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Population structure of lake-type and river-type sockeye salmon in transboundary rivers of northern British Columbia

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The population structure of 'lake-type' and 'river-type' sockeye salmon *Oncorhynchus nerka*, primarily in transboundary rivers in northern British Columbia, was examined with a survey of microsatellite variation. Variation at 14 microsatellite loci was surveyed from *c*. 3000 lake-type and 3200 river-type sockeye salmon from 47 populations in six river drainages in British Columbia. The mean F_{ST} for the 14 microsatellite loci and 47 populations was 0·068, and 0·034 over all river-type populations. River-type sockeye salmon were more genetically diverse than lake-type sockeye salmon, with expected heterozygosity of river-type sockeye salmon 0·72 and with an average 12·7 alleles observed per locus, whereas expected heterozygosity of lake-type sockeye salmon was 0·65 with and average 10·5 alleles observed per locus. River drainage of origin was a significant unit of population structure. There was clear evidence of genetic differentiation among river-type populations of sockeye salmon from different drainages over a broad geographic range in British Columbia.

Key words: genetic variation; microsatellites; population structure; sockeye salmon.

INTRODUCTION

Sockeye salmon *Oncorhynchus nerka* (Walbaum) can display considerable variation in life history. The 'lake-type' form typically spawns in lakes, or in tributaries associated with lakes, its offspring rear in these nursery lakes for at least 1 year before migrating to the ocean (Burgner, 1991), and it is generally the most widespread and abundant life-history type. Where lake-rearing habitat is inaccessible or unavailable, such as in some rivers in northern British Columbia, however, sockeye salmon spawn in tributaries or mainstem side channels, and the juveniles rear for several months ('sea-type') or at least 1 year ('river-type') in the river environment before migrating to the ocean (Wood *et al*., 1987; Wood, 1995). Sea-type and river-type sockeye salmon are similar in that the juveniles both rear in river habitats prior to smolt migration to the ocean, but sea-type juveniles do not spend a winter in fresh water, and thus lack a freshwater annulus.

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Genetic relationships among the life-history forms of sockeye salmon has been an area of considerable interest. For lake-type sockeye salmon, analysis of variation at allozymes indicated that there is considerable differentiation among sockeye salmon spawning in different lake systems, and genetic differentiation among sockeye populations in different lakes is a key level of genetic differentiation. Within a major river drainage, there can be significant differentiation among sockeye salmon populations in the different lakes (Wood *et al.*, 1994; Wood, 1995). Although there is strong differentiation among sockeye salmon populations in different lakes, and to some degree among river drainages, regional structuring of the populations is less apparent, as the nearest geographic populations are not necessarily the most similar genetically (Varnavskaya *et al.*, 1994; Wood *et al.*, 1994; Wood, 1995; Winans *et al.*, 1996). Although lake-type sockeye salmon populations from different lakes in a river drainage display significant genetic differentiation at allozyme loci, little differentiation has been observed among sea-type or river-type (hereafter referred to as riverine sockeye salmon) sockeye salmon populations within a river drainage (Wood *et al.*, 1987). Indeed, no differentiation was observed between riverine sockeye salmon in the Stikine and Taku Rivers in northern British Columbia, with the river mouths separated by 220 km (Wood, 1995). More surprisingly, little differentiation at allozyme loci was observed for riverine sockeye salmon populations across a very broad geographic area ranging from south-east Alaska to Puget Sound, Washington, a distance of *c.* 2000 km (Gustafson & Winans, 1999).

The patterns of genetic differentiation as determined from allozymes showed distinct differences among lake-type and riverine sockeye salmon populations. Differentiation among lake-type populations has been attributed to the strong homing fidelity to their natal streams or lakes, whereas lack of differentiation among riverine populations has been interpreted as reflecting high rates of gene flow among populations (Wood, 1995; Gustafson & Winans, 1999). The apparent high rate of gene flow among riverine populations led Wood (1995) to suggest that riverine sockeye are a colonizing form of the species, able to colonize and adapt to new environments, whereas the lake-type form is more genetically distinct, adapted to specific environments, and in some sense an evolutionary dead end if the environment changes.

