Genetic evidence for the persistence and divergence of native and introduced sockeye salmon (*Oncorhynchus nerka*) within Lake Washington, Washington

Andrew P. Hendry, Thomas P. Quinn, and Fred M. Utter

Abstract: The genetic population structure of Lake Washington sockeye salmon (*Oncorhynchus nerka*) was investigated using the analysis of variation in allelic frequencies at protein-coding loci. Population subdivision was considerable (average F_{ST} using the four highly polymorphic loci was 0.057) and two divergent population groups were identified (separated by an average genetic distance of 0.014). One population group (Cedar River, Issaquah Creek, and a Lake Washington beach) showed a genetic affinity to collections of sockeye salmon from Baker Lake, Washington. In contrast, the other population group (Bear Creek and Cottage Creek) was distinct from either of the putative non-native ancestral populations (Cultus Lake, B.C., and Baker Lake). We inferred that the former group was comprised of fish of the Baker Lake lineage (transplanted to Lake Washington in the 1930s and 1940s) and that the latter population group was predominantly of native ancestry. Cultus Lake fish were not closely related to any of the other populations but there was some evidence for introgression among the different ancestral lineages within Lake Washington. Allelic frequency differences among several populations of a common origin provided evidence for two possible types of genetic divergence: between ancestral and derived groups and among different derived populations.

Résumé : On a étudié la structure génétique de la population de saumons sockeye (*Oncorhynchus nerka*) du lac Washington en examinant la variation de fréquences alléliques aux locus assurant le codage des protéines. Il y avait subdivision considérable de la population (la valeur moyenne de F_{ST} établie avec quatre locus hautement polymorphes était de 0,057), et on a identifié deux groupes de population divergents (séparés par une distance génétique moyenne de 0,014). Un groupe de population (rivière Cedar, ruisseau Issaquah et une plage du lac Washington) présentait une affinité génétique vis-à-vis des collections de saumons sockeye du lac Baker, Washington. Par contraste, l'autre groupe de population (ruisseau Bear et ruisseau Cottage) était distinct des deux populations ancestrales présumées non indigènes (lac Cultus, en Colombie-Britannique, et lac Baker). Nous avons déduit que le premier groupe de population était constitué de poissons de la lignée du lac Baker (transplantés dans le lac Washington dans les années 1930 et 1940) et que le dernier groupe était surtout d'origine ancestrale indigène. Les poissons du lac Cultus n'étaient pas étroitement apparentés à ceux des autres populations, mais certaines données semblaient indiquer qu'il y avait eu introgression parmi les différentes lignées ancestrales du lac Washington. Les différences de fréquences alléliques chez plusieurs populations d'origine commune venaient appuyer deux types possibles de divergence génétique, soit entre des groupes ancestraux et des groupes dérivés et entre des populations dérivées.
[Traduit par la Rédaction]

Introduction

Unlimited migration among conspecific populations (discrete breeding aggregations) can homogenize genetic variation and lead to apparent panmixia (Wright 1978; Allendorf and Phelps 1981). Natal homing, a phenomenon exhibited by Pacific salmon (*Oncorhynchus* sp.) and many other organisms, can reproductively isolate different populations, limiting gene flow among them (Labelle 1992; Quinn 1993; Tallman and Healey 1994). This restriction on gametic exchange allows the genetic divergence of populations through random processes (genetic drift and mutation) and natural selection (Ehrlich and Raven 1969; Endler 1986; Slatkin 1987; Altukhov and Salmenkova 1991). Although undisturbed populations may eventually approach an equilibrium between genetic drift, selection, and migration (Wright 1969; Slatkin 1994), introduced fish can disrupt this balance (Hindar et al. 1991; Krueger and May 1991).

An interaction between introduced (non-native) and indigenous (native) conspecifics can lead to (*i*) success of the introduced fish through replacement of the native fish, (*ii*) persistence of the native fish coupled with failure of the introduced fish, (*iii*) introgression of the native and introduced fish, or (*iv*) coexistence of both native and introduced fish as reproductively isolated populations that breed at different times and (or) in different places. If both native and non-native fish contribute to a population mixture, the relative genetic influence of each ancestral group may vary among the derived populations,

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reflecting some combination of stocking intensity and variation in adaptive life history traits. Pacific salmon provide an opportunity to investigate the outcome of such genetic interactions because many introductions have been made into locations that already harbored conspecifics.

Outside their native range, the transplantation of salmonids has been extensive, establishing a number of new populations (Withler 1982; Krueger and May 1991; Harache 1992). Within their native range, however, only two introductions provide unequivocal evidence for the establishment of self-perpetuating, anadromous salmon populations (Withler 1982). In Frazer Lake, Alaska, sockeye salmon (*Oncorhynchus nerka*) became self-sustaining after intensive stocking and the removal of a barrier to anadromous migration (Blackett 1979). In Lake Washington, Washington, sockeye salmon transplants also became self-perpetuating within a modified drainage (see below), which nonetheless lacked blockages to migration both before and after the introductions (Ajwani 1956). Thus, the success of sockeye salmon introduced to Lake Washington represents a rare and possibly unique example, within the native range of the species, of a Pacific salmon transplant that established a self-perpetuating anadromous population in a system without a historical barrier to anadromy (Withler 1982).

