Origin and genetic structure of chinook salmon, *Oncorhynchus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence

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Abstract.—Chinook salmon, *Oncorhynchus tshawytscha*, transplanted from the Sacramento River, California, to the Waitaki River catchment of New Zealand at the turn of the century rapidly colonized many South Island rivers. Allozyme genotype and mtDNA haplotype frequencies were obtained from tissue samples from chinook salmon in Waitaki, Rakaia, Waimakariri, and Clutha rivers in New Zealand and compared with data from populations in the Sacramento River to provide further information on the origin of the NZ populations and to ascertain the genetic changes that have taken place since the transplant. Neither allozyme nor mtDNA unequivocally identified an ancestral "seasonal" run (fall, winter, or spring) for the NZ chinook salmon. Sacramento River samples collectively diverged from the NZ samples at allozyme loci, and mtDNA indicated greater similarity between NZ samples and fall-run rather than winter and spring runs from the Sacramento River. Significant variation was detected by mtDNA analysis between only two of the four populations within NZ, one of which has been landlocked by an impassable dam since 1956. The allozyme data identified significant variation within NZ, although less than has been documented among Sacramento River populations. The NZ populations also showed less genetic diversity (mean number of alleles per locus, proportion of loci that were polymorphic, and mean heterozygosity) than the Sacramento River populations. These lower values are consistent with a population bottleneck in the first generations after transplantation into the Waitaki River catchment and with founder effects during the formation of populations in the other NZ rivers. The combination of genetic differences and phenotypic variation among the NZ populations indicates that Pacific salmon populations can develop rapidly after colonizing suitable habitat.

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Salmonids display great interpopulation variation in life history traits, structure, behavior, and other characteristics, reflecting differences in rearing conditions and genetic adaptation to local environments (Ricker, 1972; Saunders, 1981; Taylor, 1991). Fisheries management attempts to be population-specific, reflecting the importance attached to these adaptations (e.g. McDonald, 1981). The past few years have seen a series of reports documenting losses of discrete Pacific salmon populations in the U.S. Pacific Northwest (Nehlsen et al., 1991; Alkire[1]) and in particular states (Washington: Palmisano et al.[2];

[1] Alkire, C. 1993. The living landscape. Vol. 1: Wild salmon as natural capital. Vol. 2: Pacific salmon and Federal lands. The Wilderness Society, Seattle, WA, 174 p.

Washington Dep. Fisheries[3]; Oregon: Lichatowich, 1989; Nickelson et al.[4]; Kaczynski and Palmisano[5]; California: Brown et al., 1994). The listing of certain populations of chinook, *Oncorhynchus tshawytscha*, and sockeye, *O. nerka*, salmon under the U.S. Endangered Species Act has further focused attention on the concepts of population differentiation and local adaptation (Waples, 1995).

Despite the importance of the "stock concept" in salmon management and the abundant examples of variation among populations, there is little direct information on genetic differentiation through the processes of selection and drift. Transplants, however, provide an opportunity to study these processes. Salmonid transplants, undertaken since at least the middle of the last century, have met with mixed success. Freshwater populations have been very widely established outside the native range of such species as brook trout, *Salvelinus fontinalis* (MacCrimmon and Campbell, 1969) and rainbow trout, *O. mykiss* (MacCrimmon, 1971), but anadromous populations have proven difficult to establish inside or outside the species' endemic range (Withler, 1982; Fedorenko and Shepherd, 1986; Harache, 1992). For example, anadromous sockeye salmon, rainbow trout (steelhead), and Atlantic salmon (*Salmo salar*) have established only freshwater populations in New Zealand (McDowall, 1990), and the pink salmon (*O. gorbuscha*) transplant to Newfoundland was unsuccessful (Lear, 1980). The most long-standing, successful establishment of an anadromous salmonid outside its native range has been the transplant of chinook salmon to New Zealand (NZ) (Fedorenko and Shepherd, 1986; Harache, 1992).

Between 1900 and 1906, chinook salmon embryos, probably originating from Battle Creek, a tributary of the Sacramento River (Fig. 1), were shipped to a hatchery on the Hakataramea River, a tributary of the Waitaki River (Fig. 2) on the South Island of NZ (McDowall, 1994). Within about 10 years, chinook salmon had established self-sustaining runs in other major rivers on the east coast of the South Island up to 230 km away (McDowall, 1990). No subsequent introductions were made, thus NZ chinook salmon developed from a discrete parent stock, relatively free from hatchery influence. The Battle Creek population has been maintained at the Coleman Hatchery (Cope and Slater, 1957); thus we had the opportunity to compare the genotypes of this and other Sacramento River populations with the NZ chinook salmon. In addition, chinook salmon from NZ rivers differ from each other in important, heritable life

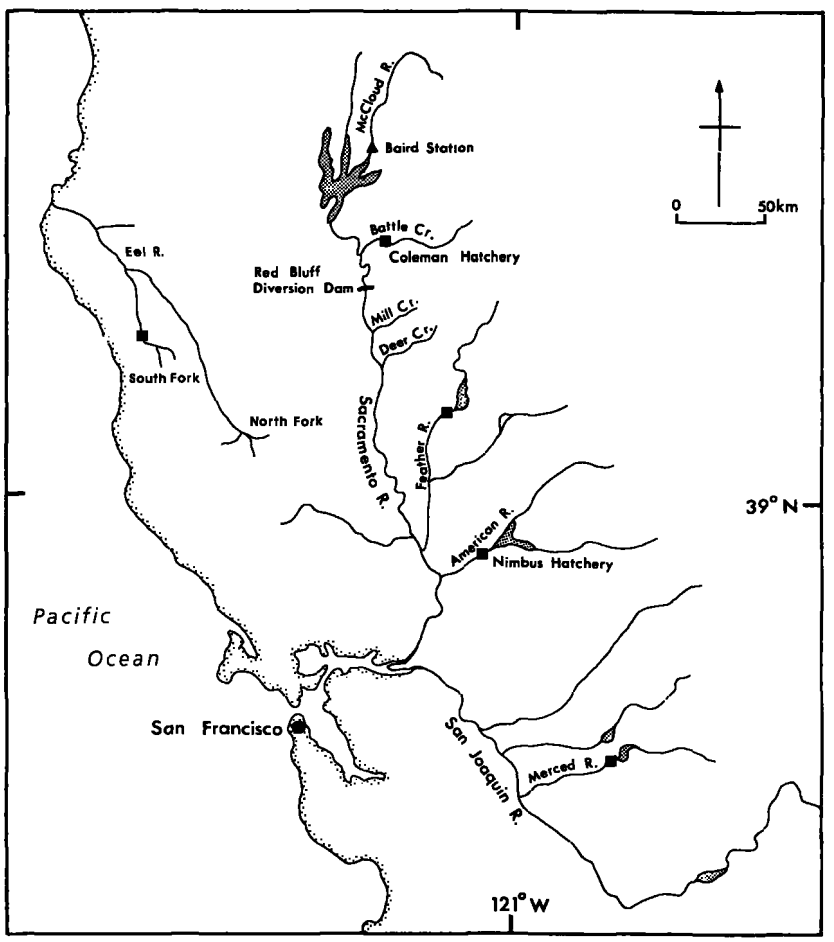

Figure 1

Map of the Sacramento River drainage showing the locations of populations of chinook salmon, *Oncorhynchus tshawytscha*, used in the genetic comparison with New Zealand populations.

