	0.088	0.004	0.024	0.069	**0.029**	0.038	0.042	0.010	**0.029**	**0.008**	**0.040**
0.050	**0.034**	**0.024**	**0.076**	**0.004**	**0.020**	**0.043**	**0.025**	**0.038**	**0.042**	**0.007**	**0.029**	**0.005**	**0.040**
0.043	**0.032**	0.031	0.029	0.018	0.012	0.056	**0.026**	0.038	0.021	0.048	**0.036**	**0.007**	**0.019**
0.035	**0.029**	**0.030**	**0.028**	**0.015**	**0.010**	**0.042**	**0.024**	**0.038**	**0.021**	**0.037**	**0.036**	**0.005**	**0.019**
0.005	**0.014**	0.035	0.010	0.029	0	0.028	**0.025**	0	0.010	0.058	**0.025**	**0**	**0.019**
0.005	**0.013**	**0.034**	**0.009**	**0.029**	**0**	**0.027**	**0.025**	**0**	**0.010**	**0.045**	**0.025**	**0**	**0.018**
0.061	**0.051**	0.085	0	0.014	0	0	**0.035**	0.087	0.073	0.019	**0.057**	**0**	**0.005**
0.050	**0.048**	**0.078**	**0**	**0.014**	**0**	**0**	**0.033**	**0.071**	**0.066**	**0.015**	**0.049**	**0**	**0.005**
0.027	**0.042**	0.022	0.039	0.018	0	0	**0.018**	0	0.042	0.010	**0.018**	**0.004**	**0.004**
0.023	**0.038**	**0.021**	**0.037**	**0.018**	**0**	**0**	**0.018**	**0**	**0.042**	**0.007**	**0.018**	**0.002**	**0.004**
0.003	**0.003**	0.025	0.010	0.05	0	0.111	**0.035**	0.013	0.031	0.038	**0.029**	**0.007**	**0.005**
0.002	**0.003**	**0.024**	**0.009**	**0.048**	**0**	**0.097**	**0.033**	**0.013**	**0.031**	**0.030**	**0.029**	**0.004**	**0.005**
0	**0.001**	0.003	0.010	0.029	0	0.069	**0.017**	0	0	0.019	**0.007**	**0**	**0.002**
0	**0.001**	**0.003**	**0.009**	**0.029**	**0**	**0.068**	**0.017**	**0**	**0**	**0.015**	**0.005**	**0**	**0.002**
0	**0**	0	0	0	0	0	**0**	0	0	0	**0**	**0**	**0.001**
0	**0.003**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.001**
0.005	**0.003**	0	0.118	0	0	0	**0**	0	0	0	**0**	**0**	**0**
0.005	**0.004**	**0**	**0.064**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
0.005	**0.004**	0	0	0	0	0	**0**	0	0	0	**0**	**0**	**0.001**
0.005	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.001**
0.060	**0.033**	0.030	0.007	0	0.163	0.027	**0.041**	0	0	0	**0**	**0.193**	**0.007**
0.153	**0.115**	**0.080**	**0.186**	**0.052**	**0.406**	**0.197**	**0.137**	**0.066**	**0.065**	**0.300**	**0.063**	**0.444**	**0.048**
*0.750	**0.764**	0.774	*0.588	*0.737	*0.390	*0.431	**0.721**	0.837	0.802	*0.721	**0.836**	0.254	0.875
0.945	**0.944**	0.915	0.896	0.921	0.938	0.919	**0.938**	0.950	0.958	0.942	**0.957**	**0.086**	**0.958**

inheritance at all three loci, although a null (nonamplifying) allele is present at *Ots*103 (Small et al., 1998). Individual samples that although amplified with both other primer sets yet produced no *Ots*103 alleles after the *Ots*103 amplification was performed three times, were scored as *Ots*103 null homozygotes. Allele frequencies at the *Ots*103 locus were then corrected according to a maximum-likelihood estimate (EM algorithm, Dempster et al., 1977) by using GENEPOP, version 1.2 (Raymond and Rousset, 1995a). Corrected frequencies were used in the genetic distance analysis. For *Ots*101 and *Ots*3, fish with a single allele were scored as homozygotes and fish with two alleles were scored as heterozygotes. Allele frequency data for individual populations in the Fraser River and Thompson River are from Small et al. (1998) and only the weighted means of total allele frequencies for these regions are presented here (Tables 1 and 2). The upper Fraser River population (Bridge River) has been grouped with the Thompson River populations in accordance with its genetic profile.