Surveys of allozyme variation have been useful in describing population structure of sockeye salmon, but surveys of DNA-level variation such as at microsatellite loci (Beacham *et al.*, 2002) may provide levels of genetic differentiation not recognized in allozyme surveys. Concordance of genetic differentiation has been reported in sockeye salmon for allozyme, microsatellite and mitochondrial DNA loci (Allendorf & Seeb, 2000), so if this is correct and based upon the results of previous allozyme surveys, then little differentiation should be observed in riverine sockeye salmon populations from throughout British Columbia. The present survey of microsatellites in British Columbia sockeye salmon has provided an opportunity to evaluate once again differentiation between lake-type and riverine populations with new classes of genetic markers.

In northern British Columbia, lake-type and riverine life-history forms of sockeye salmon are found in three major transboundary river drainages, the Alsek River (Pahlke & Riffe, 1988), Taku River (Eiler *et al.*, 1992) and the Stikine River (Wood *et al.*, 1987), and the riverine form can constitute a

substantial portion of the total sockeye salmon return to the drainage (Eiler *et al.*, 1992). The riverine form is also found in the Nass River in northern British Columbia (Rutherford *et al.*, 1994), as well as the Skeena River, but is relatively less abundant than in the three transboundary rivers. The riverine form is also found in a single population (Harrison River) (Gilbert, 1918) in the Fraser River in southern British Columbia.

The objective of the present study was to evaluate microsatellite genetic differentiation between lake-type and riverine populations within the same river drainage, among riverine populations in the same drainage, and among riverine populations in different drainages in British Columbia. In particularly it was important to confirm the finding from allozyme surveys that little genetic differentiation would be observed among riverine populations in British Columbia.

MATERIALS AND METHODS

COLLECTION OF DNA SAMPLES AND LABORATORY ANALYSIS

Tissue samples were collected from adult sockeye salmon in the Alsek, Taku, Stikine, Nass, Skeena and Fraser Rivers in British Columbia (Fig. 1 and Table I) and DNA extracted from the samples as described by Withler *et al.* (2000). PCR products at 14 microsatellite loci: *Ots2*, *Ots3* (Banks *et al.*, 1999), *Ots100*, *Ots103, Ots107* and *Ots108* (Beacham *et al.*, 1998; Nelson & Beacham, 1999), *Oki1a, Oki1b, Oki6*, *Oki10, Oki16* and *Oki29* (Smith *et al.*, 1998), *One8* (Scribner *et al.*, 1996) and *Omy77* (Morris *et al.*, 1996) were size-fractionated on denaturing polyacrylamide gels and allele sizes determined with the ABI 377 automated DNA sequencer. Allele sizes were determined with Genescan 3.1 and Genotyper 2.5 software (PE Biosystems, Foster City, CA, U.S.A.).

DATA ANALYSIS

Each population at each locus was tested for departure from Hardy–Weinberg equilibrium (HWE) using genetic data analysis (GDA) (Lewis & Zaykin, 2001). Linkage disequilibrium between loci in each population was also evaluated using GDA. With 14 loci, there were 91 different two-locus combinations to evaluate. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice, 1989). All annual samples available for a location were combined to estimate population allele frequencies, as was recommended by Waples (1990). F_{ST} estimates for each locus were calculated with GDA. Cavalli-Sforza & Edwards (1967) chord distance (CSE) was used to estimate distances among populations. An unrooted consensus neighbour-joining tree based upon 500 replicate trees was generated with the CONSENSE programme from PHYLIP (Felsenstein, 1993). Computation of the number of alleles observed per locus was carried out with FSTAT (Goudet, 1995). Estimation of variance components of riverine population differences within and among drainages was determined with GDA. Allele frequencies for all location samples surveyed in this study are available at http://www.pac.dfo-mpo.gc.ca/sci/aqua/bgsid_e.htm.

RESULTS

VARIATION WITHIN POPULATIONS

All loci surveyed were polymorphic in all populations sampled. The number of observed alleles at each locus ranged from 7 to 79, with lower heterozygosity