The historical distribution and abundance of *O. nerka* within Lake Washington is poorly understood, owing to a lack of detailed records. Nevertheless, substantial numbers of kokanee (the non-anadromous form) and limited runs of sockeye salmon (the anadromous form) were probably present at the turn of the century (Seale 1895; Evermann and Meek 1898; Rathbun 1900; Cobb 1911). In 1917, the Cedar River (formerly a tributary to the Duwamish River) was diverted into Lake Washington and a ship canal was constructed that connected the lake more directly to Puget Sound (Ajwani 1956). Associated changes in the drainage pattern and lake level (a drop of 3 m) were generally assumed to have resulted in the extinction or severe depletion of anadromous sockeye salmon within the watershed (Ajwani 1956; Woodey 1966). Nevertheless, there is some genetic evidence that native populations may have persisted in certain areas (Seeb and Wishard 1977).

The first recorded introduction of non-native sockeye salmon into Lake Washington occurred in 1917, but the exact source of these fish is unknown and they apparently did not establish any substantial populations (Woodey 1966). No other introductions occurred until the late 1930s, when an intensive stocking program began (Royal and Seymour 1940). Juvenile sockeye salmon from Baker Lake in the Skagit River system, Washington, were stocked into Bear Creek (576 000 in 1937), Issaquah Creek (1 553 000 from 1937 to 1944), and Cedar River (969 000 from 1937 to 1945). Returns of these fish to Issaquah Creek were then used for hatchery supplementation in Cedar River until 1945 and in Issaquah Creek until 1963 (Woodey 1966). The only other external source of sockeye salmon planted into Lake Washington was Cultus Lake in the Fraser River system, British Columbia, from which fingerlings were planted into North Creek (24 000 in 1944) and Issaquah Creek (60 000 from 1950 to 1954). For detailed reviews of sockeye salmon introductions into the Lake Washington drainage, see Ajwani (1956), Woodey (1966), and Hendry (1995). Currently, anadromous sockeye salmon and non-anadromous kokanee spawn throughout the Lake Washington watershed but are only abundant in certain areas (Ron Egan, Washington Department of Fish and Wildlife, 600 Capitol Way North, Mail Stop 43151, Olympia, WA 98501–1091, U.S.A., unpublished data).

The present study investigated the genetic population structure of Lake Washington sockeye salmon using the analysis of variation in allelic frequencies at protein-coding loci. This approach has frequently been used to investigate ancestral relationships and to evaluate population differentiation in Pacific salmon (Allendorf and Phelps 1981; Gharrett and Thomason 1987; Utter 1991). For sockeye salmon, biochemical genetic analysis has succeeded in discriminating broad geographical population groups (e.g., Withler 1985; Foote et al. 1989; Wood et al. 1994), populations from nearby lakes and streams (e.g., Wilmot and Burger 1985; Quinn et al. 1987; Grant et al. 1980; Varnavskaya et al. 1994*a*), and populations from different spawning locations within lake systems (e.g., Altukhov and Salmenkova 1991; Varnavskaya et al. 1994*b*). For Lake Washington, ancestral origins of the different sockeye salmon populations were inferred through comparisons with the fish currently found in Baker and Cultus lakes. Distinctions noted within and among native and introduced groups were then evaluated for evidence of genetically distinct populations within the Lake Washington drainage. The results were considered with respect to the interaction of native and introduced conspecifics and the dynamics of population divergence after an introduction.

Methods

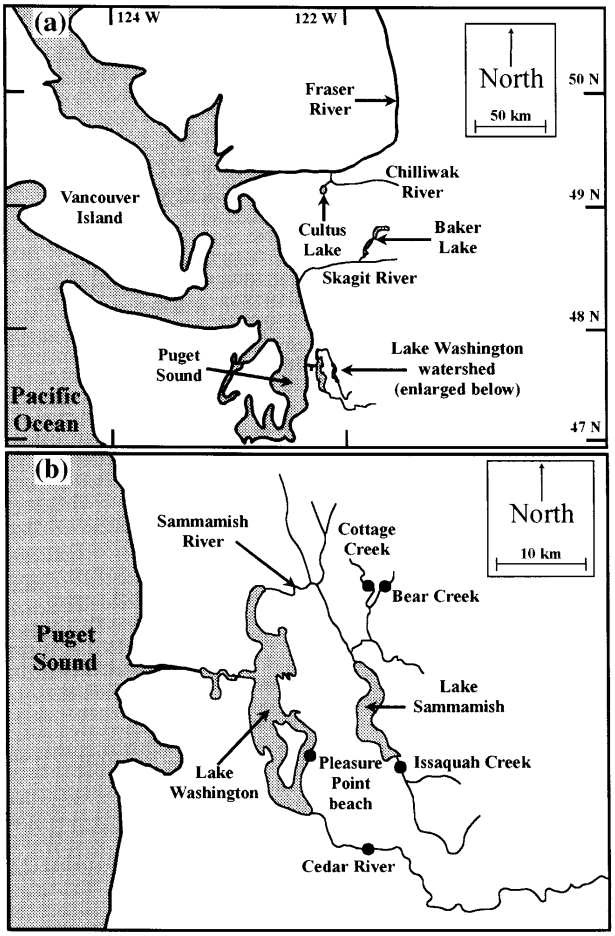
Collections

In the fall of 1992 and 1993, adult sockeye salmon were collected from each of five spawning areas within the Lake Washington drainage (Cedar River, Issaquah Creek, Bear Creek, Cottage Creek, and the Pleasure Point beach; Fig. 1*b*). The numbers of fish collected from each location varied in proportion to the size of the spawning population. Additional collections included adult sockeye salmon from Baker Lake in 1992 and 1993 and juvenile sockeye salmon from Cultus Lake in 1992 (the latter were provided by Chris Wood, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada). Kokanee were collected from Issaquah Creek in 1993 (13 adults) and from Bear and Cottage creeks in 1992 (3 adults). Few kokanee were collected because the spawning populations in both years were extremely limited.