Hardy-Weinberg equilibrium (HWE) was tested with the probability test of HWE (an exact HW test, Guo and Thompson, 1992) with GENEPOP (version 1.2). *F*-statistics and their standard deviations were calculated according to Weir and Cockerham (1984) using FSTAT (Goudet, 1995). We use the notations F_{st}, F_{is} and F_{it} for Weir and Cockerham's θ, f, and F, respectively. *P*-values for $\alpha = 0.05$ in all data analyses were corrected for simultaneous multiple tests (Lessios, 1992). Pairwise comparisons of populations for differences in allele distributions were conducted at all three loci with Fisher's exact tests (Raymond and Rousset, 1995b). In populations with multiple year classes, annual variability in allele frequencies was tested with 1000 simulations in a Monte Carlo analysis (Roff and Bentzen, 1989) and populations were divided into year classes for a neighbor-joining (NJ) analysis (Saitou and Nei, 1987). A NJ dendrogram illustrating genetic relationships among populations was constructed with PHYLIP 3.5c software (Felsenstein, 1993). The allele frequency matrix was resampled 500 times and Cavalli-Sforza and Edward's (1967) chord distances were estimated for population pairs. NJ dendrograms were constructed for each matrix and a consensus NJ dendrogram was generated with CONSENSE (see Felsenstein, 1993). Individual fish were classified to specific populations with a jackknife discriminant analysis (SAS Institute Inc., 1989).

Estimation of stock composition

Microsatellite allele frequency data were examined for use in estimating stock composition in a mixed-stock fishery. We pooled low-frequency alleles in adjacent bins (so that each bin contained at least 6% of the alleles) to reduce the number of genotypes for which frequencies were estimated. This pooling resulted in 13 "analysis" bins (91 genotypes) for *Ots*101, 10 bins (65 genotypes) for *Ots*3, and 13 bins (91 genotypes) for *Ots*103 (Table 3). Genotype frequencies at *Ots*101 and *Ots*3 were estimated for each population from the allele frequencies by assuming a Hardy-Weinberg distribution of genotypes. Because genotype frequencies at the *Ots*103 locus were generally not in HWE owing to the presence of the null allele, the observed genotype frequencies were used to characterize each population for *Ots*103. Genotype frequencies at all three loci were used as input in a maximum likelihood mixed-stock fishery analysis (Fournier et al., 1984).

Two types of hypothetical mixed-stock fishery samples were simulated: single-region fishery samples composed of fish from lower Fraser River and the Thompson River coho salmon populations, and multiregion fishery samples composed of fish from populations from several regions. Populations contributing to the multiregion samples were chosen on the basis of known or inferred migration patterns. For the Fraser River fishery simulation, only populations from the lower Fraser and Thompson rivers were present in the baseline and in the mixed-stock fishery samples. In the multiregion fishery simulations, all 34 populations were used in the baseline. In all simulations, fishery samples of 200 fish were generated from specified populations in the

Table 3

Method of pooling low-frequency alleles for *Ots*101, *Ots*3, and *Ots*103 to reduce the number of genotypes for baseline populations in mixed-stock analyses.

	Microsatellite allele bin numbers		
Analysis bin no.	*Ots*101	*Ots*3	*Ots*103
1	1–7	1	1, 2, 3
2	8, 9	3–11	4–7
3	10	12	8–11
4	11	13	12
5	12	14	13
6	13, 14	15	14, 15
7	15, 16, 17	16	16–20
8	18, 19	17	21, 22
9	20, 21	18	23, 24
10	22	19	25, 26, 27
11	23, 24		28,29
12	25, 26		30–38
13	27–32		39

baseline by sampling randomly, with replacement, thus simulating the randomness present in data collection. For each simulated mixed-stock fishery, stock contributions were estimated in 50 independent simulations, and means and standard deviations for the estimated contributions of each population were obtained.

Results

Allele frequencies and heterozygosity

Observed heterozygosity was high in all populations at *Ots*101, ranging from 0.72 for Nitinat River to 0.97 for Waukwaas River (Table 1). Heterozygosity was slightly lower at *Ots*3, ranging from 0.70 for Zolzap River to 0.82 for Cluxewe River (Table 1). At *Ots*103, observed heterozygosity varied widely among regions, ranging from 0.25 in the Thompson River (TR) to 0.89 in North Coast Vancouver Island populations (NCVI) (Table 2). For Thompson River populations, the apparently low heterozygosity values were due to high frequencies of the null allele. Of the 22 populations with data for multiple year classes, Atnarko was the only one for which allele frequencies differed significantly among year classes at all loci. Allele frequencies differed significantly among year classes in the Kitimat, Sustut, and Toboggan populations at *Ots*3, in the Kitimat River and Pallant Creek populations at *Ots*101, and in the Quinsam and Toboggan populations at *Ots*103. Year-class variation in the Fraser and Thompson River populations are reported in Small et al. (1998). Multiple samples from individual populations clustered together in NJ analyses (except for three lower Fraser River populations as noted in Small et al., 1998), indicating that allele frequency differences among year classes were less than those among populations. Thus, all fish collected from the same location in different years were pooled and treated as a single population in subsequent analyses.

