Intact genetic structure and high levels of genetic diversity in bottlenecked sockeye salmon (*Oncorhynchus nerka*) populations of the Fraser River, British Columbia, Canada

Ruth E. Withler, Khai D. Le, R. John Nelson, Kristina M. Miller, and Terry D. Beacham

Abstract: Analysis of six microsatellite loci in 5800 sockeye salmon (*Oncorhynchus nerka*) from 29 Fraser River populations provided little evidence of genetic bottlenecks or mass straying in upper Fraser sockeye salmon resulting from reduced abundances following 1913–1914 rockslides in the Fraser canyon and successive decades of high exploitation. Upper Fraser populations were not characterized by a paucity of rare alleles, a sensitive indicator of populations in which effective size has been recently reduced. Heterozygosity and allelic diversity did not differ consistently between lower and upper Fraser populations. Throughout the watershed, early-migrating populations had lower allelic diversity and a lower proportion of rare alleles than did late-migrating ones. Genetic differentiation between upper and lower Fraser populations and heterogeneity among lower Fraser populations supported the suggestion that Fraser sockeye salmon are descendants of at least two postglacial "races." Variation among lakes within regions was the strongest component of genetic structure, accounting for five times the variation among populations within lakes and more than two times the variation among regions. Extensive historical transplants of eggs and juveniles apparently resulted in little gene flow among regions, but three populations were reestablished or rebuilt as the result of more recent transplants.

Résumé : L'analyse des locus microsatellites chez 5800 saumons rouges (*Oncorhynchus nerka*) provenant de 29 populations du Fraser a donné peu d'indications de l'existence de goulots d'étranglement génétiques ou de vagabondage en masse parmi les saumons rouges du cours supérieur du Fraser à la suite des réductions de l'abondance causées par les éboulements survenus dans le canyon du Fraser en 1913–1914, puis par des décennies successives de forte exploitation. Les populations du cours supérieur du Fraser ne se caractérisaient pas par un appauvrissement en allèles rares, ce qui constitue un indicateur sensible des populations chez lesquelles l'effectif a été réduit depuis peu. L'hétérozygotie et la diversité allélique ne différaient pas de façon constante entre les populations du cours supérieur et du cours inférieur du Fraser. Partout dans le bassin, les populations à migration hâtive présentaient une diversité allélique et une proportion des allèles rares plus faibles que les populations à migration tardive. La différenciation génétique des populations du cours supérieur et du cours inférieur du Fraser et l'hétérogénéité des populations du cours inférieur du fleuve peuvent confirmer que les saumons rouges du Fraser sont les descendants d'au moins deux « races » post-glaciaires. La variation entre les lacs au sein des régions était la composante la plus forte de la structure génétique, et elle représentait cinq fois la variation parmi les populations au sein des lacs, et plus de deux fois la variation entre les régions. Les importantes transplantations d'oeufs et de juvéniles effectuées dans le passé semblent avoir produit peu de flux génique entre les régions, mais trois populations ont été rétablies ou reconstituées par suite de transplantations plus récentes.

[Traduit par la Rédaction]

Introduction

The extensive river and lake systems of the Fraser River drainage in British Columbia constitute one of the most important sockeye salmon (*Oncorhynchus nerka*) habitats in North America, with as many as 100 million sockeye salmon spawning within their confines in the early 1900s (Ricker 1987). The typical sockeye salmon life history is centered on a nursery lake. Adults spawn in lake inlet or outlet streams, juveniles rear in the lake for a year before undertaking an extensive marine migration, and adults return with great fidelity to spawn in their natal streams at 3–5 (predominantly 4) years of age. Fraser sockeye salmon populations display a cyclical 4-year pattern in which adult abundance is consistently much greater every fourth year (the dominant cycle year), lower in the following year, and much lower in the succeeding 2 years (Ricker 1950; Ward and Larkin 1964).

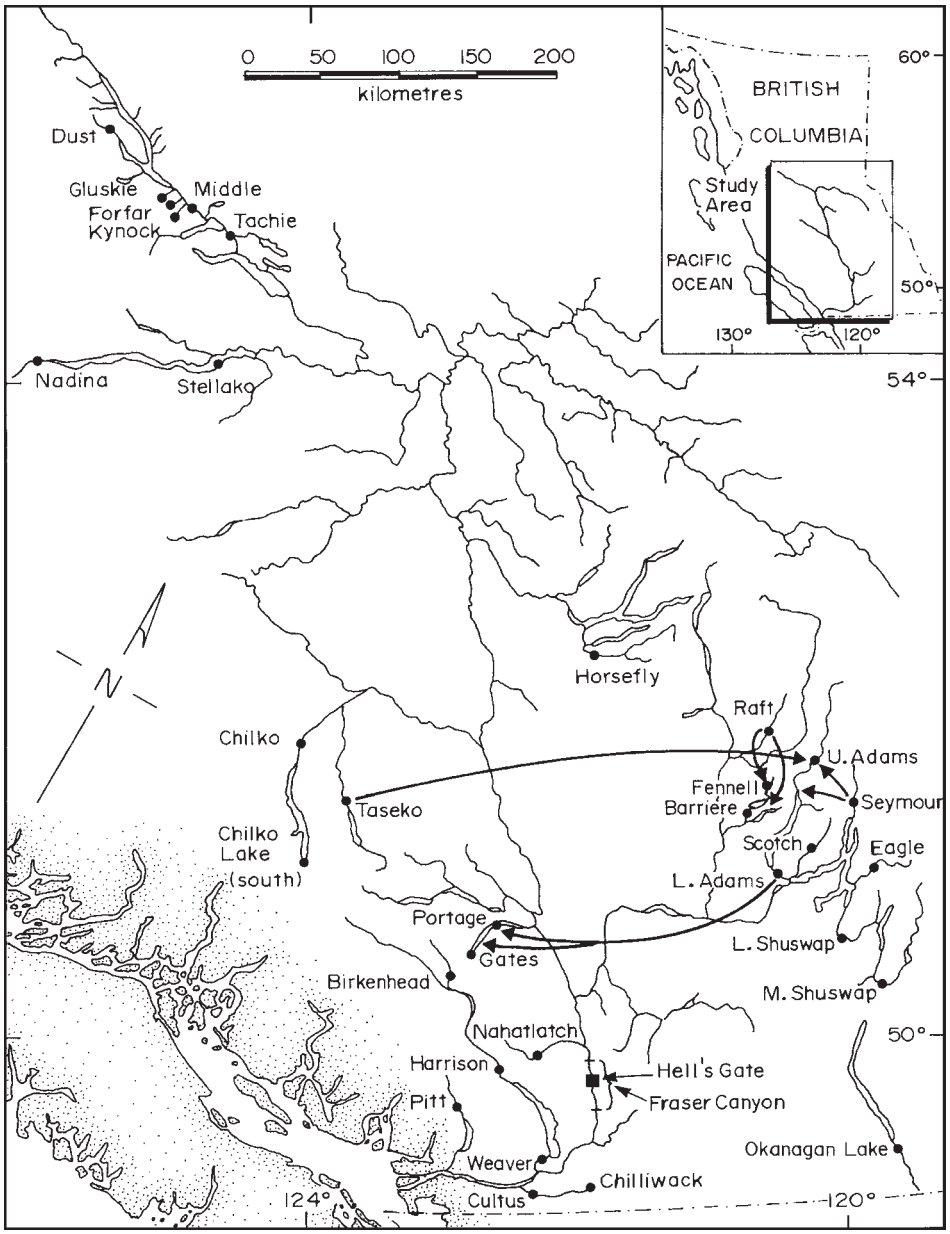
The Fraser drainage is divided into lower and upper portions by the Fraser canyon, located about 170 km upstream from the river mouth (Fig. 1). The vast upper Fraser drainage encompasses numerous tributary systems including the Thompson River, itself a major drainage. Approximately

Received August 10, 1999. Accepted July 18, 2000.
J15283

R.E. Withler,[1] K.D. Le, R.J. Nelson,[2] K.M. Miller, and T.D. Beacham. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada.

[1]Author to whom all correspondence should be addressed.
e-mail: withlerr@dfo-mpo.gc.ca
[2]Present address: Seastar Biotech Inc., Box 32056, 3749 Shelbourne Street, Victoria, BC V8P 5S2, Canada.

Fig. 1. Locations of sockeye salmon populations sampled within the Fraser River drainage. Donor and recipient populations involved in three apparently successful transplants of sockeye salmon within the upper Fraser River drainage are also shown. Transplants of Raft River sockeye salmon eggs and juveniles apparently established the extant Fennell River population. Egg and juvenile transplants from the Seymour River apparently established the extant upper Adams River population, whereas transplants from the more distant Taseko River were unsuccessful. Egg and juvenile transplants from the lower Adams River resulted in replacement or introgression of the Portage Creek population.



90 Fraser sockeye salmon populations utilizing about 24 nursery lakes have been identified (Gable and Cox-Rogers 1993). They show atypically large and consistent differences in timing of the upstream migration, presumably as a result of adaptation to the diverse spawning habitats utilized within the drainage (Burgner 1991).