[2] Palmisano, J. F., R. H. Ellis, and V. W. Kaczynski. 1993. The impact of environmental and management factors on Washington's wild anadromous salmon and trout. Washington Forest Protection Association and Washington Department of Natural Resources.

[3] Washington Department of Fisheries, Washington Department of Wildlife and Western Washington Treaty Indian Tribes. 1993. 1992 Washington State Salmon and Steelhead Stock Inventory, Olympia, WA, 211 p.

[4] Nickelson, T. E., J. W. Nicholas, A. M. McGie, R. B. Lindsay, D. L. Bottom, R. J. Kaiser, and S. E. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Dep. Fish and Wildlife, 83 p.

[5] Kaczynski, V. W., and J. F. Palmisano. 1993. Oregon's wild salmon and steelhead trout: a review of the impact of management and environmental factors. Oregon Forest Industries Council, 328 p.

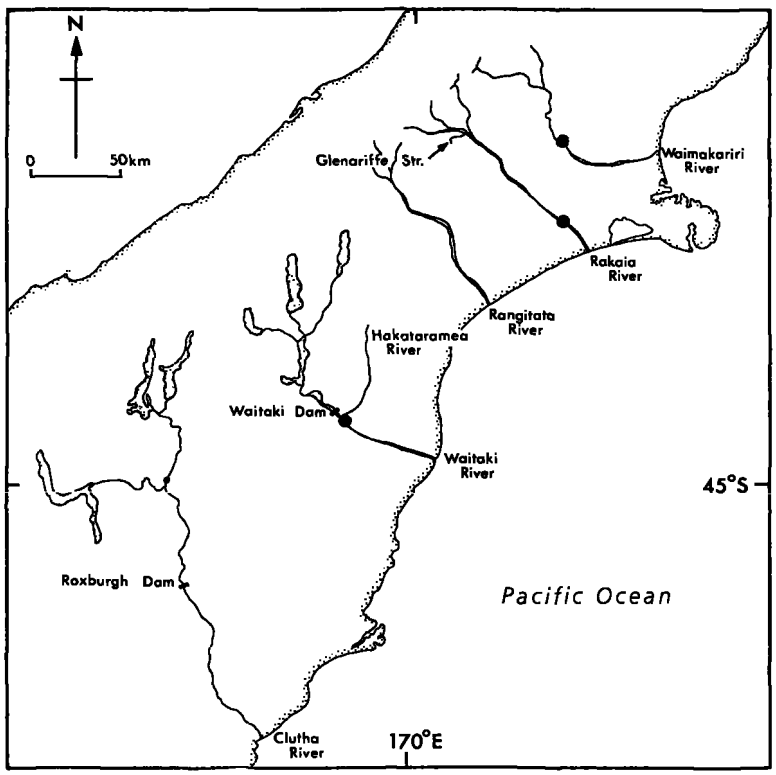

Figure 2

Map of the South Island of New Zealand showing the locations of populations of chinook salmon used in the genetic analysis.

history traits (Quinn and Bloomberg, 1992; Quinn and Unwin, 1993), raising the possibility that genetically distinct populations have evolved within about 20–25 generations and presenting the opportunity for an in-depth study of salmon population differentiation.

Genetic differentiation among populations may arise through selection regimes operating on heritable traits and through genetic drift at the time of colonization (founder effects) and after colonization. Examination of traits not subject to strong selection can provide insights into the importance of genetic drift. Allelic variation at protein-coding loci detected by protein electrophoresis, and more recently, direct examinations of mitochondrial (mt) and nuclear DNA have provided valuable sources of largely neutral molecular genetic markers that permit estimates of degrees of divergence among populations (e.g. Utter, 1991; Carvalho and Pitcher, 1994). Such techniques have helped identify source populations (Hendry et al., in press) and have shown differences between transplanted populations and their source population (Gharrett and Thomason, 1987; Ward et al., 1994) or differences among populations founded by colonization in the new habitat (Krueger and May, 1987). However, population divergence after transplantation is not always detected (Snowdon and Adam, 1992).

There is a substantial database for protein-coding loci on North American chinook salmon (e.g. Utter et al., 1989, 1992; Bartley and Gall, 1990; Bartley et al., 1992), including the Battle Creek population, and a growing database of mtDNA variation (Nielsen et al., 1994, a and b). These two types of data can be more powerful than either alone for studying relatively recent colonization events (Wade et al., 1994). The purposes of the present investigation were to use variation at protein-coding loci and mtDNA to investigate 1) the nature of the founding population (e.g. fall, winter, or spring), 2) whether NZ fish differ in gene frequencies from the descendants of the source population, 3) whether NZ populations differ from each other, and 4) whether NZ fish differ in the levels of genetic variation from descendants of the source population.

Materials and methods

History and origins of NZ chinook salmon

The first shipment of fertilized chinook eggs to NZ was collected from spring-run adults captured in the McCloud River, a tributary of the upper Sacramento River (Fig. 1), 2–27 Sept. 1875 (United States Commission of Fish and Fisheries, 1874–1901). Subsequent shipments of 100,000–500,000 chinook embryos from Baird Station on the McCloud River to the South Island continued to the end of the century, but no self-sustaining populations were established and records of even isolated individual salmon are subject to doubt (McDowall, 1994). There were apparently five shipments from California in the 1900's, arriving in NZ in January–February 1901 (500,000 embryos), 1904 (300,000), 1905 (300,000), 1906 (500,000), and 1907 (500,000; McDowall, 1994). McDowall (1994) concluded that the shipment which arrived in 1904 produced the first returns to the Hakataramea Hatchery in 1907 and that this and the subsequent shipments founded the NZ runs. These embryos were shipped from Battle Creek, but it is unclear whether they originated from Mill Creek or Battle Creek.

Collection of samples

Juvenile salmon (100 per population) were collected from the Waimakariri, Rakaia, and Waitaki rivers

(Fig. 2), three of the four major salmon-producing rivers in NZ (McDowall, 1990). Collection sites in the Waimakariri, Rakaia, and Waitaki rivers were 55, 18, and 57 km above the river mouths, respectively. All collections were made in mid-late summer (12 January to 2 February 1993), early enough in the season to ensure that both ocean-type and stream-type juveniles (Healey, 1991) would have been present (Hopkins and Unwin, 1987; Unwin and Lucas, 1993). Mean fork lengths (FL) ranged from 61 mm (Waitaki) to 76 mm (Waimakariri). Only 63 parr were caught in the Rakaia River mainstem, so another 38 (83 mm mean FL) were collected from the downstream trap on Glenariffe Stream, a major spawning tributary 94 km upstream from the mouth (Unwin, 1986). We also sampled 62 landlocked adults (409 mm mean FL) from Lake Dunstan, a hydroelectric impoundment in the upper Clutha River formed in 1992.