Hardy-Weinberg equilibrium

The degree of deviation from HWE varied substantially among the 3 loci (Table 1). After correction for multiple tests ($P<0.0015$), three populations (Atnarko, Deadman and Upper Pitt) deviated from HWE at *Ots*101, and three populations (Kitimat, Big Qualicum, and Sustut) were out of HWE at *Ots*3 (Table 1). In most populations, observed heterozygosity was lower than expected heterozygosity (Table 1), and this lower heterozygosity was reflected in single-locus F_{is} values of 0.0435 (SD 0.009) for *Ots*101 and 0.0617 (SD 0.008) for *Ots*3 (both $P<0.005$). HWE was rejected for *Ots*103 in 25 out of 34 populations (Table 2), reflecting the presence of the null allele. The single locus F_{is} value was 0.2738 (SD 0.008). Fish homozygous for the null allele were scored in most populations and corrected *Ots*103 allele frequencies were generated for all populations (Table 2).

Population differences

In pairwise tests, all populations had significantly different allele frequencies at one or more loci, with the exception of two geographically proximate populations in the Thompson River (Lemieux River and Dunn Creek), and two sets of populations from the adjacent Skeena and Nass River systems: (Cedar River [Skeena])and Zolzap River [Nass]; and Sustut River [Skeena] and Meziadin River [Nass]). The single- and multilocus F_{st} values indicated significant differentiation among populations with values of 0.040 (SD 0.006) for *Ots*101, 0.054 (SD 0.009) for *Ots*3, 0.059 (SD 0.009) for *Ots*103 (all $P<0.005$) and a multilocus value of 0.051 (SD 0.006, $P<0.005$).

Allele frequencies

With the exception of *Ots*101 allele 96, found only in the Robertson Creek population, all alleles were present in more than one population and region. Thus, population- or region-specific alleles were generally nonexistent, but allele frequencies varied among populations and regions. At *Ots*101, lower Fraser River populations had high frequencies of smaller alleles (74% shorter than 143 bp in length) and relatively low frequencies of large alleles, whereas Thompson River populations had low frequencies of small alleles (64% longer than 161 bp). In the Thompson River populations, *Ots*3 allele 66 was absent and allele 94 was more common than in populations from other regions. *Ots*3 alleles 104 and 106 were found only in the Skeena and Nass River populations. The most striking differentiation provided by *Ots*103 was the high frequency (0.44) of the null allele in Thompson River populations. This was three times the next highest frequency (0.15) that occurred in the north and west coast Vancouver Island populations.

Population structure

The unrooted consensus NJ dendrogram possessed three major branches that provided regional definition among coho salmon populations of British Columbia (Fig. 2). The best defined branch contained the Thompson River (and Bridge River of the upper Fraser drainage) populations, that occurred together

in all 500 trees used to construct the consensus tree. The branch containing all lower Fraser River populations was also well supported. Populations from the northern Skeena and Nass rivers were interspersed on the third branch, but only the upper Skeena and Nass populations formed a well-supported group (Fig. 2). Lower Skeena and Nass populations were more similar to a diverse central cluster of Vancouver Island and mainland coastal coho salmon populations. Within the coastal group, east coast (Big Qualicum and Quinsam), west coast (Robertson and Nitinat), and north coast (Cluxewe, Waukwaas and Stephens) Vancouver Island populations were as well distinguished from each other as they were from the more northern mainland coastal populations or the Queen Charlotte Island population of Pallant Creek.

