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Abstract

We used the variation at 64 allozyme loci to examine genetic relationships among 32 samples of sockeye salmon *Oncorhynchus nerka* and kokanee (resident sockeye salmon) from the Snake River basin and other North American locations. The genetic differentiation among populations was pronounced: Wright's F_{ST} was higher (0.244) than has been reported in any other study of Pacific salmon. A detailed examination of the *O. nerka* from lakes in the Sawtooth Valley of Idaho was undertaken to help guide recovery planning for the endangered Redfish Lake population and to help resolve the relationships between the resident and anadromous forms. In Redfish Lake, adult sockeye salmon that returned in 1991–1993 were genetically distinct from local kokanee but similar to a small group of "residual" sockeye salmon discovered in the lake in 1992. This result is consistent with the hypothesis that the original sockeye salmon population was not extirpated by Sunbeam Dam early in this century. Populations of *O. nerka* that appear to be native to the Snake River were also found in Alturas Lake, Stanley Lake, and Warm Lake, although the latter two lakes also showed evidence of nonnative gene pools. Kokanee sampled from Pettit Lake are clearly the result of an introduction of late-spawning kokanee from northern Idaho, and we found evidence of two *O. nerka* gene pools in Wallowa Lake, both traceable to introductions of nonnative kokanee.

Two centuries of anthropogenic changes to ecosystems inhabited by Pacific salmon *Oncorhynchus* spp. have taken a considerable toll on these species. Gustafson et al. (2007) estimated that in the 48 contiguous states of the United States about 29% of the historic populations of Pacific salmon and steelhead (the anadromous form of rainbow trout *O. mykiss*) are now extinct, and about half of the remaining populations have been listed as threatened or endangered under the U.S. Endangered Species Act (ESA). Extinctions have been most severe for sockeye salmon *O. nerka*, with an estimated 47% of the historical populations now being extinct. The only remaining population of Snake River sockeye salmon occurs in Redfish Lake in the Sawtooth Valley area near Stanley, Idaho. This population is unique in that it undergoes a longer freshwater migration (nearly 1,500 km) and spawns at a higher elevation (>2,000 m) than any other *O. nerka* population in the world (Waples et al. 1991a); it is also the southernmost population of sockeye salmon in North America. In 1990, no sockeye salmon were observed entering Redfish Lake to spawn, and in 1991 just four adults returned. Later that year, Snake River sockeye salmon became the first Pacific Northwest salmon to be afforded ESA protection.

Although only Redfish Lake has supported an anadromous Snake River run in recent years, historical records indicate that sockeye salmon were also native to several other lakes in the Sawtooth Valley area (Alturas, Stanley, Pettit, and perhaps Yellowbelly lakes; Figure 1). Currently, Alturas, Stanley, and Pettit lakes all have populations of kokanee (a nonanadromous form of sockeye salmon), but the origins of these populations are uncertain because of past efforts to eradicate native populations and subsequent releases of exogenous *O. nerka* (Bjornn et al. 1968; Hall-Griswold 1990; Welsh 1991). Outside the Sawtooth Valley area, Snake River populations of sockeye salmon were also present historically in Payette Lake, Warm Lake (in the South Fork Salmon River drainage), and Wallowa Lake (in the