Tissue samples (liver, heart, eye, and skeletal muscle) were obtained from all adult and juvenile fish and stored at −80°C. These samples were then processed using horizontal starch gel electrophoresis and stained for specific enzyme activity reflecting distinct allozyme loci and alleles (Aebersold et al. 1987). Twelve enzyme systems coded by 20 loci (Table 1) were screened in a minimum of 40 fish from each sockeye salmon collection. Two other loci (*LDH-B2** and *TPI-1.2**) were screened in a minimum of 40 individuals from each of the 1993 sockeye salmon collections. All of the kokanee were screened for all 22 loci. Samples were run in several tissues and using several buffer systems to ensure accurate scoring. Banding patterns were interpreted using established protocols (Utter et al. 1987) and standardized gene nomenclature (Shaklee et al. 1990).

Allelic frequencies were determined by direct count for all loci except *PGM-1** and *LDH-A1**. For these two loci, heterozygotes could not be readily distinguished and so allelic frequencies were estimated from the square root of the frequency of null homozygotes (assuming Hardy–Weinberg equilibrium). Loci were categorized as high polymorphic ($q > 0.05$), low polymorphic ($0.05 > q > 0$), or

Fig. 1. Locations of the different collection areas. (*a*) The relative locations of Cultus Lake, Baker Lake, and Lake Washington. (*b*) Collection locations within the Lake Washington watershed, designated with a ●.



monomorphic ($q = 0$), where q was the frequency of variant alleles in one or more collections.

In each collection (population- and year-specific), genotype frequencies were tested for deviations from those expected under Hardy–Weinberg equilibrium using χ^2 tests for each locus (except *LDH-A1** and *PGM-1**). Allelic frequencies at each locus were then compared between years for each population using χ^2 tests. Differences between years were rare (see Results) so allelic counts for the 2 years were pooled and compared among populations using contingency χ^2 analysis for each locus and for all loci combined. These among-population comparisons excluded the kokanee and were performed twice, once including the collections from Baker and Cultus lakes and a second time with only the Lake Washington populations. Log-likelihood G tests (Sokal and Rohlf 1981) for all loci combined were then used to test for differences in all pairwise comparisons between populations (years pooled). The α level was set at 0.05 for statistical analyses and was then corrected for multiple comparisons (α/n, where n is the number of comparisons) in the tests for deviations from Hardy–Weinberg equilibrium ($n = 42$, $p < 0.001$), the tests for differences in allelic frequencies between years ($n = 22$, $p < 0.002$), and the pairwise G tests ($n = 21$, $p < 0.002$).

Nei's (1978) unbiased genetic distance and Cavalli-Sforza and Edwards' (1967) chord distance were calculated among the populations using data for all loci. These genetic distance measures were then used to construct a UPGMA dendrogram (Sneath and Sokal 1973) and a neighbor-joining tree (Saitou and Nei 1978), respectively.

Table 1. Tissues and buffer systems that provided the best resolution for investigating genetic variation at allozyme loci.

Enzyme	EC No.	Locus	Tissue	Buffer
Adenosine deaminase	3.5.4.4	*ADA-1**	H	TBE
Alanine aminotransferase	2.6.1.2	*ALAT**	M	TBE
Aspartate aminotransferase	2.6.1.1	*sAAT-2**	H	ACE7
Creatine kinase	2.7.3.2	*CK-A1,2**	M	TBE
		*CK-B**	M	TBE
Glucose-6-phosphate isomerase	5.3.1.9	*GPIA**	M	TBCLE
		*GPIB1,2**	M	TBCLE
L-Iditol dehydrogenase	1.1.1.14	*IDDH-1**	L	TBCL
		*IDDH-2**	L	TBCL
Lactate dehydrogenase	1.1.1.27	*LDH-A1**	M	ACE7
		*LDH-A2**	M	ACE7
		*LDH-B1**	M	ACE7
		*LDH-B2**	L	TBCL
		*LDH-C**	E	TBE
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	H	TBE
Tripeptide aminopeptidase	3.4.*.*	*PEPB1**	M	TBE
		*PEPB2**	M	TBE
Proline dipeptidase	3.4.*.*	*PEPD1**	M	TBE
Phosphoglucomutase	5.4.2.2	*PGM-1**	M	ACE7
		*PGM-2**	M	TBCLE
Superoxide dismutase	1.15.1.1	*sSOD-1**	L	TBE
Triose-phosphate isomerase	5.3.1.1	*TPI-1.2**	H	TBE

Note: Tissues are as follows: H, heart; M, skeletal muscle; E, eye; and L, liver. Buffers were made using the recipes provided in Aebersold et al. (1987).

Both cluster analyses included the sockeye salmon populations from Lake Washington and Baker Lake (years pooled), as well as the collections of kokanee from Issaquah Creek and juvenile sockeye salmon from Cultus Lake.

Fixation indices (F statistics) can provide a useful measure of the degree of population subdivision on the basis of the correlation between random gametes drawn from a population, relative to the total for all populations (Wright 1969; Chakraborty and Leimar 1987). Within Lake Washington, Wright's (1978) nonhierarchical fixation index (F_{ST}) was calculated for each highly polymorphic locus (excluding kokanee) using the formula

$$F_{ST} = \sigma_q^2/\bar{q}(1 - \bar{q})$$

where $\bar{q}$ and σ_q^2 are the interpopulation mean and variance of allelic frequencies.