Allozyme analysis

Samples collected from NZ were frozen on dry ice and transported to the National Marine Fisheries Service Auke Bay Laboratory where they were stored at –80°C. Tissue extraction and protein electrophoresis procedures followed those described in Aebersold et al. (1987). Following initial screening for activity and variation at 71 loci, 24 polymorphic loci (Table 1) were selected for comparison with parallel allelic data reported for five Sacramento River populations by Bartley et al. (1992): fall chinook salmon from the Coleman Hatchery (Battle Creek), the Nimbus Hatchery (American River), and the Feather River Hatchery (all on tributaries of the lower Sacramento River); fall chinook salmon from the Merced River Hatchery on a tributary of the San Joaquin River; and wild winter-run chinook salmon from the upper Sacramento River. To provide additional perspective on the levels of genetic variation observed, we also analyzed data on fall chinook salmon from the South Fork of the Eel River, which enters the Pacific Ocean north of the Sacramento River (Bartley et al., 1992; Fig. 1). Compatible data within a subset of 10 out of the 24 polymorphic loci for three Sacramento River samples (Coleman Hatchery fall-run and both fall-run and spring-run from the Feather River Hatch-

Table 1

List of names and Enzyme Commission (E.C.) numbers of variable enzymes, and of designations, tissue distributions (E=eye, H=heart, L=liver, M=skeletal muscle, listed in sequence of optimal resolution) and relative mobilities of variant allelic forms of polymorphic loci.

Enzyme name	E.C. no.	Locus	Relative mobilities of variants	Tissue distribution
Aspartate aminotransferase	2.6.1.1	*mAAT-1**	-104	M, H
		*mAAT-2**	-125, -90	M, H
Adenosine deaminase	3.5.4.4	*ADA-1**	83, 108	M, E, H
Aconitate hydratase	4.2.1.3	*sAH**	86, 112	L
		*mAH-4**	119, 112	L
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B2**	60, 135	M
		*GPIr**	[1]	M
Glutathione reductase	1.6.4.2	*GR**	110	M, E, H, L
Hydroxyacylglutathione hydrolase	3.1.2.6	*HAGH**	65	M, H, L
L-iditol dehydrogenase	1.1.1.14	*IDDH-2**	61	L
Isocitrate dehydrogenase	1.1.1.27	*mIDHP-2**	150	M, E
		*sIDHP-1**	142, 83	M, H, E, L
		*sIDHP-2**	127, 50, 83, 66	H, E, L
Malate dehydrogenase	1.1.1.37	*sMDH-B2**	121, 70, 126	M, H, L
Malic enzyme	1.1.1.40	*sMEP-1**	78	M, H
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	109	M, H, E
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	90	M, E, H
Phosphoglucomutase	5.4.2.2	*PGM-2**	166	M, H, L
Phosphoglycerate kinase	2.7.2.3	*PGK-2**	90, 74	M, E, L
Dipeptidase	3.4.- -	*PEP-A**	90	M, E, H, L
Proline dipeptidase	3.4.- -	*PEP-D2**	107	M, H
Tripeptide aminopeptidase	3.4.- -	*PEP-B2**	108	M, H
Triose-phosphate isomerase	5.3.1.1	*TPI-2.1**	104, 106	M, E, H
		*TPI-2.2**	102	M, E, H

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

ery) reported in Utter et al. (1989) were also included 1) to provide data for spring-run fish from the Feather River Hatchery that were not examined by Bartley et al. (1992) and 2) for comparison among different year classes of fall-run fish. Genetic nomenclature followed Shaklee et al. (1990).

Genetic data for NZ and California populations were analyzed with the BIOSYS-1 program[6] to calculate pairwise measures of genetic distances (Cavalli-Sforza and Edwards, 1967; Nei, 1972), gene diversity (F_{ST}, Wright, 1969), chi-square comparisons of heterogeneity, and to construct phenograms through the unweighted pair-group method (Sneath and Sokal, 1973). A neighbor-joining tree (Saitou and Nei, 1987) was constructed from a matrix of arc distances (from Cavalli-Sforza and Edwards [1967]) through the NTSYS-pc program (Rohlf, 1994). Conformance of genotypic proportions of NZ collections to those expected under Hardy-Weinberg (binomial) equilibrium was tested by Levene's (1949) formula for small sample size; the variant alleles were pooled in tests involving loci with more than two alleles.

mtDNA analysis

Total genomic DNA was extracted from a small section of caudal fin tissue from 172 juvenile NZ salmon with Chelex-100 (Walsh et al., 1991) according to the protocol in Nielsen et al. (1994a). A 2-μL aliquot of the chelex-treated supernatant containing salmon DNA was used as a template for amplification with the polymerase chain reaction (PCR) and conserved primers. Our PCR protocol used primers (S-phe and P2; sequences in Nielsen et al., 1994a) that amplify a highly variable segment of the mtDNA control region in salmonids. Amplification, purification, and sequencing of salmon mtDNA were done according to the protocol in Nielsen et al. (1994a). Sequencing reactions were separated in linear 9% polyacrylamide-7 M urea gels and were autoradiographed for 24 to 72 h at room temperature. Mitochondrial DNA sequences were scored with base-pair (bp) differences found within the amplified control region sequence (Nielsen et al., 1994a).

Data on NZ chinook salmon mtDNA sequence frequencies were compared with data from Sacramento River chinook salmon with known spawning seasons (Nielsen et al., 1994b) as follows: winter-run: 72 fish taken from 1991 to 1993 broodstock program at the Coleman Hatchery; fall-run: 359 fish taken from 1992 to 1994 at hatcheries on the American, Merced, and Feather rivers; and spring-run: 32 wild fish collected in Deer and Mill creeks (1991–93) and 27 adults from the Butte Creek spring-run population (1994).

To test for differences in mtDNA frequency among the NZ chinook salmon populations and between the NZ and Sacramento River runs we used an unbiased estimate of Fisher's exact test for population differentiation with a Markov chain analysis (GENEPOP[7]). The Markov model in GENEPOP was run with 4 seeds for the pseudo-random number generator, and the dememorisation number was set to 1,000, the number of batches to 50, and with the number of iterations/batch to 1,000.

Results

Protein-coding loci: genetic variation within populations

Tests for conformance to Hardy-Weinberg genotypic proportions in the NZ populations indicated no deviation from proportions expected in a random mating population. Two tests out of 42 deviated significantly from expected proportions at the 5% level of significance; deficiencies of heterozygotes were observed for *sAH** in the Waimakariri and for *PEPA** in the Waitaki populations. This proportion of deviations (0.048) would be expected by chance at this level of significance. Similar findings were reported by Bartley et al. (1992) for wild California populations, although somewhat higher rates of deviation occurred among hatchery samples. No deviations with Sacramento River samples were reported in Utter et al. (1989). Levels of genetic variation were generally higher in the Sacramento River collections than in the NZ or South Fork Eel River samples (Table 2). The highest mean number of alleles per locus, percentage of loci polymorphic, and mean heterozygosity were seen in the Sacramento River collections, and no overlap in percentage of polymorphic loci occurred between these and any of the other collections.

Protein-coding loci: genetic variation among populations

Allele frequencies at 24 polymorphic protein-coding loci (Table 3) varied considerably among populations. The gene diversity among populations (F_{ST}) averaged

[6] Swofford, D. L., and R. B. Selander. 1989. BIOSYS-1: a computer for the analysis of allelic variation in population genetics and biochemical systematics, release 1.7. Illinois Natural History Survey, 43 p.