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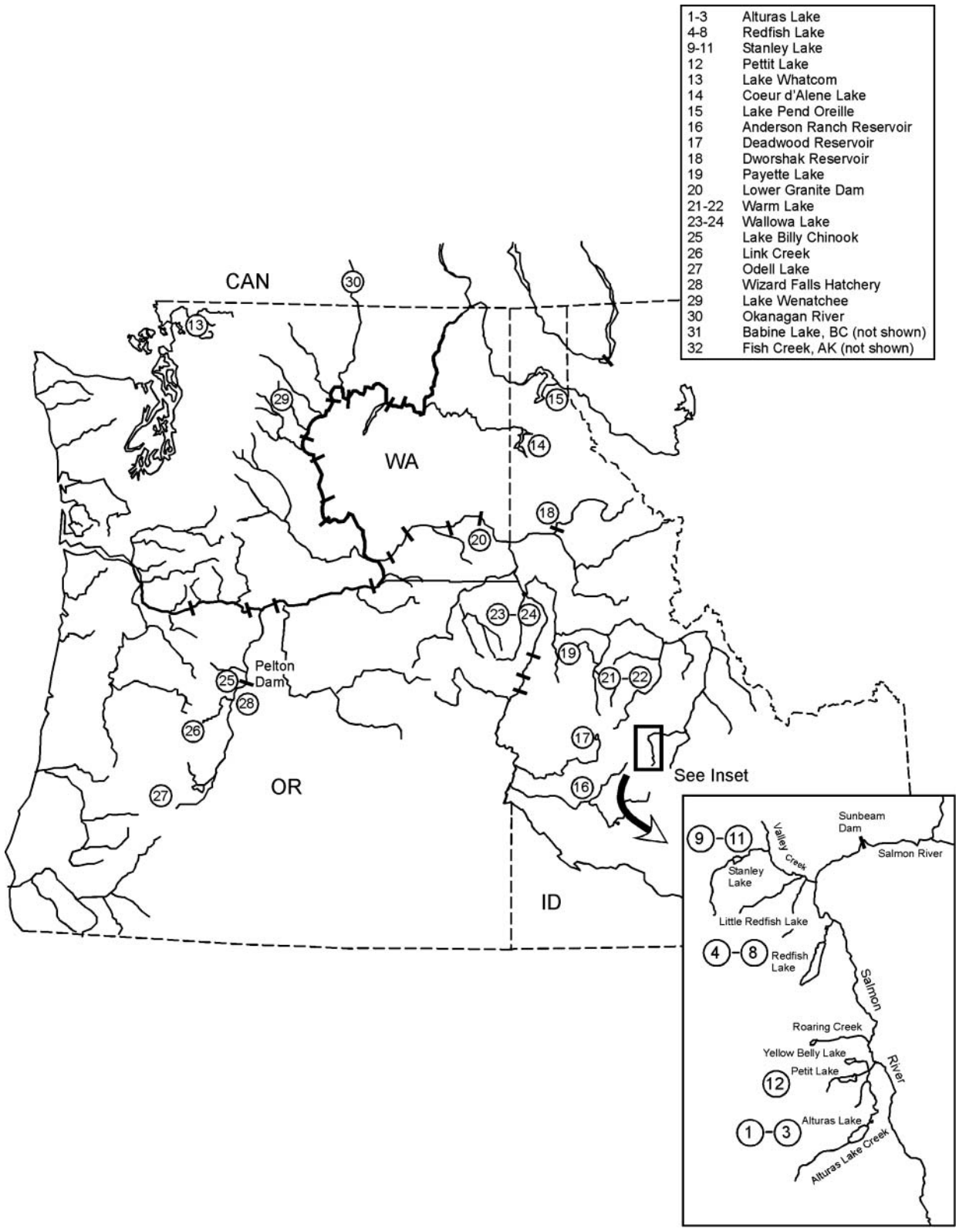

FIGURE 1. Map showing the locations (numbered circles) at which *O. nerka* samples were collected; see Table 1 for additional information on these samples.

Grande Ronde River drainage in northeastern Oregon). Anadromous populations disappeared long ago from these lakes as well, and the current populations of *O. nerka* consist entirely of resident forms.

In addition to the population of anadromous sockeye salmon, Redfish Lake supports a native population of kokanee, which mature at a much smaller size than anadromous sockeye salmon (~15–20 cm versus ~45–55 cm). Whereas all recent observations of sockeye salmon spawning have been on the lake shore in October and November, the kokanee population spawns in August and September in Fishhook Creek, the major inlet stream to Redfish Lake. At the time an ESA listing determination had to be made for Snake River sockeye salmon, there remained substantial uncertainty on several key issues, including (1) the relationship between the anadromous and resident forms in Redfish Lake, (2) the relationship between the *O. nerka* in Redfish Lake and those in other Sawtooth Valley lakes, and (3) the relationship between various forms of *O. nerka* in the Columbia River basin (Waples et al. 1991a).

In spite of these substantial uncertainties, the National Marine Fisheries Service (NMFS) proposed that Snake River sockeye salmon be listed as endangered in April 1991, and the listing was finalized later that year (U.S. Office of the Federal Register 1991). Because of the critically endangered status of the population, a captive broodstock program was initiated, seeded initially by juvenile *O. nerka* collected as they migrated out of Redfish Lake in spring 1991 and supplemented later by a total of 16 anadromous adults that returned in 1991–1998 (Flagg et al. 1995, 2004). Subsequently, peer-reviewed publications that detailed genetic and other analyses have established the following:

1. According to DNA-band sharing analyses, resident and anadromous *O. nerka* from Redfish Lake are more similar to each other than to sockeye salmon from the upper Columbia River (Thorgaard et al. 1995);
2. Kokanee from the Sawtooth Valley are genetically different from other Columbia River *O. nerka* populations (Winans et al. 1996);
3. Anadromous sockeye salmon in Redfish Lake are genetically distinct from Fishhook Creek kokanee (Cummings et al. 1997);
4. Sockeye salmon and kokanee are genetically divergent in some upper Columbia River locations (Winans et al. 1996);
5. In some cases, there is genetic evidence of the effects of stock transfers of kokanee (Waples 1995; Thorgaard et al. 1995; Winans et al. 1996); and
6. A report on the variation in mitochondrial DNA (mtDNA; Faler and Powell 2003) supported a number of these observations.