F_{ST} can be used to indirectly estimate realized gene flow among populations (Wright 1969; Slatkin and Barton 1989; Cockerman and Weir 1993). This technique has been advocated for estimating levels of migration among fish populations (Chakraborty and Leimar 1987; Ryman 1991) and has been used in some studies of salmonid population structure (e.g., Berg and Gall 1988; Tallman and Healey 1994). Within Lake Washington, the average F_{ST} value for the highly polymorphic loci was used to estimate realized gene flow ($N_e m_e$) among the sockeye salmon populations using the formula

$$F_{ST} = \frac{1}{1 + 4\,N_e\,m_e\left(\frac{n}{n-1}\right)^2}$$

Table 2. Variant allelic frequencies and sample sizes for highly polymorphic loci ($q > 0.05$).

		*ALAT**			*PGM-1**		*PGM-2**		*LDH-A1*	
Population	Year	*N*	**91*	**95*	*N*	**NULL*	*N*	**136*	*N*	**500*
Baker Lake	1992	40	0.563	0.075	39	0.320	56	0.170	56	0.000
	1993	43	0.512	0.047	40	0.387	64	0.117	64	0.000
	Total	83	0.536	0.060	79	0.356	120	0.142	120	0.000
Cultus Lake	1992	40	0.050	0.000	40	0.962	40	0.175	64	0.000
Lake Wash. Beach	1992	40	0.400	0.075	40	0.387	41	0.037	41	0.156
	1993	40	0.275	0.050	39	0.599	39	0.051	40	0.000
	Total	80	0.338	0.063	79	0.503	80	0.044	81[b]	0.111
Bear Creek	1992	40	0.225	0.150	40	0.671	63	0.127	40	0.224
	1993	43	0.279	0.163	40	0.592	52	0.154	12	0.408
	Total	83	0.253	0.157	80	0.632	115	0.139	52	0.277
Cedar River	1992	76	0.382	0.072	40	0.447	134	0.086	135	0.086
	1993	115	0.361	0.074	40	0.354	115[a]	0.096	117	0.000
	Total	191	0.369	0.073	80	0.403	249	0.090	252[b]	0.063
Cottage Creek	1992	40[a]	0.375	0.113	40	0.632	52	0.144	40	0.158
	1993	40	0.213	0.088	40	0.689	40	0.138	38	0.281
	Total	80	0.294	0.100	80	0.661	92	0.141	78	0.226
Issaquah Creek	1992	40	0.313	0.063	40	0.224	83	0.060	40	0.000
	1993	60	0.317	0.067	40	0.316	64	0.047	83	0.000
	Total	100	0.315	0.065	80	0.274	147	0.054	123	0.000
kokanee	1993	16	0.357	0.071	16	0.433	16[a]	0.250	16	0.559

Note: The frequency of the **100* allele is not shown but is equal to 1 minus the frequency of the other allele(s). Allelic frequencies for *PGM-1** and *LDH-A1** were determined by the square root of the frequency of null homozygotes (assuming Hardy–Weinberg equilibrium).

[a]Collections for which allelic frequencies, at a given locus, deviated from Hardy–Weinberg equilibrium ($p < 0.05$).

[b]Populations for which allelic frequencies, at a given locus, differed between years ($p < 0.05$).

where N_e is the effective population size, m_e is the effective rate of migration, and n is the number of populations (Chakraborty and Leimar 1987).

All statistical analyses were performed using three computer programs. BIOSYS-1 (release 1.7, Swofford and Selander 1981) was used to test for deviations from Hardy–Weinberg equilibrium; to calculate F_{ST} values, Nei's (1978) unbiased genetic distances, and Cavalli-Sforza and Edwards' (1967) chord distances; and for the construction of the UPGMA dendrogram. PHYLIP (version 3.57c; J. Felsenstein, University of Washington, Department of Genetics, Box 357360, Seattle, WA 98195-7360, U.S.A.) was used to construct the neighbor-joining tree. A *G* test program (David Teel, National Marine Fisheries Service, Coastal Zone and Estuarine Studies Division, Northwest Fisheries Science Center, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, U.S.A.) was used for the pairwise comparisons between populations.

Results

Variation within populations

Of the 22 loci, four (*ALAT**, *PGM-1**, *PGM-2**, and *LDH-A1**) were highly polymorphic (Table 2), three (*LDH-B2**, *GPI-B1,2**, and *TPI-1.2**) exhibited low polymorphism, and the remainder were monomorphic. Variant alleles for the loci at which polymorphism was low included *LDH-B2*110* (found at a frequency of 0.013 in each of the Cedar River, Cottage Creek, Cultus Lake, and beach populations), *LDH-B2*85* (found in the beach (0.038), Cedar River (0.050), Cottage Creek (0.025), and Issaquah Creek (0.025) populations), *GPI-B1,2*13* (found in the Bear Creek (0.005), Cedar River (0.003), and Cottage Creek (0.003) populations), and *TPI-1.2*-54* (found at a frequency of 0.006 in the Cottage Creek and Issaquah Creek populations).

Only one of the allelic variants detected in this study had not been described previously in the literature. This *LDH-A1** variant was a phenotypic analog to a similar polymorphism described in brown trout, *Salmo trutta* (Allendorf et al. 1984), where the variant allele either synthesizes a homotetrameric band that comigrates with the homotetramer for the common allele of *LDH-A2** or is not synthesized (i.e., a null allele). For this polymorphism, the four-banded phenotype of the heterozygote cannot be consistently distinguished from the five-banded phenotype of the common homozygote. However, the frequency of the allele can be estimated from the frequency of the homozygous variant phenotype (assuming Hardy–Weinberg proportions). We interpreted the variant as an active allele rather than a null on the basis of variation in band intensity for each phenotype (P. Aebersold and G. Winans, National Marine Fisheries Service, Coastal Zone and Estuarine Studies Division, Northwest Fisheries Science Center, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, U.S.A., unpublished data). The allele was designated *LDH-A1*500* on the basis of its mobility in the buffer system that we used. In a TBCLE type buffer system, it had a mobility of **86*.