[7] Raymond, M., and F. Rousset. 1994. GENEPOP, version 1.0, January 1994. Available through M. Raymond, Laboratoire de Génétique et Environnement, URA CNRS 327, Place E. Bataillon, 34095 Montpellier cedex 05, France. E-mail: Raymond@univ-montp2.fr.

Table 2

Genetic variability at 24 polymorphic protein-coding loci of chinook salmon from rivers in the Sacramento River drainage and South Eel River, California (CA), and from New Zealand (NZ). A locus was considered to be polymorphic if the frequency of the most common allele did not exceed 95%. Mean heterozygosity was the Hardy-Weinberg expected value (Nei, 1978). Standard errors are in parentheses. CA data are from Bartley et al. (1992).

Population	Mean sample size per locus	Mean no. of alleles per locus	% of loci polymorphic	Mean heterozygosity
Battle Creek, CA	100.0	2.1 (0.1)	58.3	0.156 (0.032)
Merced River, CA	100.0	1.8 (0.1)	46.2	0.141 (0.029)
Feather River, CA	100.0	2.0 (0.1)	50.0	0.151 (0.032)
American River, CA	100.0	2.0 (0.1)	58.3	0.164 (0.032)
Upper Sacramento River, CA	94.0	1.9 (0.1)	45.8	0.142 (0.033)
South Eel River, CA	95.8	1.6 (0.1)	29.2	0.113 (0.035)
Rakaia River, NZ	80.9	1.7 (0.1)	29.2	0.111 (0.033)
Waimakariri River, NZ	77.3	1.9 (0.1)	41.7	0.137 (0.032)
Waitaki River, NZ	67.1	1.8 (0.1)	33.3	0.117 (0.033)

over all loci was 0.051, and ranged among individual loci from 0.002 for *mAAT-2** and *PEP-D2** to 0.217 for *GPI-B2** (Table 4). Matrices of pairwise comparisons of two measures of genetic distance (Cavalli-Sforza and Edwards, 1967; Nei, 1972) among populations (Table 5) provided the basis for identifying possible distinct population groupings reflected in this diversity. The UPGM projection of pairwise measures of Nei's distance (Fig. 3A) separated the South Fork Eel River fish from the remaining collections. Two subgroups, comprising the Sacramento and NZ populations, were also apparent. In the Sacramento River subgroup, the Merced Hatchery (San Joaquin River) fall-run fish diverged from the Battle Creek (Coleman Hatchery), Feather River, and American River (Nimbus Hatchery) fall-run fish and from the wild Sacramento River winter-run fish. The three NZ populations grouped more closely within their subgroup than did the Sacramento River populations within theirs. The matrix of Cavalli-Sforza and Edwards distances (Table 5) revealed a comparable UPGM clustering (not pre-

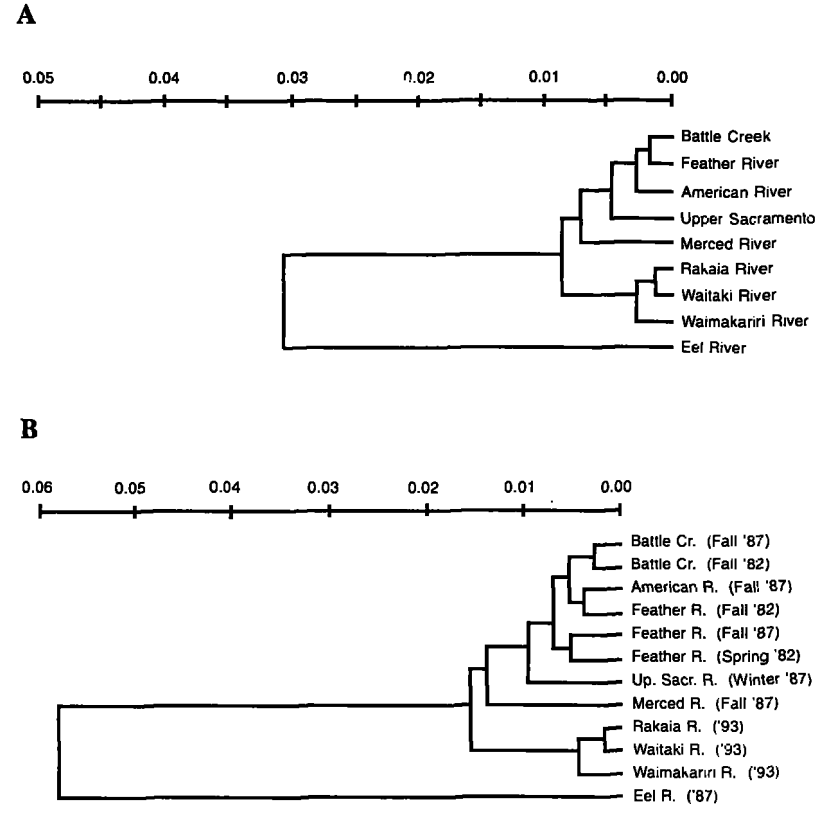

Figure 3

UPGM phenograms of chinook salmon populations from California and New Zealand based on pairwise Nei's (1972) relative genetic distance measures. (**A**) Data from 24 polymorphic loci for collections 1–9. (**B**) Data from 10 polymorphic loci for collections 1–12 (see Table 4 for details).

Table 3

Allele frequencies of 24 polymorphic protein-coding loci for chinook salmon collections (year follows in parentheses) from California: 1 = Battle Creek, fall-run (1987); 2 = Merced River, fall-run (1987); 3 = Feather River, fall-run (1987); 4 = American River, fall-run (1987); 5 = Upper Sacramento River, winter-run (1987); 6 = South Eel River, fall-run (1987) and New Zealand; 7 = Rakaia River (1993); 8 = Waimakariri River (1993); and 9 = Waitaki River (1993). Data for collections 1–6 are from Bartley et al. (1992). Additional California data for 10 loci (from Utter et al., 1989) are provided: 10 = Feather River, spring-run (1982); 11 = Battle Creek fall-run (1982); and 12 = Feather River, fall-run (1982).