Major determinants of population structure in North American sockeye salmon are three postulated races isolated during the last glacial period and the nursery lakes in which juveniles rear (Wood 1995). Sockeye salmon of the upper Fraser drainage are considered the primary representatives of the Cascadian race, isolated in the Columbia River system during the last glaciation (Wood et al. 1994; Bickham et al. 1995). The Columbia River itself now supports only a remnant of its historical sockeye salmon population (Burgner 1991). Sockeye salmon of the lower Fraser likely originated from Beringia, a refuge on the Bering land bridge, or from a smaller coastal refugium (Wood et al. 1994).

Historically, the cyclical abundance of the upper Fraser sockeye salmon populations was synchronized, with up to 100 million Fraser sockeye salmon spawning in dominant cycle years (i.e., 1905, 1909, 1913, etc.). By 1900, a large

commercial fishery was established, operating in coastal marine waters and the lower Fraser. In 1913 and 1914, abundances of sockeye salmon populations in the upper Fraser and Thompson drainages were sharply reduced as the result of rock dumping and rockslides at Hell's Gate that obstructed migration of adults through the Fraser canyon. The obstruction not only prevented the passage of most mature adults but also skewed the sex ratio and worsened the condition of fish that did reach the spawning grounds to the extent that many failed to spawn. Estimates of spawners reaching tributaries of Shuswap Lake in the Thompson drainage ranged from zero to several hundred, among which only one sixth were female (Ricker 1987). The effect of the slides was compounded by continued high levels of exploitation, and the two combined may have "reduced the upriver runs to a point dangerously close to extinction" (Ricker 1950).

Recovery of upper Fraser sockeye salmon began in the 1920s for some populations but occurred as recently as the 1980s for others. Among the first to rebuild were late-migrating populations in the Shuswap River system that benefited from end-of-the-season fishery restrictions imposed relatively quickly after the slides. Populations in waters tributary to the upper Fraser mainstem tended to migrate earlier and did not increase in abundance until much later. Rebuilding populations tended to maintain their historic migration times, even when recovery was delayed by decades, indicating that increasing abundances were based on improved survival of local fish, as opposed to mass straying and recolonization or successful transplantation. However, synchrony of the dominant cycle year in the upper Fraser drainage was lost, with some rebuilding populations developing dominance in each of the four possible cycle lines.

The effect of reduced population sizes, and of the increased fish culture activities that they engendered, on the genetic structure of sockeye salmon populations above Hell's Gate is largely unknown. An extensive transplant program underway in the Fraser drainage by 1900 was intensified after the 1913–1914 rockslides. Between 1884 and 1934, approximately 85 million sockeye salmon eggs and 395 million juveniles were transplanted within the Fraser, including transplantation between the upper and lower watershed (Aro 1979; Williams 1987). Determination that the transplants failed to increase sockeye salmon abundance led to the program closure, although some transplant efforts in the upper Fraser continued (Aro 1979).

Examination of the distributions of allele frequencies in extant populations can be used to detect historical bottlenecks, even in the absence of historical allele frequency data (Luikart et al. 1998). In this study, we surveyed 29 Fraser sockeye salmon populations and one Columbia population at six microsatellite loci and examined the data for a paucity of rare alleles that would indicate the occurrence of severe bottlenecks (i.e., effective population sizes as small as 20 individuals) during or after the 1913–1914 rockslides. We also examined upper Fraser sockeye salmon populations for evidence of low levels of heterozygosity and allelic diversity that might be attributable to small population sizes and examined the relationship between genetic and geographic distances for evidence of high levels of gene flow in rebuilding upper Fraser populations. Genetic distances between donor and recipient populations were examined for supporting evidence in three cases of putatively successful transplantation in the upper Fraser drainage.

Materials and methods

Collection of DNA samples and polymerase chain reaction (PCR)

Sockeye salmon DNA was extracted from dry scales, or previously collected frozen samples stored at –20°C, or punches of operculum tissue preserved in 95% ethanol for 29 populations in the Fraser drainage and one population (Okanagan Lake) in the Columbia drainage (Fig. 1). Approximately 5800 and 85 fish were sampled on the spawning grounds in the Fraser and Columbia drainages, respectively. Between one and five brood years were sampled from each population, with a maximum time span of sample collection for any one population of 14 years (Table 1). Microsatellite loci were amplified using the PCR conditions of Beacham et al. (1998) and included the dinucleotide repeats *Omy77* (Morris et al. 1996) and *Ots3* (Banks et al. 1999) and the compound tetranucleotide repeats *Ots100* (Nelson et al. 1998), *Ots103* (Beacham et al. 1998), and *Ots107* and *Ots108* (Nelson and Beacham 1999). PCR of *Omy77*, *Ots3*, *Ots100*, *Ots103*, *Ots107*, and *Ots108* was accomplished with annealing temperatures of 48, 50, 57, 55, 48, and 46°C, respectively. Annealing times were 30 s for *Omy77* and *Ots100* and 60 s for the other loci.

Gel electrophoresis and fragment analysis

PCR products were size fractionated on 16 × 17 cm nondenaturing polyacrylamide gels run with 20 base pair (bp) ladder DNA (Gensura Labs Inc., Del Mar, Calif.) (Nelson et al. 1998). We identified alleles using a binning procedure (Gill et al. 1990). Peaks in the allele frequency distributions were used to identify main alleles. Bin widths generally corresponded to the microsatellite repeat units and were defined so that the modal size estimate for an allele was centered in each bin. Precision of estimation of allele size was evaluated with a standard heterozygous fish run on each gel for each locus. There were two loci for which the bin width was not simply the size of the repeat unit (*Omy77* and *Ots100*). Ten alleles were defined at *Omy77* ranging from 82 to 118 bp, as were 17 alleles at *Ots3* ranging from 72 to 105 bp and 16 alleles at *Ots100* ranging from 146 to 205 bp. Twenty-three alleles were observed at *Ots103* ranging from 130 to 224 bp, as were eight alleles at *Ots107* ranging from 81 to 133 bp and 21 alleles at *Ots108* ranging from 110 to 192 bp.

Data analysis

Variation in allele frequencies among brood years within populations, genetic differentiation among populations, and departures from Hardy–Weinberg equilibrium by population were tested with GENEPOP version 3.1 (Raymond and Rousset 1995). Tests of differentiation among populations consisted of all pairwise comparisons of allele frequencies with the dememorization number set at 1000. Fifty batches were run for each test with 1000 iterations per batch. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice 1989). The Cavalli-Sforza and Edwards (1967) chord distance was used to estimate distance among populations. Values of F_{ST} (θ) for each locus were estimated with GENEPOP. Variance components for the effects of populations and brood years within populations were estimated with BIOSYS-1 (Swofford and Selander 1981). A hierarchical gene diversity analysis was conducted to assess geographic structuring of genetic variation among the five geographic regions, 23 nursery lakes, and 30 spawning populations (Table 1).

Table 1. Population, nursery lake, sample collection years, number of fish sampled per year, and total number of fish sampled for 29 populations of Fraser River sockeye salmon and one Columbia River population (Okanagan Lake).

Population	Nursery lake	Years	Number	Total
Lower Fraser				
Pitt River	Pitt	1986	145	145
Weaver Creek	Harrison	1982, 1986, 1996	83, 135, 49	267
Chilliwack River	Chilliwack	1996	59	59
Birkenhead River	Lillooet	1992, 1995, 1997	99, 136, 48	283
Harrison River	Harrison	1986, 1995	132, 27	159
Cultus Lake	Cultus	1992, 1995	61, 69	130
Mid-Fraser				
Portage Creek	Seton	1986, 1995, 1997	98, 13, 115	226
Gates Creek	Anderson	1986, 1992, 1995	91, 49, 60	200
Nahatlatch Lake	Nahatlatch	1995, 1996, 1997	6, 106, 130	242
Upper Fraser				
Nadina River	Francois	1986, 1990, 1992, 1995	39, 12, 98, 15	164
Stellako River	Stellako	1992, 1995, 1996	99, 143, 35	277
Chilko Lake (south)	Chilko	1996, 1997	97, 102	199
Chilko River	Chilko	1992, 1995, 1996, 1997	99, 60, 106, 119	384
Horsefly River	Quesnel	1986, 1993, 1996, 1997	96, 97, 94, 95	382
Middle River	Trembleur	1993, 1994, 1995, 1996, 1997	40, 11, 18, 36, 51	156
Tachie River	Stuart	1994, 1995, 1996, 1997	29, 76, 96, 56	257
Kynock Creek	Trembleur	1992, 1994, 1997	12, 74, 98	184
Forfar Creek	Trembleur	1997	148	148
Gluskie Creek	Trembleur	1997	149	149
Dust Creek	Takla	1997	105	105
Thompson				
Lower Adams	Shuswap	1982, 1990, 1995, 1996	84, 34, 103, 97	318
Upper Adams	Adams	1996	278	278
Lower Shuswap	Mara	1983, 1986, 1990, 1996	30, 36, 24, 6	96
Middle Shuswap	Mabel	1995	11	11
Eagle River	Shuswap	1986, 1990	78, 75	153
Scotch Creek	Shuswap	1994, 1995, 1996	100, 77, 112	289
Seymour River	Shuswap	1986, 1996	143, 108	251
Raft River	Kamloops	1996	101	101
Fennell Creek	North Barriere	1996	200	200
Columbia				
Okanagan Lake	Okanagan	1997	85	85

The binning process described above to identify alleles likely resulted in the occasional misclassification of alleles into adjacent bins. For this reason, and because of the large numbers of fish sampled per population (generally 100+), we included only those alleles present at a frequency of 0.01 or greater in a test to determine if rare alleles were lost in Fraser sockeye salmon due to population bottlenecks (Luikart et al. 1998). This test, based on the premise that rare alleles are lost disproportionately during bottlenecks, is generally carried out on populations represented by sample sizes of 30–50 individuals (Luikart et al. 1998), in which most alleles at frequencies <0.01 would be undetected. In the present study, the indication of a population that had lost genetic diversity due to a recent bottleneck (effective breeding size of 20 or fewer individuals) was a lower abundance of alleles at frequencies between 0.01 and 0.05 than at frequencies between 0.051 and 0.10 or some higher allele frequency interval (Luikart et al. 1998). Allelic diversity, the total number of alleles present in each population divided by 6 (the number of loci), was also calculated using alleles present at frequencies of 0.01 and greater.