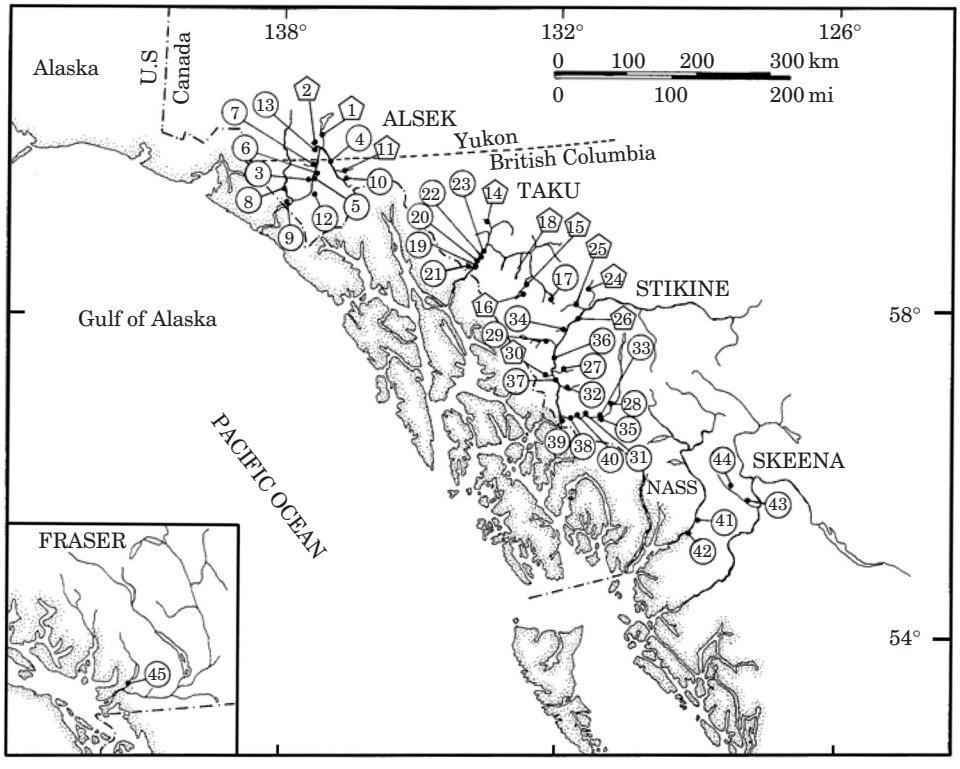

FIG. 1. Locations of sockeye salmon populations (○, a riverine and ⬠ a lake-type population) in the Alsek, Taku, Stikine, Nass, Skeena and Fraser Rivers. Numbers and locations are indicated in Table I.

observed at those loci with 15 or fewer alleles (*Oki1a, Oki1b* and *Ots107*) (Table II). Heterozygosity varied both among loci and among the populations surveyed. In the Stikine River drainage, riverine populations were more heterozygous than were lake-rearing populations, and expected heterozygosity of riverine populations ranged from 0·76 to 0·78, whereas that of lake-rearing populations ranged from 0·62 to 0·70. In the Taku River drainage, riverine populations were also more heterozygous (range 0·76–0·77) than were lake-rearing populations (0·55–0·71). In the Alsek River drainage, however, there was no difference between riverine populations (0·69–0·74) and lake-rearing populations (0·70–0·72). Expected heterozygosities of riverine populations were 0·72–0·74 in the Nass River, 0·65–0·69 in the Skeena River and 0·71 in the Fraser River. Although riverine populations in the Stikine and Taku Rivers were more heterozygous than lake-rearing populations in each drainage, heterozygosities of riverine populations in these rivers were higher than heterozygosities expected in riverine populations in other major river drainages. Over all populations surveyed, expected heterozygosity of riverine populations was 0·72, and that of lake-type populations was 0·65.

Riverine populations were more genetically diverse than were lake-type populations. Riverine sockeye salmon displayed greater numbers of alleles per locus than did lake-type sockeye salmon for 12 of the 14 loci surveyed, with equal

TABLE I. Population, life-history type, sample collection years, number of fish sampled per year and total number of fish sampled for Alsek, Taku, Stikine, Nass, Skeena and Fraser River sockeye salmon populations