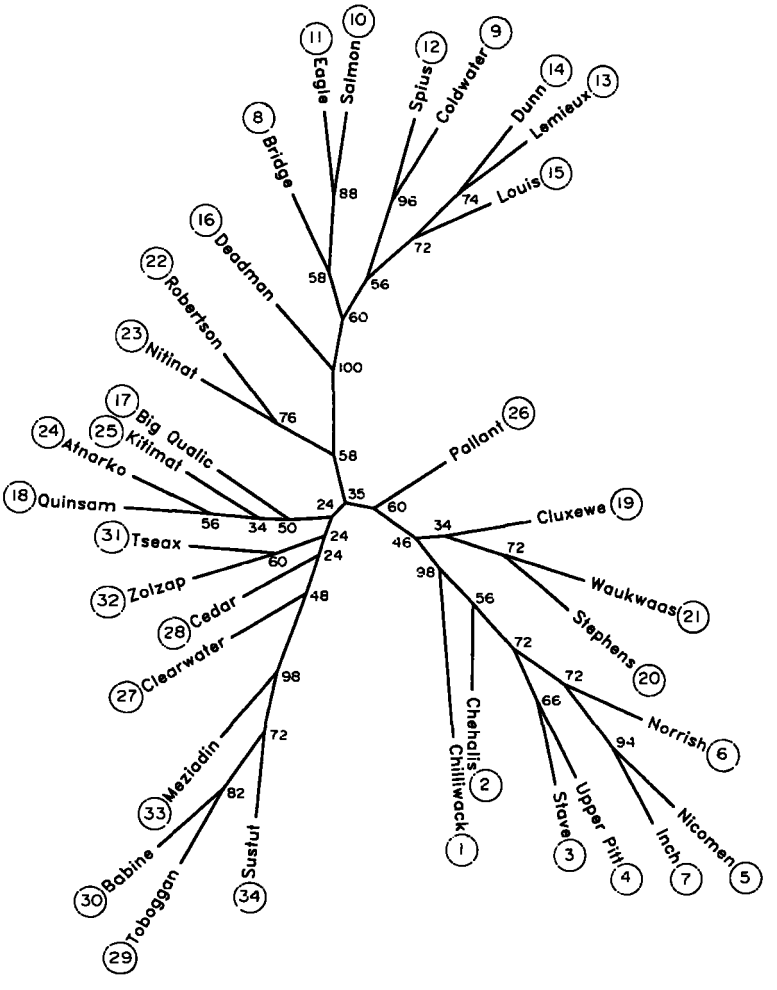

Figure 2

Unrooted neighbor-joining tree relating 34 British Columbia coho salmon populations. The tree was constructed from a consensus of Cavalli-Sforza and Edward's chord distances. Bootstrap values at the tree nodes were computed over 500 replications by resampling the allele frequency matrix. Bootstrap values indicate the percentage of trees in which the populations beyond the node occurred together. All names correspond to population names given in Tables 2 and 3 with the exception of Big Qualicum River which is shortened to Big Qualic. The number of the population (from Fig. 1) is next to the name.

Estimation of stock composition

In the mixed-stock fishery simulated within the Fraser River, estimates of stock composition were accurate and precise, with an average of 2.3% of the mixture incorrectly assigned to each population (Table 4). In general, misassigned portions of the mixture were assigned to closely related populations. For instance, the 30% contribution of Coldwater River fish to the mixture was underestimated as 26.4%, but 3.1% of the mixture was assigned to the genetically similar Spius River population, although no Spius fish were included in the mixture. Fish misassigned to population were almost invariably assigned to the correct region. Less than 1% of fish were misclassified between the Thompson River and Lower Fraser regions (Table 4). Thus, within the Fraser River drainage, populations contributing to a mixed-stock sample can be identified to region and to individual population, or population group within region, with a high degree of accuracy and precision.

Accuracy and precision of stock composition estimates were also high in the simulated mixed-stock samples to which populations from different regions contributed (Table 5). Average error of individual population contributions to the mixed fishery was 1.5% (3% for populations actually contributing to the mixture), and average error of regional contributions was 2.2% (higher for regions actually contributing). In most simulations, the contributions of populations present in the mixture were underestimated because a small proportion of the mixture was allocated to baseline populations not present in the mixture. In general, misassigned fish were allocated to genetically similar populations and thus were

correctly identified to region. Regions with no populations present in the mixture were allocated less than 5% of the fish, except in the mixture composed of Vancouver Island populations (mix 1, Table 5). In that case, 10% of the fish were allocated to the lower Fraser River. The regional misclassification of Vancouver Island coho salmon as fish of lower Fraser origin in mix 1 was due largely to the allocation of 4% of the mixture to Chilliwack River, the lower Fraser population most genetically similar to the northern Vancouver Island populations (Fig. 2). Similarly, Vancouver Island and central coast fish were underestimated in mix 5, and some of them attributed to the lower Fraser rather than to other coastal island, mainland, or lower Skeena and Nass populations as might be expected from the dendrogram (Table 5; Fig. 2). Conversely, when lower Fraser coho salmon formed a high proportion of the mixture (mix 3), they were underestimated and misidentified fish tended to be attributed to Vancouver Island populations (Table 5).

In contrast, the genetic distinctiveness of Thompson River coho salmon resulted in their accurate identification in mixtures in which they were present (mixes 3 and 5) and little misrepresentation in mixtures from which they were absent (mixes 1, 2, and 4). Nass and Skeena populations were well-separated (mix 4), and contributions from lower Skeena (Cedar and Clearwater) populations were identified as well as those from the upper Skeena-Nass populations. Given the lack of separation of Skeena and Nass in the NJ dendrogram (Fig. 2), this result needs to be confirmed by more extensive sampling and further mixture analysis for populations within these two watersheds. Individual classification of Nass and Skeena fish (see below), and the lack of significant allele frequency differences between two Nass-Skeena pairs of populations, indicated that additional genetic markers may be required for accurate differentiation of Nass and Skeena coho salmon. Nevertheless, the results of these preliminary analyses indicate that a mixed-stock sample of coho salmon collected in the field can generally be resolved into its regional components by using microsatellite genetic markers.