	Collection											
Locus	1	2	3	4	5	6	7	8	9	10	11	12
mAAT-1*												
(*n*)	100	100	100	100	94	98	80	83	80			
**100*	0.960	1.000	0.975	1.000	0.995	1.000	1.000	1.000	1.000			
**-104*	0.040	0.000	0.025	0.000	0.005	0.000	0.000	0.000	0.000			
*mAAT-2**												
(*n*)	100	100	100	100	94	46	80	83	80			
**100*	0.995	1.000	0.995	1.000	1.000	0.989	1.000	0.982	1.000			
**-125*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**-90*	0.000	0.000	0.005	0.000	0.000	0.011	0.000	0.018	0.000			
ADA-1*												
(*n*)	100	100	100	100	94	99	81	83	23	50	300	200
**100*	1.000	0.870	0.955	0.960	1.000	1.000	1.000	0.982	0.978	1.000	0.999	1.000
**83*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.001	0.000
**108*	0.000	0.130	0.045	0.040	0.000	0.000	0.000	0.006	0.022	0.000	0.000	0.000
sAH*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.775	0.765	0.885	0.835	0.862	0.995	0.778	0.831	0.850	0.720	0.815	0.797
**86*	0.200	0.165	0.105	0.130	0.128	0.005	0.210	0.157	0.131	0.240	0.173	0.195
**112*	0.025	0.070	0.010	0.035	0.011	0.000	0.012	0.012	0.019	0.040	0.012	0.007
mAH-4*												
(*n*)	100	100	100	100	94	99	81	74	55			
**100*	0.925	0.905	0.860	0.925	0.957	0.874	0.938	0.858	0.891			
**119*	0.020	0.065	0.035	0.020	0.011	0.126	0.062	0.142	0.100			
**112*	0.055	0.030	0.105	0.055	0.032	0.000	0.000	0.000	0.009			
GPI-B2*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.940	0.965	0.925	0.930	0.777	0.535	1.000	1.000	0.994	1.000	0.945	0.900
**60*	0.040	0.035	0.065	0.070	0.064	0.465	0.000	0.000	0.006	0.000	0.055	0.100
**135*	0.020	0.000	0.010	0.000	0.160	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPIr*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	0.715	0.755	0.615	0.655	0.644	1.000	0.469	0.392	0.538	0.576	0.705	0.689
**r*^{1}	0.285	0.245	0.385	0.345	0.356	0.000	0.531	0.608	0.462	0.424	0.295	0.311
GR*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	1.000	1.000	1.000	1.000	1.000	1.000	0.981	0.958	1.000	1.000	1.000	1.000
**110*	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.042	0.000	0.000	0.000	0.000
HAGH*												
(*n*)	100	100	100	100	94	99	81	78	8			
**100*	1.000	1.000	1.000	0.990	1.000	1.000	0.975	0.865	1.000			
**65*	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.135	0.000			

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Table 3 (continued)

	Collection											
Locus	1	2	3	4	5	6	7	8	9	10	11	12
IDDH-2*												
(*n*)	100	100	100	100	94	97	81	25	59			
**100*	0.990	0.990	0.975	0.990	0.984	0.985	1.000	1.000	1.000			
**61*	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000			
**20*	0.000	0.010	0.025	0.010	0.016	0.000	0.000	0.000	0.000			
mIDHP-2*												
(*n*)	100	100	100	100	94	98	81	69	56			
**100*	0.905	0.885	0.950	0.830	0.941	0.990	1.000	1.000	0.973			
**150*	0.095	0.115	0.050	0.170	0.059	0.010	0.000	0.000	0.027			
*sMDH-B2**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.920	0.935	0.955	0.905	0.979	1.000	0.957	0.928	0.956	0.945	0.968	0.977
**121*	0.070	0.040	0.045	0.065	0.021	0.000	0.043	0.072	0.044	0.055	0.032	0.023
**70*	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
**126*	0.010	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*sMEP-1**												
(*n*)	100	100	100	100	94	79	81	74	20			
**100*	0.805	0.860	0.810	0.775	0.851	0.557	0.895	0.858	0.775			
**78*	0.195	0.140	0.190	0.225	0.149	0.443	0.105	0.142	0.225			
*MPI**												
(*n*)	100	100	100	100	94	99	81	79	78	50	300	200
**100*	0.585	0.700	0.580	0.545	0.617	0.818	0.556	0.570	0.551	0.510	0.586	0.487
**109*	0.415	0.300	0.420	0.455	0.383	0.182	0.444	0.430	0.449	0.497	0.414	0.513
*PGDH**												
(*n*)	100	100	100	100	94	99	81	83	78			
**100*	0.975	0.900	0.960	0.920	0.979	1.000	0.975	0.976	1.000			
**90*	0.025	0.100	0.040	0.080	0.021	0.000	0.025	0.024	0.000			
*PGM-2**												
(*n*)	100	100	100	100	94	99	81	83	71			
**100*	0.990	1.000	0.995	1.000	0.995	1.000	0.994	0.988	0.972			
**166*	0.010	0.000	0.005	0.000	0.005	0.000	0.006	0.012	0.028			
*PGK-2**												
(*n*)	100	100	100	100	94	99	81	83	71	50	300	200
**100*	0.495	0.670	0.490	0.605	0.590	0.480	0.704	0.705	0.718	0.540	0.592	0.651
**90*	0.505	0.330	0.510	0.395	0.410	0.520	0.296	0.289	0.282	0.460	0.408	0.349
**74*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000
*PEP-A**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.810	0.950	0.850	0.875	0.894	0.965	0.951	0.952	0.938	0.890	0.869	0.905
**90*	0.190	0.050	0.150	0.125	0.106	0.035	0.049	0.048	0.063	0.110	0.131	0.095
PEP-D2												
(*n*)	100	100	100	100	94	98	81	82	70			
**100*	0.995	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000			
**107*	0.005	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000			

continued on next page

Table 3 (continued)

	Collection											
Locus	1	2	3	4	5	6	7	8	9	10	11	12
*TPI-2.1**												
(*n*)	100	100	100	100	94	99	81	83	76			
*100	0.945	0.830	0.915	0.870	0.936	0.899	0.988	1.000	0.974			
*104	0.055	0.170	0.085	0.130	0.064	0.000	0.012	0.000	0.026			
*106	0.000	0.000	0.000	0.000	0.000	0.101	0.000	0.000	0.000			
*TPI-2.2**												
(*n*)	100	100	100	100	94	99	81	83	80			
**100*	0.930	0.965	0.950	0.960	1.000	0.975	0.988	0.982	1.000			
**102*	0.070	0.035	0.050	0.040	0.000	0.025	0.012	0.018	0.000			
*PEP-B2**												
(*n*)	100	100	100	100	94	99	81	45	69	50	300	200
**100*	0.890	0.955	0.950	0.940	0.862	0.965	0.957	0.900	0.949	0.950	0.842	0.889
**108*	0.110	0.045	0.050	0.060	0.138	0.035	0.043	0.100	0.051	0.050	0.158	0.111
*sIDHP-1**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.995	1.000	1.000	1.000	0.952	1.000	1.000	1.000	1.000			
**142*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**83*	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000			
*sIDHP-2**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.905	0.995	0.895	0.875	0.910	0.859	0.914	0.873	0.956			
**127*	0.090	0.005	0.105	0.125	0.085	0.141	0.086	0.120	0.032			
**50*	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000			
**83*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**66*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.013			

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

sented), and a neighbor-joining tree (Fig. 4) also displayed similar clustering, that separated the NZ and Sacramento River populations.

Relationships from the subset of 10 polymorphic loci (Fig. 3B) paralleled those indicated with 24 loci (Fig. 3A). Each of the additional three samples from Utter et al. (1989) were grouped within the clustering of Sacramento River collections reported by Bartley et al. (1992). Notably, the spring-run collection from the Feather River Hatchery was indistinct from fall-run collections from the Feather River and from other Sacramento River hatcheries. Furthermore, the stability of allele frequencies at these loci was evident for fall-run fish collected as juveniles in 1982 (Utter et al., 1989) and 1987 (Bartley et al., 1992).