Population	Type	Years	Number	Total
Alsek River				
(1) Klukshu River-mixed	L	1992, 2000, 2001	77, 238, 30	345
-early	L	2000, 2001, 2002	85, 95, 48	228
-late	L	2000, 2001, 2002	167, 95, 49	311
(2) Neskataheen	L	2000, 2001, 2002	346, 206, 40	592
(3) Lower Tatshenshini	R	2000, 2001	14, 24	38
(4) Upper Tatshenshini	R	2001, 2002	27, 126	153
(5) Kudwat Creek	R	2001	83	83
(6) Detour Creek	R	2001	22	22
(7) Stinky Creek	R	2001	64	64
(8) Mainstem Alsek River[a]	R	2001	32	32
(9) Mainstem Alsek River[b]	R	2001	27	27
(10) Stanley Creek	R	2001	10	10
(11) Blanchard River	L	2001	23	23
(12) O'Connor Creek	R	2001	22	22
(13) Kane Creek	R	2001	26	26
Taku River				
(14) Kuthai	L	1986, 1987	75, 40	115
(15) Little Tatsamenie	L	1985, 1987, 1993	80, 70, 49	199
(16) Big Tatsamenie	L	1992, 1993	100, 51	151
(17) Hackett	R	1985, 1987	61, 30	91
(18) Little Trapper	L	1992	70	70
(19) Tuskwa	R	2000	134	134
(20) King Salmon	R	2000	12	12
(21) Tulsequah	R	2000	43	43
(22) Shustahini	R	2000	13	13
(23) Takwahoni	R	2000	31	31
Stikine River				
(24) Tuya River	L	1996	46	46
(25) Tahltan	L	1987, 1996, 2002	21, 405, 48	474
(26) Upper Stikine mixed	L	1996	368	368
(27) Scud River	R	1985, 1987, 2000, 2001	60, 81, 49, 186	376
(28) Iskut River	R	1985, 2002	50, 37	87
(29) Chutine River	R	1985, 2000, 2001, 2002	50, 17, 200, 104	371
(30) Christina Lake	L	1984	51	51
(31) Verrett River	R	1986, 2000, 2001, 2002	116, 145, 40, 26	327
(32) Porcupine River	R	2000, 2001	20, 50	70
(33) Bugleg Creek	R	2001	42	42
(34) Shakes Creek	R	2001, 2002	44, 6	50
(35) Bronson Slough	R	2001	26	26
(36) Devil's Elbow	R	2001	58	58
(37) Mainstem Stikine River	R	2001	144	144
(38) Craig River	R	2001	39	39
(39) Katete River	R	2001	25	25
(40) Twin River	R	2002	23	23

TABLE I. Continued

Population	Type	Years	Number	Total
Nass River				
(41) Gingit River	R	1987, 1988, 1997	73, 93, 169	335
(42) Zolzap	R	1996, 1997	36, 24	60
Skeena River				
(43) Kispiox River	R	2002	56	56
(44) Nangeese River	R	2002	33	33
Fraser River				
(45) Harrison River	R	1986, 1995, 2000	132, 50, 100	282

[a], upstream from confluence of Alsek and Tatshenshini Rivers; [b], downstream from confluence of Alsek and Tatshenshini Rivers; L, lake; R, riverine.

numbers observed at two loci (Table III). The two loci (*Oki1a* and *Ots107*) at which equal numbers of alleles were observed were among the loci with the fewest total number of observed alleles. Overall, after standardization to a sample size of 82 fish per river drainage and life-history type, 12·7 alleles were observed per locus for riverine sockeye salmon, whereas 10·5 alleles were observed for lake-type sockeye salmon.

Genotypic frequencies at each locus within sampling location generally conformed to those expected under Hardy–Weinberg equilibrium (Table II). There was no strong evidence of null or non-amplifying alleles at any locus except *Oki10*, where 11% of Hardy–Weinberg equilibrium tests were significant. At

TABLE II. Number of alleles, expected heterozygosity (H_e), observed heterozygosity (H_o), per cent significant Hardy–Weinberg equilibrium tests (HWE, $n = 47$ tests), and $F_{ST} \pm$ S.D. among 47 sockeye salmon populations for 14 microsatellite loci

Locus	Alleles	H_e	H_o	HWE	F_{ST} (riverine only)	F_{ST} (all populations)
Oki1a	7	0·49	0·48	0·0	0·0388 ± 0·0112	0·0764 ± 0·0159
Oki1b	9	0·53	0·52	0·0	0·0385 ± 0·0137	0·0424 ± 0·0089
Oki6	28	0·71	0·71	2·2	0·0454 ± 0·0157	0·0551 ± 0·0104
Oki10	79	0·93	0·84	10·6	0·0145 ± 0·0035	0·0241 ± 0·0045
Oki16	24	0·68	0·68	2·2	0·0611 ± 0·0222	0·1572 ± 0·0371
Oki29	34	0·84	0·82	4·3	0·0166 ± 0·0038	0·0299 ± 0·0055
Omy77	16	0·74	0·73	4·3	0·0333 ± 0·0091	0·0591 ± 0·0109
One8	22	0·75	0·77	4·3	0·0402 ± 0·0109	0·0865 ± 0·0183
Ots2	22	0·77	0·77	4·3	0·0354 ± 0·0103	0·0942 ± 0·0297
Ots3	21	0·57	0·57	4·3	0·0357 ± 0·0160	0·0434 ± 0·0122
Ots100	32	0·84	0·79	8·7	0·0545 ± 0·0159	0·0975 ± 0·0197
Ots103	27	0·89	0·88	6·5	0·0252 ± 0·0050	0·0704 ± 0·0119
Ots107	14	0·50	0·50	0·0	0·0135 ± 0·0039	0·0248 ± 0·0049
Ots108	26	0·86	0·83	6·5	0·0244 ± 0·0062	0·0690 ± 0·0183
All loci					0·0338 ± 0·0039	0·0678 ± 0·0095