Identifying individuals

Accuracy of the classification of individual fish to region with discriminant analysis varied among regions (Table 6), but individual classification was generally much less accurate than was estimation of stock composition. An average of 48% of fish, ranging from 85% of Thompson to 20% of Nass individuals, was correctly classified to region. Misclassified fish were most commonly attributed to the most genetically similar region according to relationships depicted in the NJ dendrogram. The Nass and Skeena populations were interspersed in the NJ analysis (Fig. 2), and an essentially equal proportion of Nass River fish (20%) were identified as Nass and Skeena fish (Table 6). Skeena River fish were identified more accurately than Nass River fish, with 53% and 11% of the Skeena River fish classified as being of Skeena and Nass origin, respectively. If only the Fraser River populations were included in the baseline, Fraser River coho salmon were assigned to region accurately, with 93% correctly identified to either the lower Fraser River or the Thompson River (data not shown).

Table 4

Accuracy and precision of estimated Fraser River coho salmon population contributions in a simulated mixed-stock sample from a 16-population Fraser River baseline. A 200-fish mixture was generated with replacement from the baseline 50 times and the population composition was estimated for each mixture. The mean percentage of the mixture allocated to each population is given, followed by the standard deviation in parentheses. Regional totals are given in the rows marked TR (Thompson River) and L Fr (lower Fraser River).

	True	Mean	SD
Coldwater	30	26.4	(4.4)
Salmon	0	1.3	(1.6)
Eagle	20	15.7	(3.4)
Spius	0	3.1	(3.5)
Lemieux	0	1.0	(1.5)
Dunn	0	0.6	(1.3)
Louis	0	1.0	(1.7)
Deadman	0	0.5	(0.9)
Bridge	0	0.7	(1.3)
TR	50	50.2	(1.4)
Chilliwack	20	16.8	(4.0)
Chehalis	0	1.4	(1.8)
Stave	15	12.6	(3.3)
Upper Pitt	0	1.8	(2.1)
Nicomen	15	12.2	(3.4)
Norrish	0	2.9	(2.5)
Inch	0	2.0	(2.4)
L Fr	50	49.8	(1.4)

Discussion

Microsatellite DNA analysis shows great promise for the elucidation of population structure in coho salmon. Very strong regional structure was apparent in the British Columbia coho salmon populations

Table 5

Estimated stock composition of five 200-fish mixtures of coho salmon from several regions in British Columbia using a 34-stock baseline. Each mixture was generated 50 times, and stock composition of the mixture was estimated by randomly resampling each baseline population, with replacement, to derive a new estimation of the fish mixture composition. The mean and standard deviations of 50 estimations are reported for each population. Individual population estimates are followed by the sum of contributions from a region (bold type).