Tests for genotypic variation within collections and for year-class variation within each population generally conformed to values expected from random breeding populations.

Table 3. Pairwise comparisons of genetic relationships among sockeye salmon populations from Lake Washington, Baker Lake, and Cultus Lake.

	Population						
Site	Cedar	Issaquah	Bear	Cottage	Beach	Baker	Cultus
Cedar		0.001	0.005	0.005	0.000	0.002	0.023
Issaquah	39.4[a] (8)		0.011	0.010	0.003	0.003	0.029
Bear	68.4[a] (8)	137.1[a] (7)		0.000	0.003	0.011	0.014
Cottage	59.3[a] (8)	133.5[a] (7)	5.7 (8)		0.002	0.010	0.011
Beach	14.0 (8)	52.3[a] (6)	37.2[a] (7)	29.6[a] (7)		0.004	0.017
Baker	51.9[a] (8)	35.1[a] (5)	134.4[a] (7)	127.4[a] (7)	70.4[a] (6)		0.032
Cultus	162.8[a] (8)	174.6[a] (6)	127.2[a] (8)	109.3[a] (7)	135.4[a] (7)	181.7[a] (5)	

Note: Nei's (1978) unbiased genetic distance is above the diagonal and *G* test values from pairwise comparisons are below the diagonal. The degrees of freedom for the *G* tests are given in parentheses. Corrections for multiple comparisons (α/n, where $\alpha = 0.05$ and $n = 21$) yield the final significance level ($p < 0.002$).

[a] $p < 0.002$.

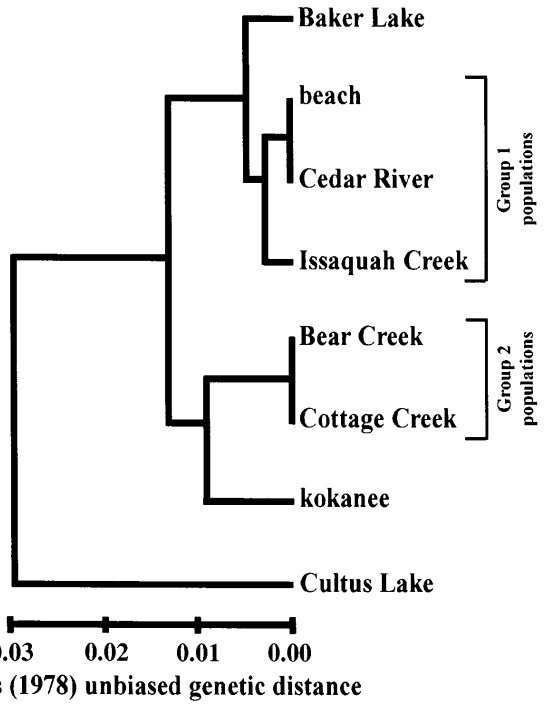
Of the 42 tests for Hardy–Weinberg proportions, three deviated from expectations at $\alpha = 0.05$ (Table 2). After correction for multiple comparisons ($p < 0.001$), only two (*PGM-2** at the Cedar River in 1993 and *ALAT** at Cottage Creek in 1992) were significant. In both cases, the deviation was due to a deficiency of heterozygotes.

Only 2 of the 24 between-year comparisons (six populations at each of the four highly polymorphic loci) showed a significant difference in allelic frequencies. After correction for multiple comparisons ($p < 0.002$), both of these (*LDH-A1** at the Cedar River and the beach) remained significant. Presumably, this year-class variation reflected the relative insensitivity of estimating allelic frequencies from the square root of the frequency of rare homozygotes (both populations had one fish that was homozygous for the **500* allele in 1 year and no such fish in the other year). Owing to the general consistency in allelic frequencies between years, data for the 2 years at each location were pooled for each locus to facilitate comparisons among the populations.