TABLE III. Mean number of alleles observed per locus at 14 microsatellite loci for riverine (R) sockeye salmon from six river drainages and lake-type (L) sockeye salmon from three drainages standardized to a sample size of 82 fish per type and drainage

Locus	Alsek R	Taku R	Stikine R	Nass R	Skeena R	Fraser R	Alsek L	Taku L	Stikine L	Riverine	Lake
Oki1a	4·2	4·0	4·2	4·7	4·0	3·5	4·3	3·9	4·0	4·1	4·1
Oki1b	4·0	4·0	4·8	4·0	2·0	4·5	3·9	3·7	2·7	3·9	3·4
Oki6	11·7	9·3	9·9	5·2	5·9	12·4	8·8	7·7	7·7	9·1	8·1
Oki10	32·4	32·3	39·5	23·8	35·3	23·9	25·9	27·2	23·1	31·2	25·4
Oki16	12·7	11·8	14·7	11·5	6·0	7·4	11·2	9·8	5·5	10·7	8·8
Oki29	20·4	25·2	24·6	18·3	14·0	19·8	15·3	18·9	16·6	20·4	16·9
Omy77	9·7	10·3	10·9	9·0	5·9	10·6	9·9	8·0	5·8	9·4	7·9
One8	13·7	14·8	13·8	9·6	8·0	9·4	10·8	7·5	6·4	11·6	8·2
Ots2	8·8	12·7	12·7	10·0	9·0	13·7	8·1	10·5	7·1	11·2	8·6
Ots3	6·5	9·6	9·8	6·0	6·8	8·3	6·2	5·8	4·8	7·8	5·6
Ots100	16·3	21·9	21·7	16·3	12·0	16·4	13·0	14·2	11·9	17·4	13·0
Ots103	18·7	20·5	18·8	15·6	15·8	18·0	16·5	17·1	15·7	17·9	16·4
Ots107	6·2	7·4	8·2	5·1	5·0	6·1	5·6	7·0	6·3	6·3	6·3
Ots108	15·9	18·3	18·1	15·7	12·0	17·7	13·6	15·1	12·2	16·3	13·6
Mean	12·9	14·4	15·1	11·1	10·1	12·3	10·9	11·2	9·3	12·7	10·5

this locus, lower heterozygosities were observed than were expected. A comparison of linkage disequilibrium in all annual baseline samples in all populations indicated that the largest number of significant cases was observed between *Ots108* and *Oki10* (4·5%), followed by *Oki10* and *Oki29* (3·7%). There was also no evidence of any significant linkage between any of the loci surveyed, and these loci were considered to be unlinked.

POPULATION STRUCTURE

Genetic differentiation among the 47 sockeye salmon populations sampled in the study was observed. The overall F_{ST} for the 14 microsatellite loci surveyed was 0·068, with individual loci values ranging from 0·024 at *Oki10* to 0·157 at *Oki16* (Table II). The 47 populations included in the analysis included riverine and lake-rearing life-history types. Genetic differentiation among lake populations, however, is typically observed, and so only differentiation among riverine populations was evaluated. There was still significant differentiation among populations, with an overall F_{ST} of 0·034, and with a range of values from 0·015 to 0·061 at individual loci. Differentiation among populations was reduced when lake-rearing populations were excluded from the analysis, but there was still significant differentiation observed among river populations.