Transplanted populations

We assessed the genetic similarity between each of three putatively transplanted Fraser sockeye salmon populations and the donor populations and examined the genetic variation within the transplanted populations to determine if genetic bottlenecks had occurred. All three transplants were the result of recent (since 1950) efforts involving donor and recipient populations in the upper Fraser drainage. The recipient populations examined were Portage Creek of the mid-Fraser region just upstream of the Fraser canyon, Fennell Creek in the North Thompson drainage, and upper Adams River in the South Thompson drainage (Fig. 1).

In 1950, a year in which the native Portage Creek fish were in low abundance, approximately 300 000 eyed eggs from the lower Adams River (Thompson drainage) were transplanted to Portage Creek and 193 000 lower Adams juvenile fish were released in Anderson Lake, upstream of Portage Creek (Aro 1979). The extant sockeye salmon population of Fennell Creek, a tributary to North Barriere Lake, was established after 1952 when dams in the Barriere River system were removed. Between 1956 and 1960, over three million Raft River sockeye eggs were transplanted into the Barriere River system, 490 000 of them into Fennell Creek in 1959 (Aro 1979). The upper Adams River sockeye population was exterminated by logging dams and poor adult returns during and after the 1913–1914 rockslides (Williams 1987). Sockeye salmon

eggs and juveniles were transplanted between 1949 and 1980 to the upper Adams River and Adams Lake from Taseko River (Chilko drainage), Seymour River (tributary to Shuswap Lake), and Cayenne Creek (a tributary to the Momich River, which enters Adams Lake close to the upper Adams River). The Cayenne Creek population, first observed in 1960, was itself likely established from the earlier transplants of Seymour and (or) Taseko eggs and juveniles to Adams Lake (Williams 1987).

Results

Precision of estimation of allele size

Standard deviations of the estimates of allele size for the heterozygous standard fish analyzed at each locus ranged from 0.22 to 1.27 bp and increased with allele size (Table 2). For the dinucleotide repeat *Ots3*, 100% of estimated sizes for the smaller allele of both standard fish fell within 2-bp intervals. For the larger alleles, 98% (203/207) of the estimated sizes were captured by 2-bp bins. Although variation at *Omy77* should be based on a dinucleotide repeat, the precision of estimation of allele size in standard fish did not enable consistent differentiation of alleles differing in size by 2 bp (Table 2). Accordingly, adjacent alleles were binned, resulting in classification of alleles into 4-bp bins. Estimated allele sizes for standard fish at other loci fell within 4-bp intervals for alleles between 100 and 175 bp in size, except for the *Ots103*^{175} allele, for which 98% (267/273) of the estimated sizes fell within a 4-bp bin. Estimated sizes of the *Ots100*^{186} standard fish allele were captured in a 4-bp bin for 98% (209/213) of measurements. For *Ots108*^{185}, estimated sizes fell within a 4-bp bin for 88% (156/178) of measurements and a 5-bp bin for 96% of measurements. The largest standard allele measured, *Ots103*^{212}, was captured in a 4-bp bin for 91% and in a 5-bp bin for 95% of 273 measurements. These results supported the binning procedure used, with the bin width generally set at the size of the repeat unit. The fact that alleles were occasionally misidentified supported the exclusion of alleles present at frequencies <0.01 in the examination of the abundance of rare alleles.

Genetic variation within populations

Heterozygosity

All six microsatellite loci examined were polymorphic in all populations surveyed. Mean observed heterozygosities by locus over all 30 populations were *Omy77* 0.75 (population range 0.58–1.00), *Ots*3 0.60 (0.43–0.70), *Ots10*0 0.64 (0.44–0.87), *Ots10*3 0.89 (0.50–0.94), *Ots10*7 0.41 (0.17–0.62), and *Ots10*8 0.80 (0.74–1.00). Mean heterozygosity over all six loci ranged from 0.57 for the Columbia sample and Cultus Lake in the lower Fraser drainage to 0.75 in the lower Shuswap population of the Thompson drainage (Fig. 2). There was no significant difference in mean heterozygosity over all six loci among regions ($F_{3,20}$ = 2.7, P > 0.05) or between early- and late-migrating populations ($F_{1,20}$ = 2.17, P > 0.1) in the Fraser drainage. Mean observed heterozygosity for the six lower Fraser populations was 0.67, for the three mid-Fraser populations was 0.69, for the 11 upper Fraser populations was 0.67, and for the nine Thompson populations was 0.71. The two populations with the lowest heterozygosity values were both from the Chilliwack River system of the lower Fraser drainage. One was the early-migrating Chilliwack Lake population (Fig. 2, bar 1) and the other was the late-migrating Cultus Lake population (Fig. 2, bar 3).

Table 2. Precision of estimation of allele size (bp) (SD in parentheses) for standard heterozygous fish analyzed repeatedly at each locus, with a single standard fish run once on each gel.

Locus	*N*	Allele size	Range	Allele size	Range
Ots3	156	93.0 (0.22)	92–94	74.1 (0.24)	74–75
	51	93.8 (0.54)	93–95	74.7 (0.48)	74–75
Omy77	138	115.6 (0.63)	114–117	104.1 (0.50)	103–106
	65	103.9 (0.52)	103–105	90.7 (0.54)	90–92
	39	116.6 (0.81)	115–118	105.4 (0.82)	104–107
	12	110.5 (0.67)	109–111	98.7 (0.49)	98–99
Ots107	247	117.7 (0.60)	117–119	109.8 (0.60)	109–111
	25	117.5 (0.59)	117–119	109.6 (0.58)	109–111
Ots108	178	184.6 (1.19)	183–187	112.0 (0.54)	110–113
Ots100	92	185.6 (0.95)	184–187	158.9 (0.77)	157–160
	121	185.8 (0.79)	184–189	155.9 (0.59)	154–157
	65	175.3 (0.75)	174–177	167.6 (0.68)	166–169
Ots103	273	212.4 (1.27)	209–215	174.9 (0.89)	173–177

Note: Between one and four standard fish, chosen to provide a range of allele sizes, were used for each locus; *N* is the number of gels for which allele sizes for each fish were estimated.