Nevertheless, these studies had some limitations. The mixed-DNA analyses are difficult to interpret in terms of standard population-genetics models. The Winans et al. (1996) study had no samples of Snake River *O. nerka* collected after 1990 and thus did not include any anadromous samples. Published evaluations of the effects of stock transfers are incomplete and cover only a fraction of the populations affected.

In this study, we used allozyme data for 64 gene loci assayed in over 2,300 individuals to examine the patterns of genetic variation in 53 collections of sockeye salmon and kokanee from 13 sites in the Snake River and 9 sites elsewhere in North America. We include replicate temporal samples (1990–1994) from all Snake River locations known to have or suspected of having native populations of *O. nerka*, as well as samples from a variety of kokanee populations used as sources for stock transfers. Together with known releases of nonnative *O. nerka* within the Snake River, these results provide a more comprehensive assessment of the status of—and genetic relationships among—native Snake River populations of *O. nerka* than has been published to date, except in contract reports (Waples et al. 1997) and other gray literature. Our results should be useful in planning long-term conservation strategies for Snake River sockeye salmon and in particular should help address two key questions: (1) What genetic lineages are represented by existing populations of *O. nerka* in Snake River lakes that originally supported sockeye salmon? (2) If recovery efforts extend beyond Redfish Lake, which lakes and stocks would be most appropriate to use?

METHODS

Study Areas and Experimental Design

A total of 53 collections, differing in geographic or temporal coverage or the life history type involved, were considered (Table 1). Both resident and anadromous forms were included, as well as some collections of uncertain parental origin. In most analyses, temporal samples were combined to form either a 46- or 32-population data set. The locations of the 32 population samples are shown on the map in Figure 1. A brief description of the types of collections made and their rationale follows.

Redfish Lake.—The 13 adult sockeye salmon that returned to Redfish Lake in 1991–1993 provided an opportunity for comparison with samples of spawning kokanee collected in 1990, 1991, and 1992. In the latter 2 years, both "early" and "late" spawning kokanee were collected to test for evidence of genetic differentiation within the run (as life history data reported by Brannon et al. 1994 suggested).

Three other types of collections of *O. nerka* were also made in Redfish Lake. In 1990, 1992, 1993, and 1994, midwater trawls were used to collect samples of mixed-age *O. nerka*. In 1991–1993, juvenile *O. nerka* out-migrating from Redfish Lake in the spring were trapped alive, and some were retained for use in a captive broodstock program (Flagg 1993; Johnson 1993). Mortalities that resulted from these trapping and rearing programs were used for genetic analysis in this study. Finally, small collections of "residual" *O. nerka* were made in 1992 and 1993; these fish are similar in size to Fishhook Creek kokanee but spawn at the same location and approximately at the same time as the sockeye salmon (Brannon et al. 1994).

TABLE 1. Collection data for the 53 samples of *O. nerka* considered in this article. In some analyses, temporal samples from the same location were combined; asterisks indicate the total number of individuals in a combined sample. Abbreviations are as follows: A = adult spawner, J = juvenile, and M = mixed or unknown.