River drainage structuring of population samples was observed in the study. For example, all populations from the Alsek River drainage clustered together 98% of the time, and these populations included by riverine and lake-rearing life-history types (Fig. 2). Similarly, the two Nass River population samples clustered together 100% of the time, as did the two populations in the Kispiox River, a tributary of the Skeena River. Populations in the Stikine and Taku

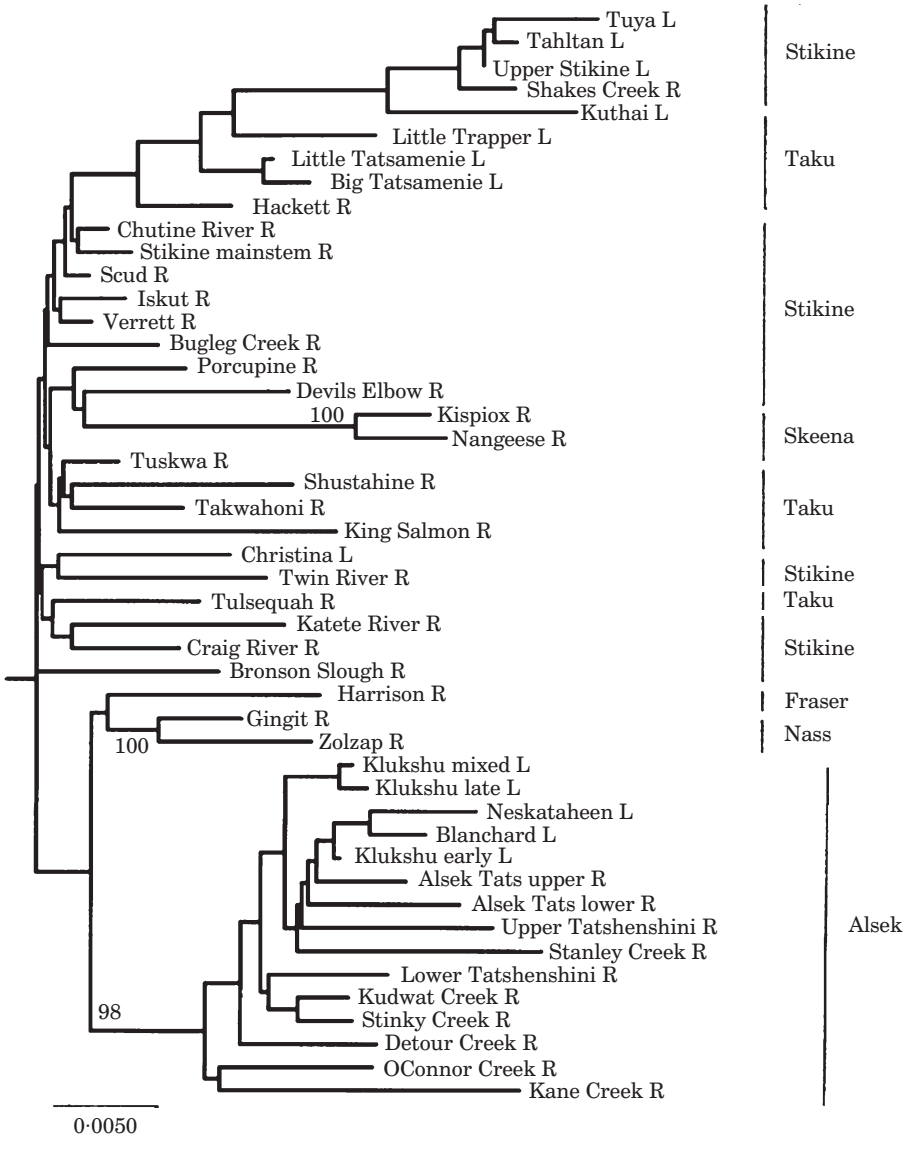

FIG. 2. Neighbour-joining dendrogram of Cavalli-Sforza & Edwards (1967) chord distance for annual samples from 47 populations of sockeye salmon surveyed at 14 microsatellite loci. Bootstrap values at the tree nodes indicate the percentage of 500 trees where samples from populations beyond the node clustered together. The life-history type (L, lake; R, riverine) is indicated after each population.

Rivers did not form distinct river clusters, but there was still some level of clustering of populations within drainages (Fig. 2). In the Stikine River drainage, the riverine Shakes Creek population clustered closely with upriver (primarily Tahltan Lake origin) samples. The Shakes Creek population was the most upstream of all riverine populations, and straying of spawners from Tahltan Lake into Shakes Creek has been observed (P. Etherton, pers. comm.), probably accounting for the genetic similarity.