Variation among populations

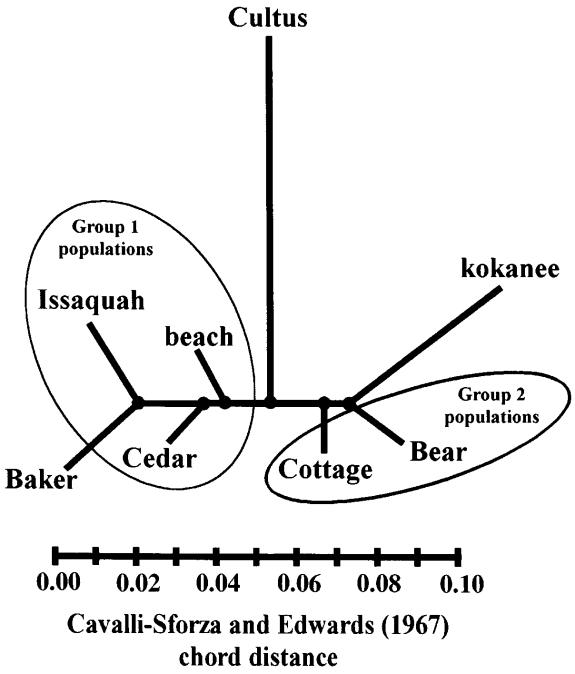
Analysis of allelic variation among the populations was based primarily on the four highly polymorphic loci because allelic variants (i.e., other than the **100*) at the less polymorphic loci were only represented by a single heterozygous individual in a few populations. For the first set of interpopulation comparisons (Baker Lake, Cultus Lake, and the five Lake Washington sockeye salmon populations), significant genetic differences were present at each locus (*ALAT**, $\chi^2 = 95.79$, df = 12, $p < 0.001$; *PGM-1**, $\chi^2 = 148.91$, df = 6, $p < 0.001$; *PGM-2**, $\chi^2 = 28.62$, df = 6, $p < 0.001$; *LDH-A1**, $\chi^2 = 168.24$, df = 6, $p < 0.001$) and when data for all loci were combined ($\chi^2 = 457.37$, df = 48, $p < 0.001$). For the second set of interpopulation comparisons (just the five Lake Washington sockeye salmon populations), significant genetic differences remained at each locus (*ALAT**, $\chi^2 = 19.23$, df = 7, $p = 0.014$; *PGM-1**, $\chi^2 = 66.61$, df = 4, $p < 0.001$; *PGM-2**, $\chi^2 = 20.87$, df = 4, $p < 0.001$; *LDH-A1**, $\chi^2 = 110.00$, df = 4, $p < 0.001$) and when data for all loci were combined ($\chi^2 = 226.58$, df = 36, $p < 0.001$).

Fig. 2. UPGMA dendrogram for all populations based on pairwise comparisons of Nei's (1978) unbiased genetic distance averaged over 6 polymorphic loci and 16 monomorphic loci.



Pairwise *G* tests (using all loci) revealed significant differences in allelic frequencies between all possible population pairs except for Bear Creek versus Cottage Creek and Cedar River versus the beach (Table 3). The highest levels of significance

Fig. 3. Neighbor-joining tree (Saitou and Nei 1987) for all populations based on pairwise comparisons of Cavalli-Sforza and Edwards' (1967) chord distance averaged over 6 polymorphic loci and 16 monomorphic loci.



were for the comparisons that involved the Cultus Lake fish. The patterns revealed by pairwise *G* tests matched those revealed by genetic distance measures (Table 3).

The UPGMA projection of Nei's (1978) unbiased genetic distance revealed several major distinctions among the populations (Fig. 2). The most divergent population, sockeye salmon from Cultus Lake, differed from populations at all of the other locations at a mean relative genetic distance of about 0.025. The other populations grouped into two distinct clusters, separated by a genetic distance of about 0.014. One cluster contained collections of sockeye salmon from Baker Lake and three of the Lake Washington populations (group 1 populations: Cedar River, Issaquah Creek, and the beach). The other cluster was comprised of sockeye salmon from Bear Creek and Cottage Creek (group 2 populations) and of kokanee from Issaquah Creek. The general pattern revealed by the UPGMA dendrogram was similar to that obtained using a neighbor-joining tree with Cavalli-Sforza and Edwards' (1967) chord distances (Fig. 3).

Different loci were involved in distinguishing among the various populations. Cultus Lake fish stood apart with near fixation of the *ALAT*100* and *PGM-1*NULL* alleles (see also Wood et al. 1994). The two major clusters that contained Lake Washington populations were best distinguished from each other by allelic frequency variation at *LDH-A1* and, to a lesser degree, at *PGM-1**. Within the first population cluster (Baker Lake, Cedar River, Issaquah Creek, and the beach), frequencies of the *ALAT*100* and the *PGM-1*NULL* alleles distinguished between the Issaquah Creek fish and those from Cedar River and the beach (Table 2). Within the other population cluster (Bear Creek, Cottage Creek, and kokanee), kokanee differed markedly from the two sockeye salmon populations

Table 4. Documented levels of genetic differentiation within sockeye salmon lake systems.

		F_{ST}			
Lake	Location	*PGM-1**	*PGM-2**	*ALAT**	*LDH-A1**
Washington	Washington	0.089	0.012	0.006	0.144
Nachiki	Russia	—	0.007	—	—
Kuril	Russia	0.029	0.012	0.006	—
Dvu-Yurta	Russia	—	0.006	—	—
Clark	Alaska	0.008	0.010	0.025	—
Iliamna	Alaska	0.005	0.008	0.017	—
Karluk	Alaska	—	0.003	—	—
Meziadin	B.C.	0.010	0.006	0.004	—
Babine	B.C.	0.006	0.003	0.010	—
Shuswap	B.C.	0.054	0.009	—	—

Note: For Lake Washington, Wright's (1978) nonhierarchical fixation index (F_{ST}) was calculated for each highly polymorphic locus using BIOSYS-1 (Swofford and Selander 1981). Values for the other lake systems are from Varnavskaya et al. (1994*b*).

at *LDH-A1** and to a lesser degree at *PGM*1* and *PGM*2* (Table 2).

Fixation indices, calculated for sockeye salmon within the Lake Washington drainage, identified varying degrees of differentiation indicated by allelic variation at the different loci (Table 4). The higher values for *LDH-A1** and *PGM-1** reflected their broader range of allelic frequencies within the drainage and contrasted with the lower F_{ST} values and more limited allelic frequency ranges of *ALAT** and *PGM-2**. The average F_{ST} value for the highly polymorphic loci was 0.057, equivalent to an estimate of 2.64 effective migrants per generation (i.e., realized gene flow among the populations).