Area and sample	*N*	Type	Age	Collection date	Population number
Sawtooth Valley					
Alturas Lake out-migrants	33	Unknown	J	May–Jun 1991	1
Alturas Lake spawners	30	Resident	A	Sep 25, 1992	2
Alturas Lake trawl	142*				3
August 1990	100	Unknown	M	Aug 20, 1990	
August 1992	32	Unknown	M	Aug 28, 1992	
September 1992	10	Unknown	M	Sep 25, 1992	
Redfish Lake kokanee	217*				4
1990	88	Resident	A	Sep 15, 1990	
1991 early	40	Resident	A	Aug 22, 1991	
1991 late	29	Resident	A	Sep 5, 1991	
1992 early	30	Resident	A	Aug 14, 1992	
1992 late	30	Resident	A	Sep 8, 1992	
Redfish Lake trawl	128*				5
August 1990	12	Unknown	M	Aug 20, 1990	
August 1992	10	Unknown	M	Aug 27, 1992	
September 1992	37	Unknown	M	Sep 24, 1992	
September 1993	43	Unknown	M	Sep 16, 1993	
September 1994	26	Unknown	M	Sep 6, 1994	
Redfish Lake out-migrants	181*				6
1991	138	Unknown	J	May–Jun 1991	
1992	17	Unknown	J	May–Jun 1992	
1993	26	Unknown	J	May–Jun 1993	
Redfish Lake sockeye	13*				7
1991	4	Anadromous	A	Nov 5, 1991	
1992	1	Anadromous	A	Oct 1, 1992	
1993	8	Anadromous	A	Oct 1, 1993	
Redfish Lake residuals	14*				8
1992	4	Resident	A	Nov 12, 1992	
1993	10	Resident	A	Oct 1, 1993	
Stanley Lake spawners, 1992	60	Resident	A	Aug 20, 1992	9
Stanley Lake trawl, 1992–1994	40*				10
1992	10	Resident	M	Aug 28, 1992	
1993	13	Resident	M	Aug–Sep 1993	
1994	17	Resident	M	Sep 7, 1994	
Stanley Lake spawners, 1994	8	Resident	A	Oct 5, 1994	11
Pettit Lake trawl	63*				12
1992	25	Resident	M	Sep 26, 1992	
1994	38	Resident	M	Sep 1, 1994	
Other Idaho					
Lake Whatcom (Washington)	60	Resident	A	Nov 5, 1990	13
Coeur d'Alene Lake	50	Resident	A	Nov 20, 1990	14
Lake Pend Oreille	60	Resident	A	Nov 20, 1990	15
Anderson Ranch Reservoir	12	Resident	M	Aug 20, 1990	16
Deadwood Reservoir	148*				17
1990	88	Resident	A	Sep 15, 1990	
1992	60	Resident	A	Sep 17, 1992	

(Continued on next page)

TABLE 1. Continued.

Area and sample	*N*	Type	Age	Collection date	Population number
Dworshak Reservoir	60	Resident	A	Sep 15, 1990	18
Payette	120*				19
Payette Lake	60	Resident	A	Sep 15, 1990	
North Fork Payette River	60	Resident	A	Sep 18, 1992	
Lower Granite Dam	18	Unknown	J	Mar 10, 1992	20
Warm Lake, 1990	60	Resident	A	Oct 26, 1990	21
Warm Lake, 1992	60	Resident	A	Sep 12, 1992	22
Oregon					
Wallowa River	60	Resident	A	Sep 29, 1992	23
Wallowa Lake	40	Resident	A	Nov 4, 1993	24
Lake Billy Chinook	47	Resident	A	Sep 15, 1992	25
Link Creek	49	Resident	A	Sep 29, 1992	26
Odell Lake	60	Resident	A	Sep 24, 1992	27
Wizard Falls Hatchery	80	Resident	J	Spring 1993	28
Washington					
Lake Wenatchee	280*				29
Brood year 1987	120	Anadromous	J	Feb 16, 1988	
Brood year 1988	160	Anadromous	J	Jan 5, 1990	
British Columbia					
Okanagan River	63	Anadromous	A	Oct 12, 1990	30
Babine Lake	60	Anadromous	A	Sep 29, 1990	31
Alaska					
Fish Creek	40	Anadromous	A	Sep 1, 1992	32

Alturas Lake.—As in Redfish Lake, the collections in Alturas Lake included samples of kokanee spawners, juvenile outmigrants, and trawled mixed-age *O. nerka*. No anadromous fish have returned to Alturas Lake in recent decades,[1] and no population comparable to the Redfish Lake "residuals" has been identified.

Other Snake River lakes.—Stanley and Pettit lakes are both within about 30 river kilometers of Redfish Lake in the Sawtooth Valley area. Historical records indicate that both lakes at one time supported sockeye salmon populations, but anadromous runs disappeared long ago following the erection of barriers to migration and lake poisonings to enhance opportunities for game fish. Both lakes currently support populations of resident *O. nerka*, but their origin is uncertain because both lakes have been stocked with nonnative sockeye salmon and/or kokanee. Warm Lake, Payette Lake, and Wallowa Lake are other Snake River sites that at one time supported runs of sockeye salmon but now have only resident forms of *O. nerka* of uncertain origin.