Decreasing heterogeneity among the 24 loci was apparent when chi-square tests within subgroups were contrasted with those involving all collections (Table 4). Within the total grouping, all but two loci were heterogeneous ($P<0.01$). A lower level of significance occurred for 9 loci within the Sacramento River and for all but one locus among the NZ collections. Standardized measures of these differences indicated more than a doubling of heterogeneity for the Sacramento subgroup relative to the NZ subgroup, and a near doubling of the total heterogeneity relative to the Sacramento collections.

Much of the total heterogeneity reflected the distinction of the South Fork Eel River collection from the remaining group, notably owing to allele frequency differences approaching or exceeding 0.4 at *GPI-B2** and *GPIr**, and to only slightly lower distinctions at *sMEP-1**, and *MPI** (see Table 3). Allelic differences between the Sacramento and NZ subgroups were more subtle. Nonoverlapping frequencies at many loci (*GPI-B2**, *GPIr**, *IDDH-2**, *IDH-2**, *PGM-2**, *PGK-2**, *TPI-2.1**) contributed to their differentiation. In addition, some variants in the NZ subgroup were either absent in all the Sacramento subgroups (*GR**) or occurred at a very low frequency

and not in the Battle Creek population (*HAGH**).

Mitochondrial DNA: genetic variation among populations

There were no new base substitutions found in the 171-bp section of the mtDNA control region of the NZ chinook sequence that we sequenced, compared with mtDNA types reported for Sacramento River chinook (Table 1 in Nielsen et al., 1994b). However, because the base change recorded at bp 183 contained a cryptic deletion that was difficult to score consistently in the NZ fish, we pooled mtDNA types 1 and 4 (as previously reported), which were originally differentiated by a single deletion at bp 183. The same cryptic nucleotide deletion was found in haplotype 3 in the NZ chinook; therefore, the base cytosine (C) and the deletion found at this site were pooled for all populations, yielding five mtDNA types used in this analysis (Table 6).

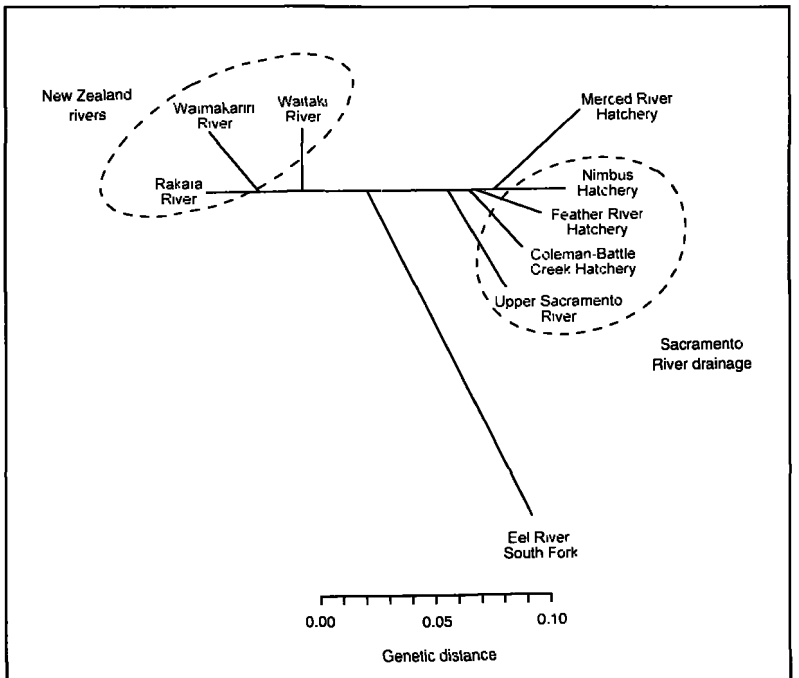

Figure 4

Neighbor-joining tree (Saitou and Nei, 1987) displaying relationships among chinook salmon populations from California and New Zealand based on a matrix of genetic distance measures (Cavalli-Sforza and Edwards, 1967; Table 5). Dashed circles enclose the three New Zealand and four Sacramento River populations.

The NZ salmon populations were dominated by mtDNA haplotype 1, representing 82% in the pooled sample compared with 69% in the Sacramento River population (Table 7). Haplotype 2 was rare in the NZ fish (only one sample was found, from the Waimakariri River) and detected only in fall-run fish from the Sacramento River. Haplotype 3 was detected at low frequencies in NZ and in the Sacramento River fall-run fish. This haplotype was found at higher frequencies in the 1994 spring-run samples taken at Butte Creek and not at all in the Deer and Mill Creeks spring-run collection (1991–93) or the winter-run California chinook. Fish carrying haplotype 5 in the Clutha and Waitaki NZ chinook shared a close frequency distribution to that observed in the Sacramento River fall-run fish. The frequency distribution of haplotype 5 in the Sacramento River fall-run population was primarily due to an increase in its relative abundance in one year class (1994). Haplotype 6 was found only in the winter-run Sacramento fish and not in any NZ population.

The Fisher's exact tests, which compared the total NZ chinook population with each of the three Sacramento River runs of chinook were compared, indicated that the NZ chinook differed significantly from the winter- and spring-run fish ($P<0.001$) but not from the fall-run samples ($P=0.08$). Haplotype frequencies varied among the four NZ populations, but the Clutha River population, with only two mtDNA variants (1 and 5), was the only population to differ ($P<0.01$) from any other population (Rakaia; Table 7).

Discussion

Contrasts among population groups

The allozyme and mtDNA data sets provided complementary and independent comparisons for considering the origin and differentiation of the NZ chinook salmon populations. At the broadest level, the Sacramento and NZ populations share a common lineage (Figs. 3 and 4). The collection from the Eel River, though geographically adjacent to the Sacramento drainage, is typical of a distinct coastal lineage, distinguished by high frequencies of *GPI-2** variation and monomorphism for *GPIr** (Utter et al., 1989; Bartley and Gall, 1990; Bartley et al., 1992). At a finer level, some details of the separate Sacramento and NZ subgroups were apparent from both data sets. The most obvious distinction was the greater degree of divergence among the Sacramento populations on the basis of comparative genetic distances (Table 4; Fig. 3), allelic heterogeneity and partitioning of gene

Table 4

Contingency chi-square (χ^2) analyses and degrees of freedom (df) among all collections (from South Fork Eel River, Sacramento River (CA), and from New Zealand) with data from 24 protein-coding loci, and the Sacramento River and New Zealand subgroups. "—" indicates fixation for common allele in compared group. Significance levels are indicated as follows: ns ($P>0.05$); * ($0.05 > P > 0.01$); ** ($0.01>P>0.001$); *** ($P<0.001$). Standardized measure is χ^2/df.