	Mix 1			Mix 2			Mix 3			Mix 4			Mix 5		
	True	Mean	SD	True	Mean	SD	True	Mean	SD	True	Mean	SD	True	Mean	SD
Pallant	**0**	**0.02**	**0.02**	**0**	**0.01**	**0.01**	**0**	**0.00**	**0.01**	**0**	**0.00**	**0.01**	**0**	**0.01**	**0.01**
Atnarko	0	0.01	0.01	0.13	0.11	0.02	0	0.00	0.01	0	0.02	0.02	0	0.02	0.02
Kitimat	0	0.01	0.02	0.13	0.10	0.02	0	0.01	0.01	0	0.02	0.02	0.20	0.16	0.04
C Coast	**0**	**0.02**	**0.02**	**0.26**	**0.21**	**0.03**	**0**	**0.01**	**0.01**	**0**	**0.04**	**0.03**	**0.20**	**0.18**	**0.04**
Cluxewe	0	0.01	0.01	0	0.01	0.01	0	0.00	0.01	0	0.00	0.01	0	0.01	0.01
Stephens	0.13	0.10	0.02	0	0.00	0.00	0	0.01	0.01	0	0.01	0.01	0	0.01	0.02
Waukwaas	0.17	0.12	0.03	0	0.00	0.00	0	0.01	0.01	0	0.00	0.01	0	0.00	0.01
NCVI	**0.30**	**0.23**	**0.03**	**0**	**0.01**	**0.01**	**0**	**0.02**	**0.02**	**0**	**0.01**	**0.01**	**0**	**0.02**	**0.02**
Nitinat	0.13	0.10	0.02	0	0.00	0.00	0	0.00	0.01	0	0.00	0.00	0	0.00	0.00
Robertson	0.13	0.12	0.03	0	0.00	0.00	0.15	0.13	0.01	0	0.00	0.01	0	0.00	0.00
WCVI	**0.26**	**0.22**	**0.03**	**0**	**0.00**	**0.01**	**0.15**	**0.13**	**0.01**	**0**	**0.00**	**0.01**	**0**	**0.00**	**0.01**
Quinsam	0.17	0.15	0.05	0	0.02	0.03	0	0.01	0.01	0	0.01	0.01	0	0.03	0.04
Big Qualic	0.26	0.22	0.04	0.17	0.14	0.03	0	0.01	0.02	0	0.01	0.01	0.25	0.19	0.04
ECVI	**0.43**	**0.37**	**0.06**	**0.17**	**0.16**	**0.04**	**0**	**0.02**	**0.02**	**0**	**0.02**	**0.02**	**0.25**	**0.22**	**0.05**
Toboggan	0	0.00	0.00	0.26	0.24	0.03	0	0.00	0.00	0.14	0.15	0.03	0	0.01	0.01
Cedar	0	0.01	0.01	0	0.01	0.01	0	0.00	0.01	0.13	0.09	0.03	0.20	0.13	0.03
Babine	0	0.00	0.01	0.17	0.16	0.02	0	0.00	0.00	0.26	0.25	0.04	0	0.00	0.00
Clearwater	0	0.00	0.01	0	0.00	0.01	0	0.00	0.00	0.17	0.14	0.03	0	0.01	0.01
Sustut	0	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0.13	0.10	0.03	0	0.00	0.01
Skeena	**0**	**0.01**	**0.02**	**0.43**	**0.42**	**0.03**	**0**	**0.00**	**0.00**	**0.83**	**0.73**	**0.04**	**0.20**	**0.15**	**0.03**
Tseax	0	0.01	0.01	0	0.00	0.01	0	0.01	0.01	0	0.01	0.01	0	0.01	0.01
Zolzap	0	0.00	0.01	0	0.01	0.01	0	0.00	0.01	0	0.01	0.01	0	0.01	0.01
Meziadin	0	0.01	0.01	0	0.01	0.01	0	0.00	0.00	0.17	0.13	0.03	0	0.01	0.01
Nass	**0**	**0.02**	**0.03**	**0**	**0.02**	**0.02**	**0**	**0.01**	**0.00**	**0.17**	**0.15**	**0.03**	**0**	**0.03**	**0.02**
Coldwater	0	0.00	0.00	0	0.00	0.00	0	0.03	0.02	0	0.00	0.00	0	0.00	0.00
Salmon	0	0.00	0.00	0	0.00	0.00	0	0.00	0.01	0	0.00	0.00	0.10	0.09	0.01
Eagle	0	0.00	0.00	0	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0	0.00	0.00
Spius	0	0.00	0.00	0	0.00	0.00	0.20	0.16	0.03	0	0.00	0.00	0	0.00	0.00
Lemieux	0	0.00	0.00	0	0.00	0.00	0	0.00	0.01	0	0.00	0.00	0	0.00	0.00
Dunn	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
Louis	0	0.01	0.01	0	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0	0.00	0.00
Deadman	0	0.01	0.01	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.01	0.00
Bridge	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
TR	**0**	**0.02**	**0.01**	**0**	**0.01**	**0.01**	**0.20**	**0.21**	**0.01**	**0**	**0.01**	**0.01**	**0.10**	**0.10**	**0.01**
Chilliwack	0	0.04	0.03	0	0.01	0.01	0.10	0.10	0.04	0	0.00	0.01	0	0.02	0.03
Chehalis	0	0.01	0.02	0	0.01	0.02	0.25	0.18	0.03	0	0.01	0.01	0	0.02	0.03
Stave	0	0.01	0.02	0	0.02	0.02	0	0.02	0.02	0	0.01	0.02	0	0.03	0.03
Upper Pitt	0	0.01	0.01	0	0.01	0.01	0	0.01	0.02	0	0.00	0.01	0.10	0.08	0.04
Nicomen	0	0.01	0.02	0	0.01	0.01	0.10	0.10	0.03	0	0.00	0.01	0	0.01	0.02
Norrish	0	0.01	0.02	0	0.01	0.02	0	0.02	0.02	0	0.01	0.02	0	0.03	0.03
Inch	0	0.01	0.01	0.13	0.09	0.03	0.20	0.17	0.03	0	0.00	0.01	0.15	0.11	0.03
L Fr	**0**	**0.10**	**0.04**	**0.13**	**0.16**	**0.03**	**0.65**	**0.60**	**0.03**	**0**	**0.04**	**0.03**	**0.25**	**0.30**	**0.05**

of our study on the basis of only three microsatellite loci, albeit ones selected for high levels of intra- and interpopulation polymorphism. The four major regional components of diversity in B.C. coho salmon almost certainly constitute the phylogeographic legacy of the last ice age, which ended 10–15,000 years ago. When the headwaters of the neighboring Columbia River system were in contact with the upper reaches of the Thompson-Fraser watershed, Columbia River coho salmon recolonized the Thompson and upper Fraser River (McPhail and Lindsey, 1986; Wehrhahn and Powell, 1987; Small et al., 1998). Coho salmon from the northern Bering Sea-Yukon River glacial refuge dispersed southward by

Table 6

Percentage of classifications of individual fish to regions for 34 populations of coho salmon from British Columbia. In this jackknife analysis the fish tested was not included in the discriminant analysis sample, which included the rest of the fish. The percentage of fish correctly classified to region is in the "correct" column and the percentage of fish from that region misclassified to other regions is read across the row. The percentage of fish from other regions misclassified to a particular region is read down the region column. *n* is the number of fish from the region.