Discussion

The use of allozymes to infer ancestral origins and reproductive isolation assumes that electrophoretically detectable genetic variation is predominantly neutral with respect to selection (Allendorf and Phelps 1981; Utter 1991). The applicability of this assumption to the present study deserves consideration. For selection to override the effects of genetic drift, the coefficient of selection (s) would need to be considerably greater than the reciprocal of the effective population size, N_e (Chakraborty and Leimar 1987, p. 118). N_e was not estimated for the Lake Washington populations but the absolute number of spawners (N) has been at least as low as 100 for the beach (several years), 707 for Issaquah Creek (1990), 1795 for the Bear–Cottage system (1989), and 76 000 for the Cedar River (1993; Ron Egan, unpublished data). In each case, N_e would likely be much smaller than N owing to fluctuations in population size, unequal sex ratios, overlapping generations, and nonrandom mating (Hartl and Clark 1989), all of which are common in salmon populations. Some studies have reported a small apparent fitness advantage for individuals that were heterozygous at certain loci (e.g., Altukhov and Salmenkova 1991). However, genotype frequencies for the Lake Washington populations rarely deviated from Hardy–Weinberg expectations and the few that did were characterized by a heterozygote deficit. Hence, it is unlikely that $s \gg 1/N_e$ and effective neutrality was probably a valid assumption in the present study.

Ancestral origins

Two genetically divergent population groups were identified within Lake Washington (Figs. 2 and 3). One of these groups was comprised of sockeye salmon from the Cedar River, Issaquah Creek, and the beach (group 1), and the other was comprised of sockeye salmon from Bear Creek and Cottage Creek (group 2). This general pattern has been corroborated by independent processing, scoring, and statistical analysis using the fish collected in this study and additional fish collected from Lake Washington in 1994 (G. Winans and P. Aebersold, unpublished data). In the present study, the group 1 and group 2 populations were distinguishable from each other at several loci (Table 2), but most conspicuously at *LDH-A1**. In the independent analysis mentioned above, a larger suite of allozyme loci were used, revealing that the distinction between group 1 and group 2 populations extended to a number of other polymorphic loci not reported here (G. Winans and P. Aebersold, unpublished data).

The populations in group 1 showed a genetic affinity to fish collected from Baker Lake (Figs. 2 and 3). Thus, in conjunction with information on hatchery supplementation and the distribution and intensity of stocking efforts (see Introduction), the genetic data supported the inference that transplants from Baker Lake made a strong contribution to the Cedar River, Issaquah Creek, and beach populations. In contrast, the populations in group 2 were not closely related to either of the major donor populations (Baker Lake or Cultus Lake). In fact, they were more similar to Issaquah Creek kokanee than they were to the other Lake Washington sockeye salmon populations (Figs. 2 and 3). Hence, the Bear Creek and Cottage Creek populations do not appear to have been derived from any of the known introductions into the Lake Washington drainage. We infer that these fish represent native stocks that somehow persisted, albeit at low levels, in the Sammamish River tributaries despite considerable anthropogenic disturbances elsewhere in the watershed.

Other than Baker Lake, two non-native sources could conceivably have contributed to the Lake Washington gene pool. The contribution of the first source (in 1917) could not be evaluated using genetic techniques because its origin was unknown. However, success for this early transplant was unlikely because (*i*) it coincided with the diversion of Cedar River and the construction of the Lake Washington ship canal, (*ii*) only one introduction was made, and (*iii*) it was directly into the lake rather than a spawning stream (Ajwani 1956; Woodey 1966; Hendry 1995). Furthermore, introgression between native fish and returns from the transplant was unlikely because populations of anadromous sockeye salmon within the watershed were very small. Another possible source of non-native fish in the drainage was Cultus Lake (Woodey 1966; Seeb and Wishard 1977). In the present study, Cultus Lake fish were genetically distinct from all of the Lake Washington populations (Figs. 2 and 3), indicating that transplants from this location probably made little contribution to the existing Lake Washington gene pool. Nevertheless, frequencies for some alleles in the Lake Washington populations (particularly *ALAT*91* and *PGM-1*NULL*) were intermediate to those found at Baker Lake and Cultus Lake (Table 2). Therefore, we do not completely discount the possibility that Cultus Lake fish made some contribution to the Lake Washington sockeye salmon populations.

Within group 1, the three Lake Washington populations were more similar to each other than they were to the Baker Lake populations (Fig. 2). This pattern could have arisen for several reasons. First, the fish introduced to Lake Washington may not have been representative of the Baker Lake population at that time. This was unlikely because more than 3 million fry and fingerlings were introduced in a total of nine transplants over 5 years (Hendry 1995). Second, the Baker Lake fish, and (or) those transplanted to Lake Washington, could have introgressed with fish of another origin (see above). Introgression probably contributed to the divergence of the Lake Washington populations because both native and introduced fish persisted within the watershed. Third, genetic drift during the 47 years of isolation (1945–1992) could have resulted in the divergence of the ancestral and derived populations. Theoretically, this length of time (12 generations) would be sufficient for the observed level of divergence in the absence of selection or migration (Allendorf and Phelps 1981). Moreover, these populations have undergone several periods of low abundance (recently for Baker Lake and during the 1940s and 1950s for Lake Washington), which would have increased genetic drift and hence accelerated population divergence in a situation analogous to that postulated for pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes (Gharrett and Thomason 1987).