DISTRIBUTION OF GENETIC VARIATION

Gene diversity analysis of the 14 loci surveyed was used to evaluate the distribution of genetic variance among populations within river drainages, as well as among river drainages. Within the Alsek River drainage, genetic differentiation was observed between riverine and lake-rearing life-history types (F-test, d.f. = 1 and 13, $0{\cdot}05 < P < 0{\cdot}10$), and among populations within life-history type (F-test, d.f. = 13 and 1961, $P < 0{\cdot}01$). In the Taku River drainage, genetic differentiation was observed between the life-history types (F-test, d.f. = 1 and 8, $0{\cdot}05 < P < 0{\cdot}10$) and among populations within life-history type (F-test, d.f. = 8 and 848, $P < 0{\cdot}01$). In the Stikine River drainage, strong differentiation was observed between the life-history types (F-test, d.f. = 1 and 13, $P < 0{\cdot}01$, Shakes Creek population excluded as a riverine population) and among populations within life-history type (F-test, d.f. = 13 and 2527, $P < 0{\cdot}01$).

For riverine populations only, the distribution of genetic variance among populations within river drainages, as well as among river drainages was evaluated. There was no marked differentiation observed between riverine populations in the Stikine and Taku rivers (F-test, d.f. = 1 and 15, $P > 0{\cdot}10$), but a clear differentiation between riverine populations in the Stikine and Alsek Rivers (F-test, d.f. = 1 and 20, $P < 0{\cdot}01$). Similarly, riverine populations in the Taku and Alsek Rivers were well differentiated (F-test, d.f. = 1 and 14, $P < 0{\cdot}01$). For all riverine populations sampled in British Columbia, the amount of variation contained within populations ranged from 93·98% (*Oki6*) to 98·33% (*Ots107*), with the average for the microsatellite loci 96% (Table IV). Variation among populations within river drainages accounted for an average 1·20% of the observed variation, and 2·60% of the variation observed was attributed to differentiation among river drainages. Significant differentiation was observed among river drainages in British Columbia (F-test, d.f. = 5 and 41, $P < 0{\cdot}01$), and this was consistent at all microsatellite loci (Table IV). Unlike allozyme loci, there was clear evidence of genetic differentiation among river populations of sockeye salmon over a broad geographic range in British Columbia.

DISCUSSION

The number of fish analysed in each population was quite variable, ranging from *c.* 10 to 600 individuals per population. Many of the populations were located in quite remote areas, and the sampling requirements proved particularly challenging in some locations. Although sample sizes were small in some cases, are the genetic relationships among the sampled populations valid? In an evaluation of genetic distance measures, Kalinowski (2002) suggested that equivalent results can be achieved by examining either a few loci with many alleles or many loci with a few alleles, such that the total number of alleles was thought to be a good indicator of precise estimates of genetic distance. Clearly there will be a fair degree of uncertainity in allele frequencies for population sample sizes of <30 fish (60 alleles), particularly for loci with larger numbers of alleles, but will this level of uncertainity obscure genetic relationships, given that the survey included 14 loci with 361 observed alleles? In the Alsek River drainage, sample sizes were <40 fish for eight of the 13 populations, yet

TABLE IV. Hierarchical gene-diversity analysis (relative diversity) of 34 populations of riverine sockeye salmon from five river drainages in northern British Columbia for 14 microsatellite loci. River drainages and populations within drainages are outlined in Table I. Only populations considered to have a riverine life history were included in the analysis. The Fraser River was not included in the analysis, as it was represented by only a single population

Locus	Within populations	Among populations within drainages	Among drainages
Oki1a	0·9487	0·0056**	0·0457**
Oki1b	0·9447	0·0080**	0·0473**
Oki6	0·9398	0·0290**	0·0312**
Oki10	0·9820	0·0093**	0·0087**
Oki16	0·9454	0·0144**	0·0402**
Oki29	0·9826	0·0079**	0·0095**
Omy77	0·9530	0·0157**	0·0313**
One8	0·9534	0·0148**	0·0318**
Ots2	0·9498	0·0239**	0·0263**
Ots3	0·9738	0·0154**	0·0108**
Ots100	0·9410	0·0138**	0·0452**
Ots103	0·9685	0·0121**	0·0194**
Ots107	0·9833	0·0110**	0·0057*
Ots108	0·9697	0·0131**	0·0172**
All	0·9600	0·0140**	0·0260**

*, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$.

drainage populations clustered together 98% of the time for 500 replicate dendrograms. If sample sizes of <40 fish were not sufficient to detect genetic differentiation between Alsek River populations and those in other drainages, it is unlikely that such solid support for the distinctiveness of Alsek River populations would have been observed. For the other four drainages in which at least two populations had been sampled, drainage populations clustered together 100% of the time in two of the four drainages (Skeena and Nass Rivers), but larger sample sizes were available for those populations. Although in some cases population samples sizes were quite small, they were probably satisfactory to detect differentiation if it existed.