		Region										
Region	*n*	Correct	Pallant	C. Coast	L. Fraser	Thompson	WCVI	ECVI	NCVI	Nass	Skeena	Total
Pallant	92	48.91		6.52	8.70	5.43	6.52	7.61	13.04	1.09	2.17	100
C. Coast	219	27.85	10.05		5.94	6.85	4.11	17.81	11.42	7.31	8.68	100
L. Fraser	1018	53.73	4.72	5.89		2.85	3.05	8.74	12.87	5.11	3.05	100
Thompson	798	84.96	1.13	2.51	2.63		0.25	3.26	3.01	1.00	1.25	100
WCVI	115	60.00	6.09	6.09	11.30	2.61		5.22	3.48	2.61	2.61	100
ECVI	338	44.08	5.03	10.36	13.61	2.37	5.03		10.06	6.80	2.66	100
NCVI	133	43.61	4.51	5.26	18.05	6.02	1.50	10.53		6.77	3.76	100
Nass	133	20.30	0.75	13.53	14.29	6.02	6.77	8.27	9.02		21.05	100
Skeena	412	52.67	3.40	5.58	6.55	6.07	1.94	6.80	6.31	10.68		100

sea, or traversed the shifting freshwater waterways of northern B.C., to recolonize the upper reaches of major watersheds as far south as the Nass and Skeena rivers (Lindsey and McPhail, 1986). Dispersal of coho salmon from a central B.C. coastal refuge(ia) located on the mainland or unglaciated portions of Vancouver or the Queen Charlotte Islands (or both) (Warner et al., 1982) likely established the heterogeneous mainland-coastal population group, of which lower Fraser coho salmon populations may be a distinctive offshoot.

Of the four regional components of biodiversity in B.C. coho salmon, the Thompson and upper Fraser is the most distinctive. Little introgression has apparently occurred between the lower Fraser and Thompson River coho salmon populations despite their common passage through the lower Fraser River on their return to spawning grounds for over 3,000 generations. Coho salmon populations are few and small in the Fraser River drainage above its confluence with the Thompson River, and our data show no evidence of introgression between the coho salmon of the Thompson-Fraser Rivers and the upper Skeena watersheds such as that postulated for sockeye salmon (Wood et al., 1994). However, our sampling of the Skeena watershed is limited to date, and the current analysis (in which larger, relatively infrequent, alleles have been binned) has limited power for the detection of historical gene exchange through an analysis of rare alleles.

The Skeena River watershed has been identified as the southern limit for freshwater fish and sockeye salmon that dispersed from a northern glacial refuge (Lindsey and McPhail, 1986; Wood et al., 1994; Bickham et al., 1995). Thus, it seems likely that the coho salmon populations of the upper Skeena and Nass watersheds are derived from Beringia. The genetic intermediacy of lower Skeena and Nass populations between upper Skeena-Nass and neighboring coastal populations suggests a hybrid nature for the lower river populations. The extent to which the composite nature of these populations reflects historical or current gene flow (or both) between the two founding groups, and the adaptive consequences of such introgression, has yet to be determined.

The coho populations of the lower Fraser drainage basin formed a cohesive genetic group in the NJ analysis of genetic distance in this study. This was in sharp contrast to the heterogeneity observed among other coastal mainland and island populations likely derived from one or more coastal refugia. The heterogeneity of central coast populations may reflect the existence of several coastal refugia, introgression from northern coho populations originating from Beringia that have yet to be well characterized, or simply founder effects in the establishment of individual coastal populations from a single refuge, as postulated for sockeye salmon (Wood et al., 1994). If the heterogeneity does result from an admixture of several founding groups among coastal coho populations, the lower Fraser River populations may better represent the original genetic profile of fish from a single, possibly southern, coastal refuge. Interestingly, Vancouver Island coho salmon were more frequently misclassified as lower Fraser than as central coast fish in the mixed-stock fishery simulations of our study, in spite of their apparently greater genetic similarity to central coast populations. If the

lower Fraser River populations are characteristic of coho salmon derived from a refuge located on, or to the south of, Vancouver Island, Puget Sound coho salmon populations might be expected to be of similar origin. This is consistent with the inclusion, based primarily on genetic data, of lower Fraser and southeastern Vancouver Island coho salmon populations in a Puget Sound and Strait of Georgia ESU (Weitkamp et al., 1995). Further sampling of Vancouver Island populations will be necessary to define the boundaries of the historical groups of coho salmon that likely converge there.