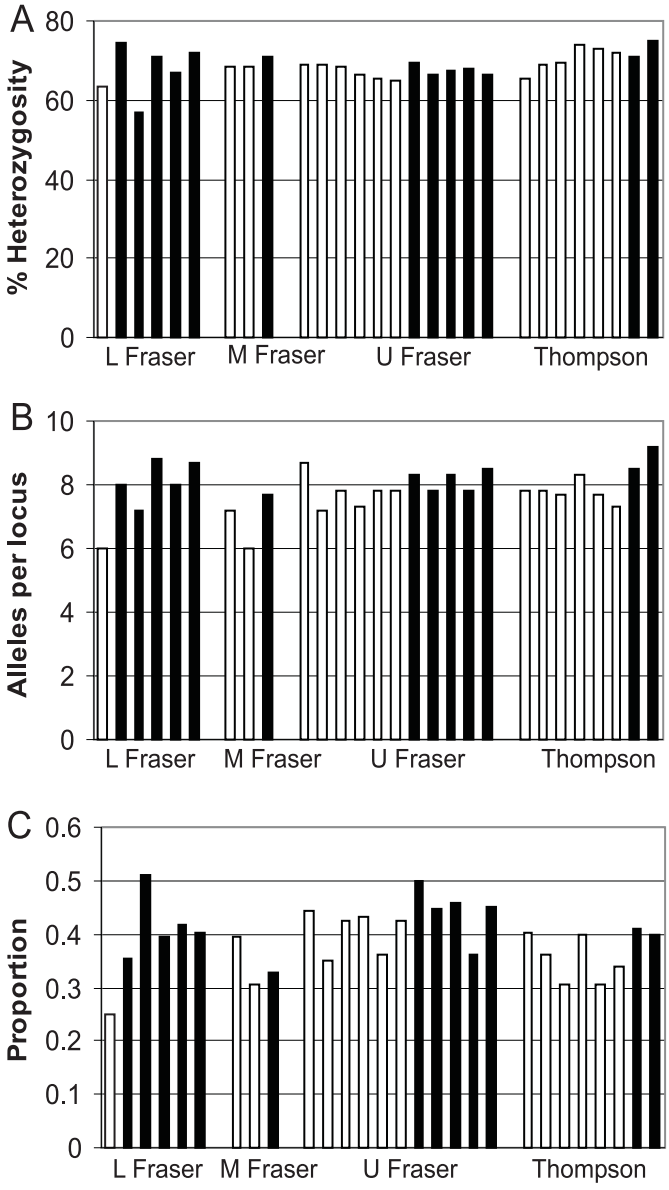
Allelic diversity and rare alleles

Allelic diversity varied significantly both among regions ($F_{3,20}$ = 6.93, P < 0.01) and between early and late populations ($F_{1,20}$ = 25.28, P < 0.01) of the Fraser drainage (Fig. 2). Among regions, the mid-Fraser populations had significantly fewer alleles per locus (6.95) than did the other three regions (7.78–8.04), but the mid-Fraser also was represented by the fewest number of populations. Early-migrating sockeye salmon populations had lower allelic diversity (7.50) than late-migrating populations (8.26) (Fig. 2). The Chilliwack Lake (lower Fraser) and Gates Creek (mid-Fraser) populations displayed the least allelic diversity, both averaging 6.0 alleles per locus.

The proportion of rare alleles (those at estimated frequencies of between 0.01 and 0.05 inclusive) within populations also differed significantly among regions ($F_{3,20}$ = 4.54, P < 0.05) and between early and late populations ($F_{1,20}$ = 6.18, P < 0.05). Upper Fraser populations had the highest proportions of rare alleles (0.44), mid-Fraser populations had the lowest proportion (0.35), and rare alleles occurred at intermediate frequencies in lower Fraser (0.40) and Thompson (0.37) populations (Figs. 2 and 3). Early populations had a lower proportion of rare alleles (0.38) than late populations (0.43), although this pattern was not evident in the mid-Fraser for which the single late population (Portage Creek) was affected by transplantation.

Only the early Chilliwack Lake population of the lower Fraser displayed a "mode shift" in allele frequencies such that alleles at intermediate frequencies (0.051–0.100) were more prevalent than rare alleles (Fig. 3). Cultus Lake, the other lower Fraser population that exhibited low heterozygosity, displayed a moderate level of allelic diversity (7.17) and the highest proportion of rare alleles (0.51) observed in the study (Figs. 2 and 3). Similarly, most other populations with low levels of heterozygosity and (or) allelic diversity had relatively high proportions of rare alleles. An exception

Fig. 2. (A) Observed heterozygosity, (B) allelic diversity, and (C) proportion of rare alleles for six microsatellite loci in sockeye salmon populations of four regions within the Fraser River drainage. Early-migrating populations are indicated by open bars and late-migrating populations by solid bars.



was Gates Creek of the mid-Fraser in which allelic diversity was 6.0 and only 31% of alleles were rare (not shown). Sockeye salmon populations of the Thompson region tended to have only a moderate level of allelic diversity and few rare alleles in spite of relatively high heterozygosity. In the early-migrating Eagle and Seymour River populations, rare alleles constituted only 30% of total alleles, and alleles at frequencies between 0.051 and 0.10 were almost as common as rare alleles (Fig. 3).

Temporal variation

For the 20 populations sampled in multiple years (Table 1), significant annual variation in allele frequencies occurred at one locus in eight populations, at two loci in five populations, and at three loci in two populations. All five populations that displayed no variation over time were late-migrating populations from the lower Fraser (Harrison River and Cultus Lake), the upper Fraser (Stellako River), and the Thompson (lower Adams and lower Shuswap rivers) regions. Samples from the lower Adams and lower Shuswap populations were those collected over the greatest time spans (14 and 13 years, respectively). The allele frequency variation observed in the remaining populations occurred at all loci except *Ots3* in both early- and late-migrating populations. Of the two populations in which significant variation was observed at three loci, one (Seymour River) was characterized by relatively few rare alleles, but the other (Nahatlatch Lake) was not. Few populations were sampled twice in the same cycle year (4 or 8 years apart), but in those that were, the allele frequency variation was as great within as between cycle years.

In spite of the observed low levels of temporal allele frequency variation, genotypic frequencies at the six loci in samples pooled by population were in Hardy–Weinberg equilibrium. A significant departure from expected genotypic frequencies was observed only at *Ots108* in Weaver Creek sockeye salmon, providing no evidence of non-amplifying alleles, inbreeding, or population admixture.

Genetic variation among populations

Allele frequencies

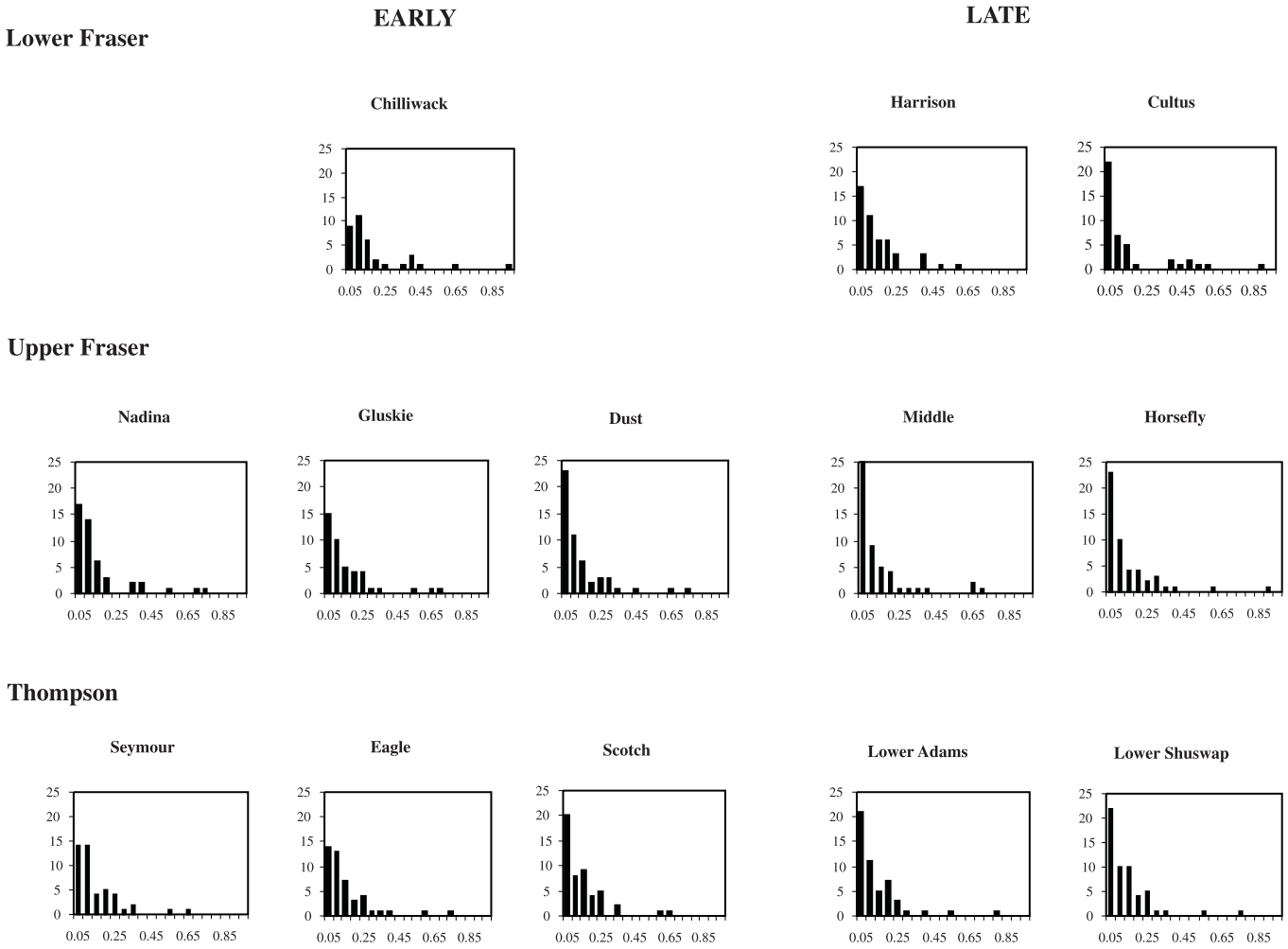
Interpopulation differentiation exceeded intrapopulation temporal variability at all loci, with the ratio of the variance components being 6.9, 51.5, 10.3, 2.8, 22.6, and 4.5 for *Omy77*, *Ots3*, *Ots100*, *Ots103*, *Ots107*, and *Ots108*, respectively. The average ratio over all loci was 7.4. For comparisons of allele frequencies among populations and regions, multiple samples from individual populations were pooled.

Considerable genetic differentiation was observed between the single Columbia sockeye salmon population, Okanagan Lake, and Fraser populations at all six loci (Figs. 4 and 5). Allele frequency differentiation among the 29 Fraser sockeye salmon populations was less than between the Columbia and Fraser drainages, but most pairwise population comparisons of allele frequencies at each locus were significant ($P < 0.0001$).