	Collections included in analysis								
	Total			Sacramento River			New Zealand		
Locus	χ^2	df	P	χ^2	df	P	χ^2	df	P
*mAAT-1**	40.052	8	***	18.035	4	**	—	—	—
*mAAT-2**	23.833	16	ns	7.886	8	ns	5.819	4	ns
*ADA-1**	117.915	16	***	53.655	4	***	5.731	4	ns
sAH	81.151	16	***	26.092	8	**	4.007	4	ns
*mAH-4**	108.921	16	***	25.984	8	**	8.349	4	ns
*GPI-B2**	606.586	16	***	106.551	8	***	2.054	2	ns
*GPIr**	202.800	8	***	11.804	4	*	6.991	2	*
*GR**	48.936	8	***	—	—	—	7.194	2	*
*HAGH**	168.593	16	***	7.896	4	ns	15.227	2	***
*IDDH-2**	48.413	24	**	13.442	8	ns	—	—	—
*mIDHP-1**	82.834	8	***	20.898	4	***	8.095	2	*
*sMDH-A2**	91.154	24	***	43.336	12	***	1.803	2	ns
*sMEP-1**	80.033	8	***	6.577	4	ns	4.105	2	ns
*MPI**	53.112	8	***	11.540	4	*	0.118	2	ns
*PGDH**	50.497	8	***	19.048	4	***	3.871	2	ns
*PGM-2**	15.185	8	ns	3.503	4	ns	2.6372	2	ns
*PGK-2**	67.987	16	***	19.290	4	***	1.915	4	ns
*PEP-A**	54.293	8	***	19.817	4	***	0.404	2	ns
*PEP-D2**	10.770	8	ns	5.249	4	ns	—	—	—
*TPI-2.1**	237.524	8	***	20.386	4	***	4.452	2	ns
*TPI-2.2**	72.565	16	***	13.327	4	**	2.729	2	ns
*PEP-B2**	29.622	8	***	17.997	4	**	3.624	2	ns
*sIDHP-1**	78.781	16	***	42.576	8	***	—	—	—
*sIDHP-2**	60.541	32	**	22.329	16	**	10.752	4	*
Totals	2,387.107	320	***	548.327	136	***	99.878	50	***
Standarized measure		7.36			4.42			2.08	
F_{ST}		0.051			0.013			0.005	

Table 5

Matrix of genetic distance coefficients based on 24 protein-coding loci. Below the diagonal (****) are estimates of Nei's (1972) genetic distance; above the diagonal are Cavalli-Sforza and Edwards (1967) chord distances.

	Collection								
Collection and site	1	2	3	4	5	6	7	8	9
1 Battle Cr.	****	0.097	0.060	0.067	0.077	0.162	0.100	0.122	0.092
2 Merced R.	0.006	****	0.082	0.072	0.107	0.172	0.111	0.133	0.093
3 Feather R.	0.002	0.006	****	0.059	0.076	0.159	0.098	0.116	0.082
4 Nimbus R.	0.002	0.004	0.002	****	0.091	0.167	0.107	0.127	0.090
5 Upper Sacra. R.	0.003	0.006	0.003	0.004	****	0.162	0.102	0.124	0.092
6 South Eel R.	0.023	0.025	0.023	0.024	0.022	****	0.180	0.190	0.166
7 Rakaia R.	0.007	0.008	0.006	0.006	0.006	0.038	****	0.053	0.063
8 Waimakariri R.	0.011	0.013	0.008	0.009	0.008	0.042	0.002	****	0.085
9 Waitaki R.	0.006	0.007	0.004	0.004	0.005	0.031	0.002	0.003	****

diversity (Table 2). Greater mtDNA haplotype diversity also occurred within the Sacramento subgroup where haplotype 6, detected in winter-run fish, was absent from the NZ fish. These observations comport with the introduction of Sacramento River chinook from a single source to NZ a century ago.

In the NZ collections, the common clustering (Figs. 3 and 4) and generally lower heterozygosities and percentages of polymorphic loci (Table 2) support the occurrence of a limited effective population size (i.e. a "bottleneck") during the founding and perhaps during the early generations of these populations. Enhanced genetic drift resulting from a bottleneck followed by a larger and more stable population size would explain the common clustering of these collections and the lower levels of genetic variation, compared with those observed in the Sacramento River collections. There are no records of population sizes in the first few generations, but natural mortality and the general tendency of salmon to home would have reduced the number of adults colonizing the rivers. Current populations (catch plus escapement) are on the order of 10,000 adults in the four major rivers, including the three sampled in this study.

Several factors might have contributed to the initial bottleneck. The founding population probably represented more females than males, as hatchery staff commonly spawn females with a few "choice" males. The founding individuals experienced a very different environment and presumably a different selection regime from the Sacramento River. The NZ chinook salmon rivers lack the estuary used by fall chinook salmon in the Sacramento River system (Kjelson et al., 1982), and smolts unable to make the abrupt transition to seawater may have died. The surviving smolts of the first generation experienced ocean currents, temperature, and other factors influencing migratory patterns and orientation that differed from those experienced off the coast of California. There may have been strong selection for coastal distribution or other behavior patterns facilitating homeward orientation. Upon return, the mature adults found short, steep, gravel-rich, unstable, recently deglaciated rivers, whose channels lacked woody debris. In addition to these habitat differences that may have exerted selection on the founding generations, the nature of the salmonid mating system (semelparous life cycle and intrasexual competition for nesting sites or mates) also generates considerable variation in reproductive success, especially among males (e.g. Fleming and Gross,

Table 6

Four variable base-pair sites and nucleotide changes found in five chinook salmon mtDNA types from four wild populations in New Zealand and from fish collected in the Sacramento River, California, 1991–93.

MtDNA type	*n*	Variable sites			
		47	125	134	183
1 and 4	479	G	T	C	C/*
2	15	A	T	C	C
3	59	G	T	A	C/*
5	107	G	T	C	A
6	2	G	81i[1]	C	C

[1] The symbol "81i" represents an 81-bp exact repeat. An asterisk (*) represents a nucleotide deletion. The complete sequence amplified in chinook salmon by the primers S-phe and P2 is given in Nielsen et al. (1994a).

Table 7

The numbers of fish (% in parentheses) found in five variable mtDNA haplotypes in populations of chinook salmon from New Zealand and the Sacramento River.

Population	*n*	mtDNA haplotype				
		1 and 4	2	3	5	6
Winter-run (CA)	72	70 (97)	0	0	0	2 (3)
Fall-run (CA)	359	233 (65)	14 (4)	35 (10)	77 (21)	0
Spring-run (CA)	59	35 (59)	0	16 (27)	8 (14)	0
CA total	490	338 (69.0)	14 (2.9)	51 (10.4)	85 (17.3)	2 (0.4)
Clutha (NZ)	62	51 (82)	0	0	11 (18)	0
Waitaki (NZ)	34	26 (76)	0	1 (3)	7 (21)	0
Rakaia (NZ)	37	30 (81)	0	6 (16)	1 (3)	0
Waimakariri (NZ)	39	34 (87)	1 (3)	1 (3)	3 (8)	0
NZ total	172	141 (82.0)	1 (0.6)	8 (4.7)	22 (12.8)	0

1994; Quinn and Foote, 1994) and may have reduced the effective population size further.

Ancestral population of New Zealand chinook salmon

Although the genetic and historical data clearly point to a seeding of NZ chinook from a Sacramento River population, identification of the specific ancestral population remains difficult. In addition to possible genetic changes in NZ chinook salmon over the years, the California populations have also undergone complex changes in abundance, habitat, and management since the turn of the century. Moreover, the seasonal runs are not monophyletic races but have apparently evolved independently in suitable habitats; hence major ancestral groups are generally based more on geography than on the timing of a run (Utter et al., 1993).