The geographic basis for population structure of coho salmon revealed in this study is remarkably similar to that described for sockeye salmon based on allozyme and mtDNA data (Wood et al., 1994; Bickham et al., 1995). A genetic discontinuity between chinook salmon originating from the Columbian and Beringial glacial refugia (Gharrett et al., 1987; Cronin et al., 1993) also lies in British Columbia, and dispersal from a coastal refuge(ia) can be traced in the microsatellite data for chinook salmon as well (Beacham, unpubl. data). Thus, the phylogeographic reconstruction of postglacial dispersal based on freshwater fish distributions in British Columbia (McPhail and Lindsey, 1970, 1986; Lindsey and McPhail, 1986) has proven to be taxonomically robust and also provides the foundation for the genetic architecture of anadromous Pacific salmon species.

The mixed-stock fishery analyses demonstrated the utility of microsatellite DNA variation for coho salmon stock identification. We obtained accurate and precise estimates both of population contributions in mixed-stock samples from a single drainage and of population and regional contributions in mixed-stock samples drawn from several regions. An important feature of the microsatellite data set is the strong regional structuring of the observed genetic variation, which means that contributions from populations present in a mixture sample, but not in the baseline, will be identified correctly to region. Identifying individual fish to correct populations is more difficult than estimating percentage contributions to a stock mixture, because only characteristics of individual fish are used in the classification. In general, the microsatellite loci of this study provided a similar level of accuracy in the classification of individual coho salmon to population and region as did minisatellite DNA markers (Beacham et al., 1996). Within the Fraser River drainage, identification of individual fish was more accurate with microsatellite data (correct identification of 54% of lower Fraser and 85% of upper Fraser Rive coho salmon) than with minisatellite data (correct identification of 30% and 60% of the respective groups). The identification of individual fish is an important enforcement tool, and may improve as more microsatellite loci are added to the database.

The results of this study are consistent with a depiction of population structure in coho salmon as distinct phylogenetic lines composed of geographically based metapopulations (McPhail, 1997). The more consistent regional grouping of coho salmon populations than of sockeye salmon (Wood et al., 1994) may reflect greater, or more recent, gene flow among geographically proximate coho salmon populations than among similar sockeye populations, or may reflect differences between allozyme- and microsatellite-based data sets. Moreover, the increasing power of genetic methods applied to coho salmon data, as demonstrated in this and other (Weitkamp et al., 1995; Beacham et al., 1996; Van Doornik et al., 1996; Miller et al., 1996; Miller and Withler, 1997; Small et al., 1998) studies, enable us not only to delineate regional (metapopulation) structure in coho salmon but also to identify the regional contributions of coho from different metapopulations in mixed-stock fishery harvests. Thus, the challenge for metapopulation-based coho salmon management may lie not so much in the delineation of metapopulation structure (McPhail, 1997) as in the evaluation of the biological and social costs associated with the loss, even if only temporary in historical terms, of the less productive components of metapopulation structure during periods of overall low abundance.

Additional aspects of metapopulation theory, as applied to Pacific salmonids, need to be addressed before this model of population structure will support practical management decisions. Managers need to know, at any given point in history, how the adaptive genetic diversity of a metapopulation is likely to be distributed among its subpopulations, and how many subpopulations can be lost before evolutionary potential is compromised. This depends on, among other things, which model of metapopulation structure is adopted. Are salmonid metapopulations of the "source-sink" variety in which gene flow is basically unidirectional from large source subpopulations to ephemeral sink subpopulations (Pulliam, 1988; Pulliam and Danielson 1991)? Or are salmonid metapopulations of the "balanced exchange" type, in which gene flow is bidirectional and migration rates are inversely proportional to subpopulation size (McPeek and Holt, 1992; Doncaster et al., 1997)? Current models of metapopulation structure have been more extensively investigated with respect to population dynamics (extinctions and recolonizations among subpopulations) than with respect to population and evolutionary genetics (the spatial and tem-

poral distribution of genetic diversity among subpopulations). The finding in this, and other molecular genetic studies on coho salmon (Beacham et al., 1996; Miller et al., 1996), of temporally stable allele frequency differences at neutral loci among local "stocks" (subpopulations in the metapopulation model) may indicate that there is very little effective gene flow among subpopulations (and few recolonization events in vacant habitat) on time scales of relevance to managers.

In summary, we have demonstrated that variation at microsatellite loci can be used both to define the regional and local components of coho salmon population structure in British Columbia and to identify these elements in stock composition estimation for mixed-stock fishery analysis. Molecular genetic technology will enable delineation of metapopulations or ESUs (or both) in the coho salmon of British Columbia, but management tools based on these concepts are lacking.

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