Populations utilizing the same nursery lake, especially those with similar migration times, displayed the greatest genetic similarities. For example, the population at the south end of Chilko Lake was not significantly different from that of the Chilko River, which drains from the north end of the lake, at three of the six loci surveyed. Allele frequencies in the four early Stuart populations of Trembleur Lake (Kynock, Forfar, Gluskie, and Dust creeks) differed significantly in pairwise comparisons at only at two or three loci. In the Thompson drainage, early-migrating populations using Shuswap Lake as a nursery (Eagle and Seymour rivers, Scotch Creek) had similar allele frequencies (Fig. 5).

Characterized by low allelic diversity (6.0) and a low proportion of rare alleles (0.31), Gates Creek sockeye salmon tended to possess one or more alleles at each locus in atypically high frequencies. Over 15 million sockeye salmon eggs and juveniles were transplanted from the Birkenhead River

Fig. 3. Numbers of alleles summed over six microsatellite loci by frequency class for early- and late-migrating sockeye salmon populations in three regions of the Fraser River drainage.



in the lower Fraser to Gates Creek and other sites within the Anderson–Seton drainage between 1915 and 1930 (Aro 1979), but there is little evidence that these resulted in introgression (Fig. 5). It seems likely that the low genetic diversity and unusual allele frequencies of the Gates Creek population reflect founder effects and (or) subsequent genetic drift at small population sizes.

Population structure

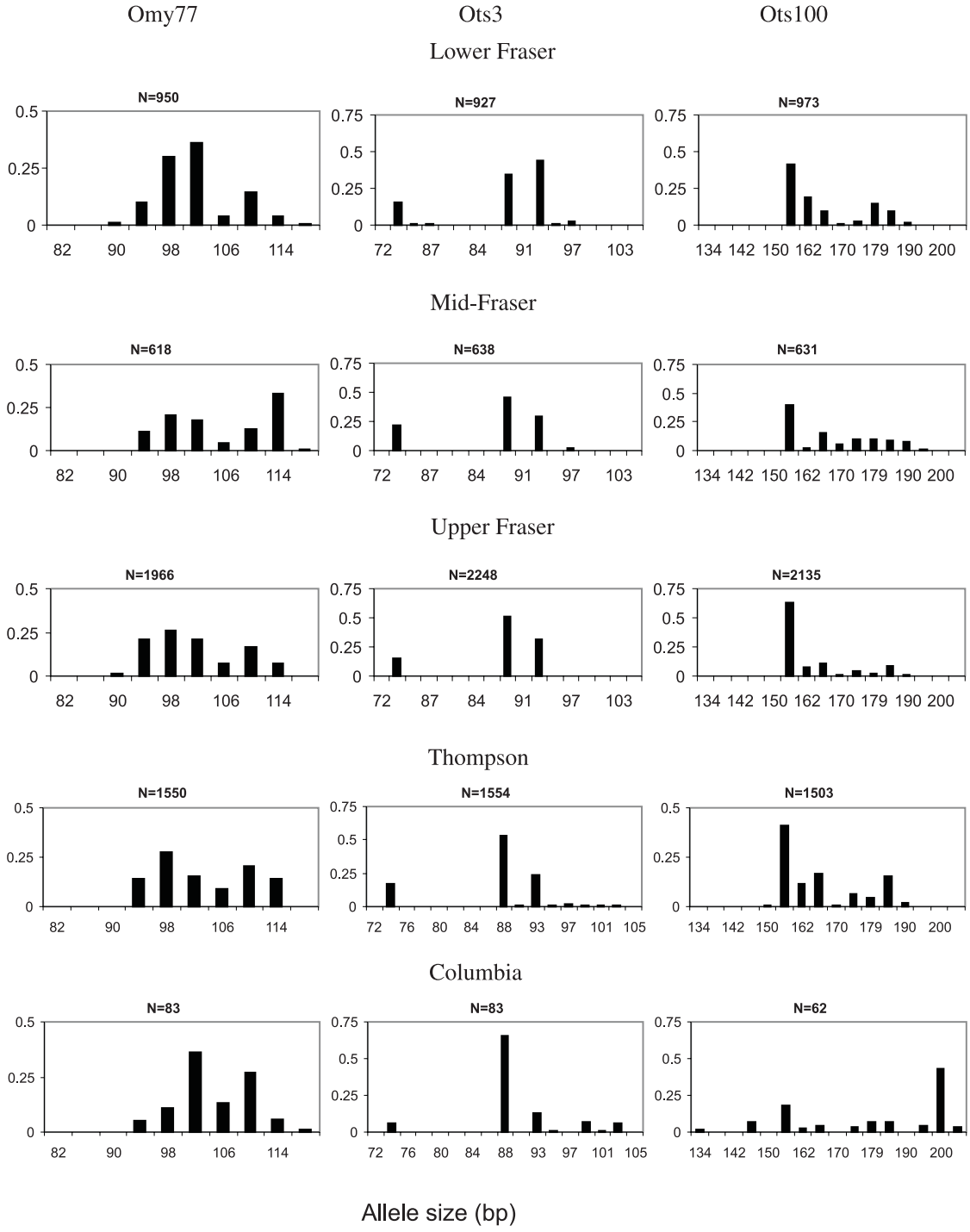
Hierarchical gene diversity analysis of sockeye salmon from the 30 spawning populations using 23 nursery lakes indicated that 94.6% of variation occurred within populations (Table 3). Variation among lakes within regions was the greatest source of the remaining variation, accounting for more than twice the variation among regions and five times the variation among populations within lakes. The greatest structuring among lakes within regions was observed at *Ots100* (5.8%) and *Ots107* (4.3%).

Greater differentiation was observed among populations within the lower Fraser and mid-Fraser regions than within either the upper Fraser or Thompson regions. The mean pairwise θ for lower Fraser populations was 0.069 (SD 0.025) and that for the mid-Fraser region was 0.084 (SD 0.045), whereas the mean pairwise θ estimate for the upper Fraser region was 0.022 (SD 0.016) and that for the Thompson region was 0.027 (SD 0.018). For the entire upper Fraser drainage (including the mid-Fraser, upper Fraser, and Thompson regions of this study), in which sockeye salmon populations are believed to be derived from Cascadia, the mean pairwise θ value was 0.042 (SD 0.029).

The larger pairwise θ estimates in the lower Fraser drainage were partially a result of the relative distinctiveness of the Cultus Lake and Chilliwack River populations. The high values for the mid-Fraser region were influenced by the fact that of only three populations sampled, one was the highly distinctive Gates Creek population and another was Portage Creek, which apparently has been altered by transplantation from the Thompson region (see below) (Fig. 5).

A degree of regional structuring of population differentiation was evident in the upper Fraser watershed. South Thompson populations tended to form a relatively distinct group, with the early-migrating populations clustering in a well-defined group 71% of the time in the 500 trees used to create the consensus tree (Fig. 5). The Stuart–Nechako drainage populations, consisting of four early Stuart, two late Stuart, and two Nechako populations (Stellako, Nadina),

Fig. 4. Regional allele frequencies of sockeye salmon at six microsatellite loci; *N* is the number of sockeye salmon sampled in each of four regions within the Fraser River drainage.