Population differentiation

The level of population differentiation, as measured by F_{ST}, was larger within Lake Washington than that documented within a number of other sockeye salmon lake systems (Table 4). This differentiation was reflected in significant genetic differences among many of the populations (Table 3). Some of this interpopulation genetic diversity was likely initiated by their multiple origins (i.e., Baker Lake or native) but subsequent gametic exchange among the populations has been insufficient to homogenize allelic frequencies. Therefore, natal homing has probably contributed to the differentiation of the various Lake Washington populations. However, significant genetic differences should not necessarily be interpreted as a complete lack of migration (Allendorf and Phelps 1981; e.g., Berg and Gall 1988). Accordingly, realized gene flow among the Lake Washington populations was estimated to be about 2.64 migrants per generation.

Estimates of gene flow from F_{ST} are subject to several assumptions that can limit their applicability in certain systems (Chakraborty and Leimar 1987; Ryman 1991). For instance, the calculation of $N_e m_e$ from F_{ST} assumes genetic and demographic equilibrium (Wright 1969; Slatkin 1994). For Lake Washington, the introductions of Baker Lake fish occurred less than 15 generations ago, a time frame where an equilibrium may not yet have been reached (Takahata 1983; Slatkin 1993). The possible violation of the equilibrium assumption dictates that 2.64 migrants per generation should be considered approximate. Nevertheless, the large genetic difference among several populations, the relatively high F_{ST}, and the indication that migration was restricted all attest to substantial reproductive isolation for several Lake Washington populations.

The greatest variation in allelic frequencies within the watershed was evident between the group 1 and group 2 populations. Within group 1, sockeye salmon from Issaquah Creek

were also distinguishable from those in Cedar River and from the beach (Table 3). This finding accords with that of Seeb and Wishard (1977), who reported genetic differences between sockeye salmon collected in Lake Sammamish and those collected in the Cedar River. Thus, there is evidence for at least three genetically distinct populations within Lake Washington: (*i*) Cedar River and the beach, (*ii*) Issaquah Creek, and (*iii*) Bear and Cottage creeks.

Allelic variation was not sufficient to distinguish between sockeye salmon from Bear and Cottage creeks or between the Cedar River and beach populations. The lack of a detectable difference in the former comparison was not unexpected because of the geographic proximity of the two creeks (<1 km) and the similar life histories of their sockeye salmon populations (Hendry and Quinn 1996). Conversely, the similarity of the Cedar River and the beach collections was surprising because other studies using allozymes (Seeb and Wishard 1977) and life history traits (Woodey 1966; Hendry and Quinn 1996) provided evidence that these populations were distinct. For example, Seeb and Wishard (1977) reported that the frequency for the *PGM-2*136* allele was 0.158 for Cedar River sockeye salmon but only 0.015 in beach fish. In the present study, this allele also occurred more frequently in the Cedar River population but the difference was smaller (0.090 vs. 0.044).

Allelic frequencies were stable in the Cedar River population but varied between years at the beach for two of the highly polymorphic loci (*ALAT** and *PGM-1**; Table 2). Temporal variation at the beach probably resulted from two factors. First, small population sizes (Woodey 1966; Ron Egan, unpublished data) would magnify the effects of genetic drift, and second, the small sample sizes would reduce the precision of allelic frequency estimates and the power of statistical tests (Utter et al. 1987). Thus, two competing hypotheses exist for the apparent similarity of the Cedar River and the beach populations. One is that straying from Cedar River, which usually has a population more than three orders of magnitude larger than the beach, may have had a homogenizing influence. Alternatively, the small N_e and small sample sizes at the beach may have limited the ability to detect differences.

Conclusions

Both native and introduced sockeye salmon contributed to the existing Lake Washington population mixture. The contribution of each lineage varied among the different spawning sites in proportion to the location and intensity of stocking. For instance, numerous transplants were made into Cedar River and into Issaquah Creek, populations that genetic analysis revealed to be primarily of non-native origin. In contrast, few transplants occurred into Bear and Cottage creeks, which appeared to have fish primarily of native origin. The intensity of stocking may also have contributed to the success of the Baker Lake transplants, relative to those from Cultus Lake, because many more fish were introduced from the former location. Nevertheless, the introductions from Cultus Lake were probably sufficient to produce some immediate returns to the watershed, thereby providing the potential for introgression with populations of native or Baker Lake origin. Consistent with this possibility, allelic frequencies in some Lake Washington populations were intermediate to those found in the Baker Lake and Cultus Lake populations.

Variation in life history, morphology, and behavior may also have contributed to the differential success of the two major donor groups. The sockeye salmon in Cultus Lake spawned primarily on lake beaches while those from Baker Lake spawned predominantly in tributary streams (Hendry and Quinn 1996). Presumably, the Baker Lake fish were adapted for reproduction in stream environments whereas the Cultus Lake fish were not. If this were true, the fitness of salmon transplanted from Baker Lake might have been higher than that of salmon transplanted from Cultus Lake because all of the introductions occurred into stream environments (primarily Cedar River and Issaquah Creek).

Among the populations derived primarily from Baker Lake, significant genetic differences were present. This result may reflect population divergence after the introduced populations became reproductively isolated from each other. The three derived populations also differed from the ancestral group. This difference between derived and ancestral populations could have resulted from introgression with native fish or with the fish introduced from Cultus Lake. Alternatively, it could indicate genetic divergence after the cessation of gene flow from Baker Lake into the Lake Washington drainage. Therefore, some evidence indicated two patterns of possible divergence: (*i*) between ancestral and derived groups, and (*ii*) among derived populations of the same lineage. The Lake Washington populations have only been completely isolated from the Baker Lake population since 1945 (12 generations). If the differences that arose during this time can be attributed to genetic drift, this study provided initial documentation of the rapidity with which neutral evolution can occur in Pacific salmon.

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