Riverine populations were surveyed from six river drainages and genetic differentiation was observed among four of the six drainages. No significant differentiation was observed between riverine populations in the Taku and Stikine River drainages, but associations among the populations in the two drainages in the dendrogram were not completely random. There was some clustering of populations within drainages. It is unlikely that the number of fish sampled in each population was not sufficient to detect significant drainage differentiation if it were present. Riverine sockeye salmon in the Taku and Stikine Rivers have been previously reported as not genetically differentiated at allozyme loci (Wood, 1995), similar to the results of the present study. The most likely explanation for the lack of distinct differentiation between riverine

populations of the Taku and Stikine Rivers is gene flow between populations in the two drainages.

Nonconformance of genotypic frequencies to those expected under HWE was most apparent at *Oki10*, with *c*. 11% of tests significant. Genotypic frequencies observed in sockeye salmon in more southern populations at *Oki10* have conformed to those expected under HWE (Beacham *et al*., 2002), so that lower observed heterozygosities than expected under HWE reflected a regional characteristic of sockeye salmon populations, rather than a systemic characteristic of the locus.

For lake-type sockeye salmon, previous surveys of allozyme variation had suggested that lake of origin was a key determinate of population structure, and the general pattern of population differentiation was essentially that of a mosaic, with sockeye salmon in nearby lakes not necessarily genetically similar (Wood, 1995; Winans *et al*., 1996; Gustafson & Winans, 1999). Surveys of microsatellite variation have indicated that in Alsek River lake-type populations, sockeye salmon from Neskataheen Lake and Klukshu River were more similar to each other than to lake-type populations in other drainages. Similarly, lake-type populations from the Taku River (Kuthai, Little Tatsamenie, Big Tatsamenie and Little Trapper) were similar and distinct from those in the Alsek and Stikine Rivers. For microsatellites, there was more similarity among lake-type populations within a drainage compared with populations in other major river drainages.

Although riverine populations have been reported as lacking differentiation at allozyme loci on a broader regional basis (Gustafson & Winans, 1999), clear differentiation at microsatellite loci was observed in the present study, with the more northern Alsek River riverine populations well differentiated from those in the Taku and Stikine Rivers. Riverine populations further south in the Nass and Skeena Rivers were also differentiated from those in the Taku and Stikine Rivers, as well as from populations in the Alsek River. Although concordance of genetic differentiation has been reported between allozymes and microsatellites in sockeye salmon (Allendorf & Seeb, 2000), there was clearly genetic differentiation among riverine sockeye salmon populations from different major river drainages in British Columbia.

Wood (1995) has suggested that riverine sockeye salmon, largely living in close proximity to glaciers or in glacially influenced drainages, are the principal colonists of new habitat following the retreat of glaciers. Riverine sockeye salmon in newly colonized river drainages would then give rise to the lake-type form which has a high degree of homing, and presumably they are adapted to environments on a very fine geographic scale. This postulated colonizing role was consistent with the lack of genetic differentiation observed at allozyme loci, and consistent with greater gene flow among riverine populations than among lake-type populations. In the present study, riverine populations tended to have more alleles and higher heterozygosity at microsatellite loci than did lake-type populations in the same river. Higher heterozygosity of riverine populations compared with lake-type populations has also been observed at allozyme loci (Gustafson & Winans, 1999). Higher heterozygosity of riverine sockeye salmon is consistent with the concept that they may be a colonizing form, retaining genetic variation that allows them to adapt to new environments. The lack of

differentiation observed among riverine populations when surveyed at allozymes (Gustafson & Winans, 1999) compared with the differentiation observed at microsatellites is probably due to the differences in mutation rates in the two classes of loci. The mutation rate of a microsatellite locus in poikilotherms is estimated to be *c*. 10–4 per generation (Shimoda *et al*., 1999), substantially higher than that of allozymes (typically *c*. 10–8). Higher rates of mutation probably reflect the differentiation observed among riverine populations when examined at microsatellite compared with previous evaluations at allozymes.

Microsatellites provide an effective means for assessing salmonid population structure. The non-lethal requirements for sampling, the differentiation observed among populations, the ease of laboratory analysis and trends towards more automation of sample processing, and the relatively reasonable costs combine to provide a powerful tool in the assessment and management of Pacific salmon (*Oncorhynchus* spp.) and other species.

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