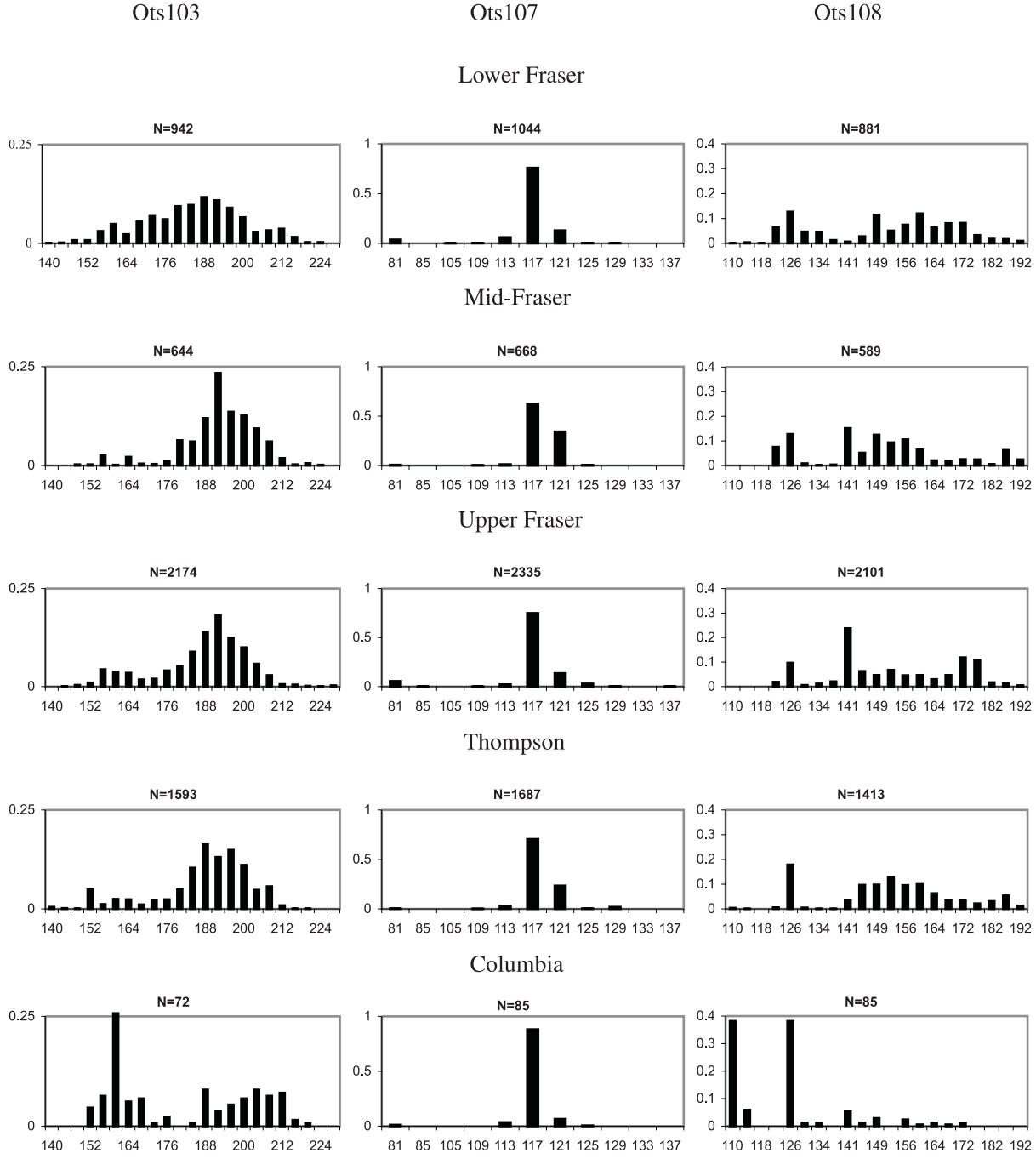
were homogeneous and distinct from the Horsefly population sampled from the Quesnel River drainage and from the two populations sampled from the Chilko River drainage.

Isolation by distance

The importance of geographic separation in accounting for genetic differentiation among populations was evaluated by examining the correlation between pairwise linearized θ values and the pairwise distance (kilometres) between populations determined as the most direct river migration route. In addition to the global comparison encompassing all 29 Fraser populations, separate comparisons were made between all populations upstream from the Fraser canyon (upper Fraser including the mid-Fraser and Thompson populations), between all populations downstream from the Fraser canyon (lower Fraser), and between all pairs of upper and lower Fraser populations.

For all populations, the correlation between θ and geographic distance was significant (r = 0.19, N = 406, P < 0.01), but this was largely a result of comparisons between

Fig. 4 (*concluded*).



upper Fraser populations (Fig. 6). For upper Fraser drainage populations only, the correlation between θ and distance was significant (r = 0.21, N = 253, P < 0.01). The genetically distinctive Gates Creek population accounted for 28 of the 29 observed θ values >0.10 (Fig. 6). With Gates Creek excluded, a larger correlation between θ and distance was observed for upper Fraser populations (r = 0.61, N = 231, P < 0.01). The significant correlation between geographic and genetic distances for sockeye salmon populations of the upper Fraser is consistent with regional structuring in the dendrogram for these populations (Fig. 5).

There was no correlation between θ and distance for lower Fraser populations (r = –0.11, N = 15, P > 0.05), largely due to the genetic differentiation of the Cultus and Chilliwack Lake populations, both from each other and the remaining populations. There was also no correlation between θ and distance for pairs of upper and lower Fraser populations (Gates Creek removed: r = 0.10, N = 131, P > 0.05), and the degree of genetic differentiation between them was higher than expected based on the relationship between genetic and geographic distances for upper Fraser sockeye salmon populations (Fig. 6). The mean θ value between pairs of upper

Fig. 5. Unrooted neighbor-joining tree outlining relationships of 29 Fraser River sockeye salmon populations and one Columbia River population. Bootstrap values at the tree nodes indicate the percentage of 500 trees in which populations beyond the node occurred together.

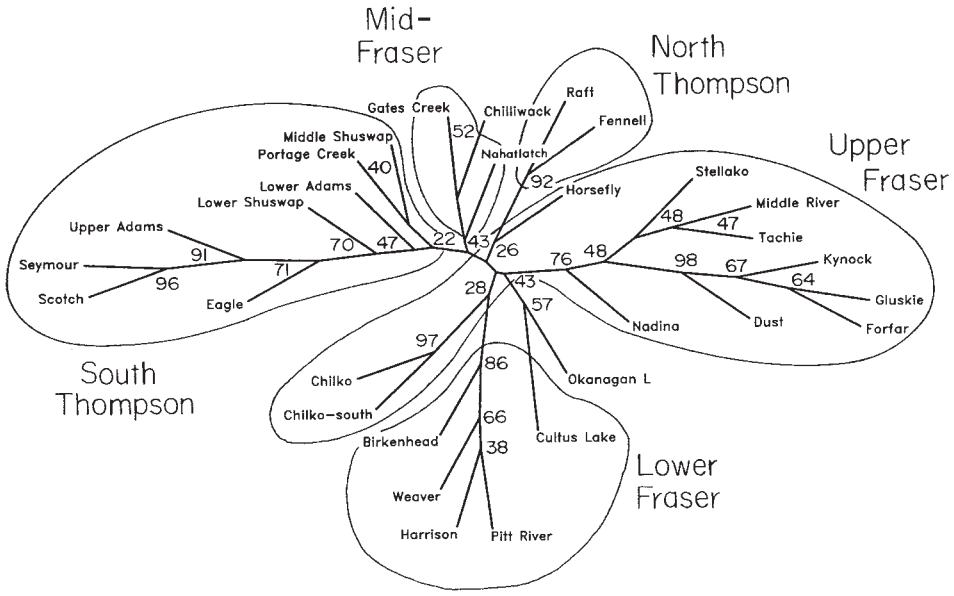


Table 3. Hierarchical gene diversity analysis of 29 populations of Fraser River and one population of Columbia River sockeye salmon for six microsatellite DNA loci.

Absolute diversity			Relative diversity			
Locus	Total	Within populations	Within populations	Among populations within lakes	Among lakes within regions	Among regions
Omy77	0.8117	0.7633	0.940	0.011*	0.037**	0.013**
Ots3	0.6408	0.6109	0.953	0.003	0.035**	0.008*
Ots100	0.7192	0.6592	0.916	0.002	0.058**	0.025**
Ots103	0.9113	0.8813	0.967	0.009*	0.019**	0.005
Ots107	0.4239	0.3988	0.941	0.008*	0.043**	0.009*
Ots108	0.9211	0.8677	0.942	0.009*	0.025**	0.025**
All			0.946	0.007*	0.035**	0.015*

Note: Values significant at the 0.05 and 0.01 levels are indicted by one and two asterisks, respectively. Regions, nursery lakes within regions, and populations within lakes are outlined in Table 1.

and lower Fraser populations was 0.069 (SD 0.024). This is consistent with the suggestion that the upper and lower Fraser drainages were colonized by sockeye salmon from different glacial refugia, with the result that the actual geographic distance between pairs of upper and lower Fraser populations has had little influence on their differentiation.