Aside from confirming a Sacramento River origin, the allozyme data provided no clues about the ancestral population. Both the absence of distinct alleles or of distinguishing frequencies of common alleles among contemporary temporal segments within the Sacramento River and the high genetic drift associated with the presumed bottlenecking in NZ precluded resolution from these nuclear variants. The mtDNA D-loop data, which theoretically provide higher resolving capabilities owing to higher mutation rates and greater population divergence of the haploid genome (Brown et al., 1982; Hoelzel et al., 1991), gave some clues but no definitive answers about the ancestral population (Table 7). The rate of molecular base changes at any one locus can vary according to the number and size of colonies, migration rates, sex ratios, type of parental transmission, as well as the expected rate of genetic drift (Birky et al., 1989; Martin and Palumbi, 1993). The haplotype profile of the Sacramento River fall-run fish resembled that of the combined NZ fish, sharing four haplotypes (1 and 4, 2, 3, 5). In contrast, the winter-run fish were the most distinct, lacking haplotypes 2, 3, and 5, and were represented by a unique haplotype 6 in two individuals. The spring-run sample contained haplotype 3 at a significantly higher frequency than that found for any NZ populations but shared a similar frequency profile for haplotype 5 with the combined NZ sample.

The genetic signatures of the spawning runs of chinook salmon found in the Sacramento River have probably changed since the transfers to NZ at the turn of the century owing to population bottlenecks (particularly the winter-run), hatchery manipulation, impacts from fisheries, changes in habitat, and changes in the thermal regime leading to overlap in temporal spawning populations. Prior to development of the Sacramento River system, Battle Creek had fall and spring runs of chinook salmon, and the current populations in the hatchery may have introgressed to some extent or been altered by interchange with chinook from other populations, despite efforts to maintain the runs separately. Cope and Slater (1957) noted that changes in the river's temperature regime delayed the arrival of spring-run fish at Battle Creek and that "This behavior, together with the fact that these two runs were forced to spawn on the same riffles, with the blocking of the river at Keswick Dam, is presumed to have brought about some mixing of the two stocks . . . when their spawning periods overlap in September. . . . At the hatchery . . . the dividing point between the spawning seasons of the two runs has been more or less arbitrarily set at September 25." Contemporary chinook salmon runs are defined by the timing of adult migration up the Sacramento River (Healey, 1991; Fisher[8]): fall-run (September–October), winter-run (November–February), and spring-run (March–May). These runs also differ in their spawning periods: fall-run (October–December), winter-run (May–June), and spring-run (August–September). Currently, there is also a putative "late fall-run," spawning in winter; unsampled in this study, these fish differed marginally from the fall-run in haplotype frequencies (Nielsen et al., 1994b). According to temporal criteria, the type of chinook embryos sent to NZ at the turn of the century were probably fall-run fish because Thomson (1922) reported that the shipments from California arrived ". . . early in January." Both the spawning season of the winter-run populations (late spring to early summer) and their mtDNA haplotype distribution indicate that they did not found the NZ chinook runs.

Some of the allozyme data raise additional questions about the ancestral population. Allelic variants at two loci occurred in two of the three NZ collections that were either rare (*HAGH*65*) or did not occur in any Sacramento River fish (*GR*110*). The occurrence of both of these variants in two populations (Rakaia and Waimakariri) and at frequencies as high as 0.135 (*HAGH*65*) minimizes the possibility of mutation after colonization. More likely, the variants were present in the founder population. If so, these alleles have drifted to a very low frequency or out of the sampled California populations or they were present in unusually high proportions in the founder population in NZ or in the two rivers in particular.

[8] Fisher, F. 1995. Calif. Dep. Fish and Game, Red Bluff, CA. Personal commun.

Interpopulation differences in NZ chinook

The reduced divergence among the three NZ populations indicated by the allozyme data, relative to the Sacramento River populations, may reflect the recent origins of the NZ groups. The similar magnitude of divergence evident among the NZ populations and between years within two Sacramento River fall-run hatchery populations (Fig. 3B) suggested no differentiation beyond year-class variation of a single population. The frequency of mtDNA types among the NZ stocks also did not indicate isolation between most populations. However, Clutha River fish (which expressed only two of the five haplotypes found in NZ samples) tended to be the most different, especially from Rakaia River fish. The Clutha River population, for which we had no allozyme data, was planted from the Hakataramea River in 1917 (McDowall, 1994) but has been landlocked since 1956 by Roxburgh Dam and may have undergone a population bottleneck after completion of the dam. The Clutha River population is thus less susceptible to genetic exchange than the three anadromous populations sampled, likely to be less polymorphic, and hence is not typical of NZ chinook.

The gene-frequency differences among the anadromous populations are consistent with panmixia caused by straying or successful transfers of salmon among the rivers. Unwin and Quinn (1993) documented straying rates of about 12% by hatchery-released chinook salmon from the Rakaia River to other NZ rivers. In addition, during the 1980's several million juvenile salmon were transferred from the Rakaia, Rangitata, and Waimakariri Rivers to virtually all major east coast rivers except the Rakaia River. Nevertheless, the populations now differ in many life history traits, including fecundity (Quinn and Bloomberg, 1992), freshwater and marine age, length at age, weight at length, date of return to freshwater, and spawning date (Quinn and Unwin, 1993), and egg size and body shape.[9] These phenotypic differences are consistent with some level of genetic isolation among the populations but do not demonstrate it (Waples, 1995).

Our results provide a perspective on the management and conservation of salmon populations. Founder effects or strong selection against certain genotypes can reduce the genetic diversity of populations established by colonization, relative to the source population. However, the NZ experience indicates that this may not prevent the transplant from being successful. The life history differences among NZ populations indicate that salmon populations may evolve quite quickly, although the genetic basis of the life history differences seen in NZ has yet to be demonstrated. The implications of such rapid evolution are open to interpretation. One might argue that it demonstrates the importance of the stock concept in salmon management because reduced gene flow and population adaptation are such fundamental aspects of salmon biology. One might be encouraged to attempt to restore salmon populations to areas from which they have been extirpated, given a suitable source population. However, skeptics of the application of the species concept (including the U.S. Endangered Species Act) to salmon populations might argue that the rapid diversification of salmon populations indicates that they are more plastic than has been assumed and that only a diverse gene pool needs be preserved, not every spatially and genetically discrete population. The concept of "evolutionarily significant unit" (Waples, 1995) provides a compromise by focusing on critical genetic and ecological variables involved in grouping and managing populations. In any case, it is important to remember that the success of the NZ chinook transplant was the exception and that the vast majority of other transplants have failed. Presumably, local adaptation was not sufficiently rapid or flexible to prevent extinction.

[9] Unwin, M. J., M. Kinnison, N. Boustead, and T. P. Quinn. In prep. Variation in body size and morphology of adult chinook salmon (*Oncorhynchus tshawytscha*) from two New Zealand populations and their ancestral Sacramento River, California, population, ninety years later. Natl. Inst. of Water and Atmosphere, P.O. Box 8602, Christchurch, New Zealand.

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