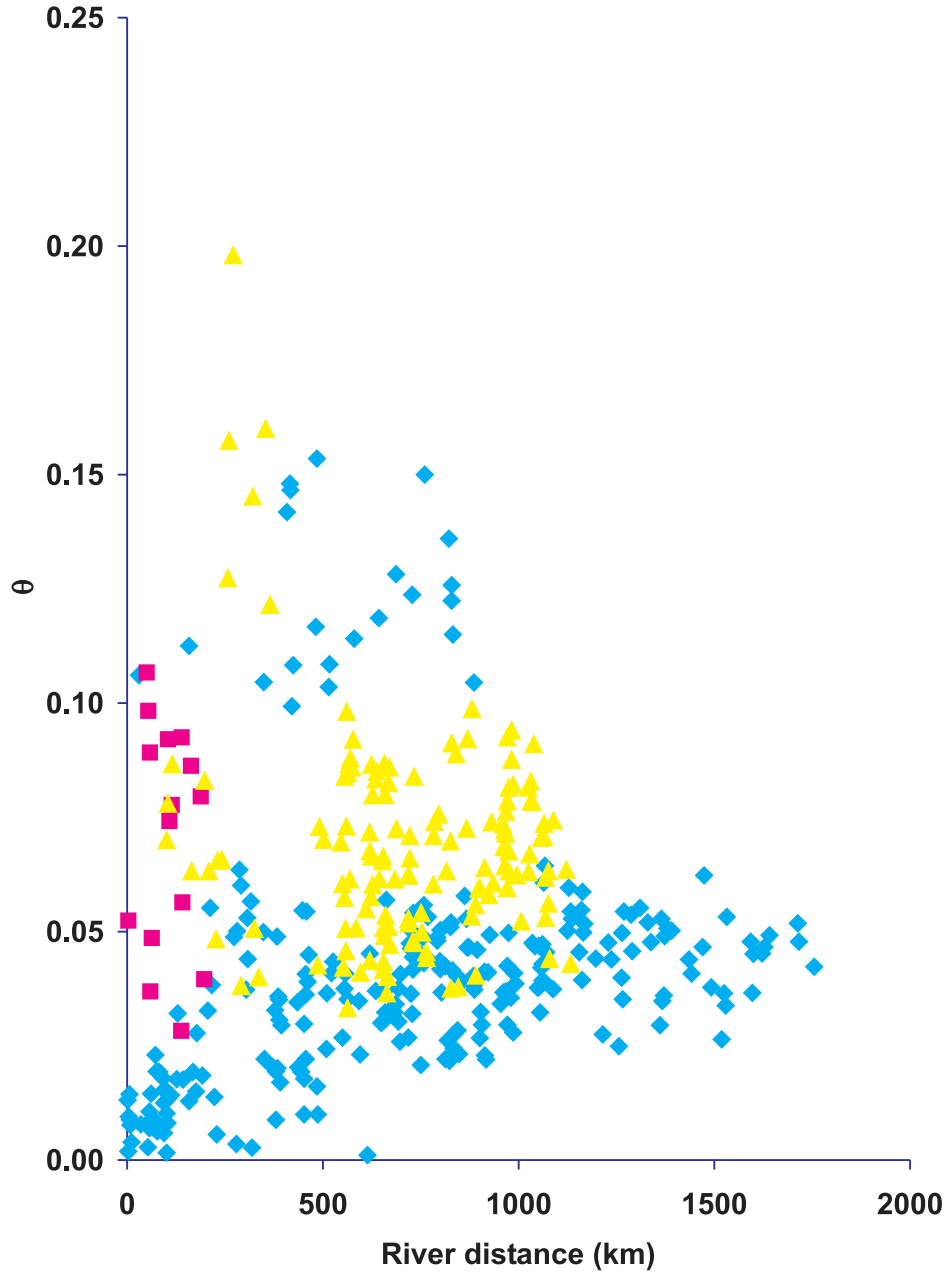
Transplanted populations

A high degree of genetic similarity at microsatellite loci between the three pairs of donor and recipient populations reputed to have been reestablished or rebuilt by transplantation was observed, supporting the contention of successful transplantation in these instances (Table 4; Fig. 5). In addition, the two sockeye salmon populations postulated to have been established entirely by multiyear transplantation displayed typical levels of intrapopulation variation, similar to the levels in the populations from which they were derived (Table 4).

The pairwise θ value between the upper Adams River and the nearby donor population, Seymour River (Fig. 1), was 0.015, equal to the average value among sockeye salmon populations in the South Thompson drainage and less than half the value between the upper Adams River and the Chilko River, sampled from the same drainage as the more distant donor population, the Taseko River (Table 4). The upper Adams population clustered most closely with the Seymour population (Fig. 5), but significant allele frequency differences between the two populations at all six loci indicated that founder effects and (or) genetic drift have occurred. The reestablished Fennell Creek population also clustered most closely with its donor population, Raft River, although allele frequencies differed significantly between the two North Thompson populations at five of six loci.

The Portage Creek sockeye salmon population was small but extant at the time that lower Adams River eggs and juveniles were transplanted to it. The high degree of genetic similarity between the Portage and lower Adams populations (Table 4; Fig. 5) indicates that replacement of or gene flow into the Portage population occurred, but the degree of introgression is not known. Allele frequencies differed significantly between the Portage and lower Adams populations at only two of the six loci examined, but the Portage popula-

Fig. 6. Relationship between pairwise θ and pairwise distance for 29 populations of Fraser River sockeye salmon. Comparisons are between the 23 populations upstream from Hell's Gate (blue diamonds), between the six populations downstream from Hell's Gate (pink squares), and between pairs of upstream and any downstream populations (yellow triangles).



tion possessed lower levels of heterozygosity, allelic diversity, and fewer rare alleles than did lower Adams sockeye salmon (Table 4).

Discussion

The study provided little evidence to support the hypothesis that sockeye salmon populations of Fraser drainage above the Fraser canyon have greatly depleted levels of genetic variation due to bottlenecks during and after the 1913–1914 rockslides at Hell's Gate. Heterozygosity levels in upper Fraser and Thompson populations were similar not only to those of lower Fraser populations but also to those of sockeye salmon populations in the Nass River system of northern British Columbia (0.66) (Beacham and Wood 1999) and in Barkley Sound on Vancouver Island (0.68) (Beacham et al. 2000) surveyed at the same loci. Sockeye salmon populations of Cook Inlet, Alaska, surveyed at four different microsatellite loci were less heterozygous (0.42) (Seeb et al. 1998). There was no difference in heterozygosity between early- and late-migrating sockeye salmon populations throughout the Fraser drainage.

Rare alleles are lost more rapidly than heterozygosity as the result of small population size (Nei et al. 1975;

Table 4. Comparisons of the Cavalli-Sforza and Edwards (1967) (CSE) chord distance and θ between, and heterozygosity, allelic diversity, and proportion of rare alleles within, putative donor and recipient transplant populations of sockeye salmon in the upper Fraser River drainage.

Type	Population	CSE distance	θ	Heterozygosity	Allelic diversity	Rare alleles
Donor 1	Chilko (Taseko)	0.019	0.044	0.665	8.5	23
Donor 2	Seymour	0.010	0.015	0.730	7.67	14
Recipient	Upper Adams			0.717	7.33	15
Donor	Raft	0.009	0.019	0.654	7.83	19
Recipient	Fennell			0.691	7.83	17
Donor	Lower Adams	0.005	0.003	0.751	8.5	21
Recipient	Portage			0.709	7.67	15

Maruyama and Fuerst 1985). Nonbottlenecked populations at or near mutation–drift equilibrium possess a large number of alleles at very low frequencies, whereas bottlenecked populations often display a mode shift distortion of allele frequencies such that the proportion of alleles at an intermediate frequency exceeds the proportion of rare alleles, even when heterozygosity levels are not detectably reduced (Luikart et al. 1998). Thus, it is possible to identify populations in which the effective size has become very low even in the absence of data on historical population sizes and allele frequencies. The absence of mode shift distortion in the allele frequency distributions of upper Fraser sockeye salmon populations indicated that these populations were not severely bottlenecked as a result of the 1913–1914 rockslides and dumping in the Fraser canyon.

Both allelic diversity and the proportion of rare alleles were slightly, but significantly, reduced throughout the Fraser drainage for early-migrating populations in comparison with late-migrating populations. However, only the early-migrating Chilliwack Lake population of the lower Fraser drainage displayed the mode-shifted allele frequency distribution that would indicate the occurrence of a bottleneck (effective population size of 20 or fewer individuals) within the past century (Luikart et al. 1998), although the abundance of rare alleles in some early-migrating upper Fraser – Thompson populations was also low. It is possible that lack of restriction on the fishery prosecuted in coastal and lower Fraser waters after 1913–1914 resulted in excessive harvest of comigrating early Chilliwack Lake and upper Fraser populations, but few populations upstream of the Fraser canyon experienced a bottleneck of sufficient severity to purge a high proportion of rare alleles.

For the early-migrating upper Fraser sockeye salmon populations, it is not clear whether the apparent lack of genetic bottlenecks is due to the fact that population sizes did not become as small as estimated after the rockslides, whether effective population sizes were bolstered by increased gene flow among populations due to increased straying among streams at low fish densities, or whether rapid expansion of population sizes once recovery was initiated prevented a great loss of allelic diversity. Certainly, there is no evidence of mass straying among populations of the upper Fraser and Thompson over the last 85 years. Upstream of the Fraser canyon, genetic distance is correlated with geographic distance, and populations of major tributary watersheds (e.g., Stuart–Nechako, Quesnel (Horsefly), Chilko, North Thompson, South Thompson) show the differentiation that typifies sockeye salmon populations within major river systems (Wood et al. 1994; Wood 1995). This genetic differentiation supports the evidence from maintained migration time differentials that the existing population structure of sockeye salmon above Hell's Gate was not destroyed by the immediate or long-term effects of the rock dumping and slides in 1913–1914. However, the possibility that increased straying occurred among populations utilizing the same nursery lake cannot be eliminated. We observed limited genetic differentiation among populations in streams tributary to the same nursery lake, but some variation associated with migration times was apparent. This is consistent with other observations that genetic differentiation among sockeye salmon populations within lakes reflects differences in spawning behavior or timing (e.g., Varnavskaya et al. 1994; Burger et al. 1995).

Rare alleles increase in abundance more rapidly than heterozygosity increases in genetically depauperate populations undergoing rapid expansion (Maruyama and Fuerst 1985). Many Fraser sockeye salmon populations rebuilt extremely rapidly after recovery was initiated, with spawning numbers increasing by 5- to 30-fold per generation (Ricker 1987). Thus, rapid increases in abundance may have prevented much loss of allelic diversity in populations that did become very small. Recovery tended to occur sooner, more rapidly, and to a greater extent in late-migrating populations such as the lower Adams and lower Shuswap rivers. Thus, the combined effects of less severe bottlenecks and more rapid postbottleneck expansion may be responsible for the higher allelic diversity exhibited by the late-migrating populations.

Genetic distances between pairs of sockeye salmon populations upstream and downstream of the Fraser canyon were relatively large and independent of the geographic distance separating them. Upper Fraser – Thompson sockeye salmon populations are also distinctive at mitochondrial DNA and allozyme loci (Wood et al. 1994; Bickham et al. 1995). This genetic differentiation has been attributed to independent postglacial colonization, but the potentially confounding effect of bottlenecks in the upper Fraser sockeye salmon populations during and after 1913–1914 had not been examined previously. The lack of evidence for severe bottlenecks in the current study provides strong support for the theory of independent colonization. Moreover, both coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) populations display concordant genetic discontinuities at the Fraser canyon (Small et al. 1998; Teel et al.

2000). Thus, differentiation of the Fraser sockeye salmon populations may be part of a phylogeographic pattern due to independent colonization of the upper and lower drainages.

The lower Fraser was likely colonized by sockeye salmon entering from the river mouth, and the genetic heterogeneity of the region, reflected in a lack of correlation between genetic and geographic distances and relatively large θ values between populations, may be an extension of the mosaic genetic structure of coastal sockeye salmon populations that have been attributed to multiple founder effects and genetic drift (Wood et al. 1994; Wood 1995). The upper Fraser drainage may have been colonized by immigration from the headwaters of one or more adjacent major river systems, such as the Skeena to the north or the Columbia to the south (Wood et al. 1994), but upper Fraser populations showed little similarity to the sole Columbia population in this study.

There is a documented general failure of efforts to establish self-sustaining anadromous sockeye salmon populations through transplants (Withler 1982; Wood 1995). The strong genetic differentiation observed between the upper and lower Fraser drainages and among nursery lakes within those regions confirms that the vast majority of transplants in the Fraser system made little or no genetic contribution to recipient populations. However, this study supported the contention that two populations extirpated by logging dams (upper Adams River and Fennell Creek) were reestablished by transplantation from nearby streams, apparently without a loss of genetic diversity. It is possible that natural straying from nearby populations contributed to the reestablishment of these two populations. The Portage Creek population, which was most distant from its donor population and which was established or introgressed by a single transplant, was genetically less variable than its donor population but showed no evidence of a bottleneck.

Small population size due to rockslides in 1913–1914 and subsequent overexploitation may have slightly reduced allelic diversity through a loss of rare alleles in early-migrating sockeye salmon populations throughout the Fraser watershed but did not have a major impact on genetic variation within or among upper Fraser sockeye salmon populations. Moreover, extensive transplantation within the Fraser and introductions from outside the drainage have not greatly affected the population structure of Fraser sockeye salmon. Major determinants of sockeye salmon population structure in the Fraser, as elsewhere, are apparently patterns of postglacial colonization and strong philopatry to the nursery lake. Maintenance of both genetic diversity and high levels of productivity in Fraser sockeye salmon would seem to be best achieved by conserving as many as possible of the populations adapted to different nursery lakes. Population-specific management of Fraser sockeye salmon will be facilitated by both the consistent and large differences in time of migration among populations and the genetic distinctiveness of Fraser sockeye salmon at microsatellite loci.

Acknowledgments

We would like to acknowledge all those people involved in spawning ground sample collections, which were conducted under the supervision of N. Schubert and L. McDonald. C. Rathlef assisted in laboratory analysis of the samples. J. Candy assisted in some of the data analysis and figure preparation. I. Williams determined the river distance between all pairwise population comparisons. Funding was provided by the Department of Fisheries and Oceans.

References

Aro, K.V. 1979. Transfers of eggs and young of Pacific salmon within British Columbia. Fish. Mar. Ser. Tech. Rep. No. 861.

Banks, M.A., Blouin, M., Baldwin, B.A., Blankenship, S.M., Rashbrook, V.K., Calavetta, M., and Hedgecock, D. 1999. Isolation and transmission genetics of microsatellites in chinook salmon (*Oncorhynchus tshawytscha*). J. Hered. **90**: 281–288.

Beacham, T.D., and Wood, C.C. 1999. Application of microsatellite DNA variation to estimation of stock composition and escapement of Nass River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **56**: 1–14.

Beacham, T.D., Margolis, L., and Nelson, R.J. 1998. A comparison of methods of stock identification for sockeye salmon (*Oncorhynchus nerka*) in Barkley Sound, British Columbia. North Pac. Anadr. Fish Comm. Bull. **1**: 227–239.

Beacham, T.D., Le, K.D., Raap, M.R., Hyatt, K., Luedke, W., and Withler, R.E. 2000. Microsatellite DNA variation and estimation of stock composition of Barkley Sound, British Columbia sockeye salmon. Fish. Bull. U.S. **98**: 14–24.

Bickham, J.W., Wood, C.C., and Patton, J.C. 1995. Biogeographic implications of cytochrome *b* sequences and allozymes in sockeye (*Oncorhynchus nerka*). J. Hered. **86**: 140–144.

Burger, C.V., Finn, J.E., and Holland-Bartels, L. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for subpopulation differentiation. Trans. Am. Fish. Soc. **124**: 1–15.

Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 3–117.

Cavalli-Sforza, L.L., and Edwards, A.W.F. 1967. Phylogenetic analysis: models and estimation procedures. Am. J. Hum. Genet. **19**: 233–257.

Gable, J., and Cox-Rogers, S. 1993. Stock identification of Fraser River sockeye salmon: methodology and management application. Int. Pac. Salmon Comm. Tech. Rep. No. 5.

Gill, P., Sullivan, K., and Werrett, D.J. 1990. The analysis of hypervariable DNA profiles: problems associated with the objective determination of the probability of a match. Hum. Genet. **85**: 75–79.

Luikart, G., Allendorf, F.W., Cornuet, J.-M., and Sherwin, W.B. 1998. Distortion of allele frequency distributions provides a test for recent population bottlenecks. J. Hered. **89**: 238–247.

Maruyama, T., and Fuerst, P.A. 1985. Population bottlenecks and nonequilibrium models in population genetics. III. Genic homozygosity in populations which experience periodic bottlenecks. Genetics, **111**: 691–703.

Morris, D.B., Richard, K.R., and Wright, J.M. 1996. Microsatellites from rainbow trout (*Oncorhynchus mykiss*) and their use for genetic study of salmonids. Can. J. Fish. Aquat. Sci. **53**: 120–126.

Nei, M., Maruyama, T., and Chakraborty, R. 1975. The bottleneck effect and genetic variability in populations. Evolution, **29**: 1–10.

Nelson, R.J., and Beacham, T.D. 1999. Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. Anim. Genet. **30**: 228–229.

Nelson, R.J., Beacham, T.D., and Small, M.P. 1998. Microsatellite analysis of the population structure of a Vancouver Island

sockeye salmon (*Oncorhynchus nerka*) stock complex using non-denaturing gel electrophoresis. Mol. Mar. Biol. Biotechnol. **7**: 312–319.

Raymond, M., and Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenism. Heredity, **86**: 248–249.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225.

Ricker, W.E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. No. 1522.

Ricker, W.R. 1950. Cycle dominance among the Fraser sockeye. Ecology, **31**: 6–26.

Seeb, J.E., Habicht, C., Olsen, J.B., Bentzen, P., Shaklee, J.B., and Seeb, L.W. 1998. Allozyme, mtDNA, and microsatellite variants describe structure of populations of pink and sockeye salmon in Alaska. North Pac. Anadr. Fish Comm. Bull. **1**: 300–318.

Small, M.P., Beacham, T.D., Withler, R.E., and Nelson, R.J. 1998. Discriminating coho salmon (*Oncorhynchus kisutch*) populations within the Fraser River, British Columbia using microsatellite DNA markers. Mol. Ecol. **7**: 141–155.

Swofford, D.L., and Selander, R.B. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. **72**: 281–283.

Teel, D.J., Milner, G.B., Winans, G., and Grant, W.S. 2000. Genetic population structure and origins of life history types in chinook salmon in British Columbia, Canada. Trans. Am. Fish. Soc. **129**: 194–209.

Varnavskaya, N.V., Wood, C.C., Everett, R.J., Wilmot, R.L., Varnavsky, V., Midanaya, V.V., and Quinn, T.P. 1994. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within lakes of Alaska, British Columbia, and Kamchatka, Russia. Can. J. Fish. Aquat. Sci. **51**(Suppl. 1): 147–157.

Ward, F.J., and Larkin, P.A. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 11.

Williams, I.V. 1987. Attempts to re-establish sockeye salmon (*Oncorhynchus nerka*) populations in the Upper Adams River, British Columbia, 1949–84. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 235–242.

Withler, F.C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. No. 1079.

Wood, C.C. 1995. Life history variation and population structure in sockeye salmon. Am. Fish. Soc. Symp. **17**: 195–216.

Wood, C.C., Riddell, B.E., Rutherford, D.T., and Withler, R.E. 1994. Biochemical genetic survey of sockeye salmon (*Oncorhynchus nerka*) in Canada. Can. J. Fish. Aquat. Sci. **51**(Suppl. 1): 114–131.