Two years of trawl samples from Pettit Lake and 3 years of trawl and spawner samples from Stanley Lake were examined in this study. In Warm and Wallowa lakes, spawning fish were sampled in two different years.

Idaho kokanee.—Kokanee have been widely planted in Idaho as well as elsewhere in the western United States. Two major stock groups occur in the state: a late-spawning group from northern Idaho (including Lake Pend Oreille and Coeur d'Alene Lake) and an early, stream-spawning group from central Idaho (including populations from Deadwood, Dworshak, and Anderson Ranch Reservoirs and Payette Lake). These stocks were included because they or their derivatives have been transplanted into many Snake River populations, including all of the Sawtooth Valley lakes. We also included a sample of kokanee from Lake Whatcom (near Bellingham, Washington) because this stock has been widely planted throughout the Pacific Northwest and it has been suggested (Waples 1995) that this was the original source of the northern Idaho kokanee populations.

Columbia River sockeye salmon.—Apart from those in Redfish Lake, the only remaining sockeye salmon populations in the Columbia River basin are from Lake Wenatchee and Lake Osoyoos on the Okanagan River (known as the Okanogan River in the United States), which were included to provide a more complete picture of the genetic variability within the Columbia River basin.

Deschutes River basin O. nerka.—Historically, a run of sockeye salmon spawned in Link Creek and reared in Suttle Lake in the Deschutes River basin of Oregon. This run was dramatically

[1]It should be noted, however, that Alturas Lake is upstream from both Redfish Lake and the weir for Sawtooth Hatchery and that since 1991 all anadromous *O. nerka* that have reached the weir have been taken for the Redfish Lake captive broodstock program.

affected by the construction of a dam at the mouth of Suttle Lake in 1930 and the construction of Pelton Dam on the Deschutes River in 1959. Although a few anadromous fish have returned to Pelton Dam in most recent years, there is no provision for fish passage. We obtained three samples of resident *O. nerka* from this river system (Odell Lake, Link Creek, and Lake Billy Chinook) as well as from a hatchery stock (Wizard Falls) that has been the source for numerous stock transfers within the Pacific Northwest.

Other samples.—Three other samples of *O. nerka* were included in this study. In the 1980s, sockeye salmon eggs from the Babine Lake system in British Columbia were outplanted in Alturas and Stanley lakes, and a sample from Babine Lake provided an opportunity to evaluate the effects of these stock transfers. An Alaskan sample (from a hatchery on Fish Creek in Cook Inlet near Anchorage) served as an outlier to provide a sense of geographic perspective to the genetic data for other U.S. populations. Finally, during a test in March 1992 of the feasibility of drawing down Columbia River reservoirs to speed migration of juvenile salmon (USACE 1993), a number of *O. nerka* were unexpectedly found in the vicinity of Lower Granite Dam. We examined a sample of 18 of these individuals to determine whether there was evidence that they were from the listed Redfish Lake population.

Sampling Methods

A variety of collection methods were employed to sample natural populations. In most localities, postspawning adults were collected by net or beach seine. Because of the large adult size difference between resident and anadromous forms, this method provided the most reliable means of distinguishing the two forms in areas where they co-occur. In the Sawtooth Valley lakes (Redfish, Alturas, Pettit, and Stanley), midwater trawls were also used to collect *O. nerka* from a mixture of age-classes. Residual *O. nerka* were collected in Redfish Lake using a floating Lake Merwin trap net. Finally, traps were used in the outlet streams of Redfish and Alturas lakes to collect *O. nerka* migrating out of the lake in the spring. Adult Redfish Lake sockeye salmon that returned to spawn in 1991–1993 were trapped for use in a captive broodstock program (Johnson 1993), and tissue samples for genetic analysis were obtained from the carcasses after the fish had spawned.

Whole fish or tissues were frozen in the field and transported on dry ice to the NMFS laboratory in Seattle, where they were transferred to an ultracold (–80°C) freezer for storage prior to electrophoretic analysis. The procedures for starch gel electrophoresis followed those described in Aebersold et al. (1987). Four tissues (skeletal muscle, liver, heart, and retinal tissue) were sampled from each fish, and extracts were loaded onto starch gels utilizing seven different buffer systems. Most of these buffers are described by Aebersold et al. (1987), with modifications described by Waples et al. (1991b). The seven electrophoretic buffers used in combination with the four tissues resulted in a screening protocol involving 16 gels for each 40 fish analyzed. Table A.1 in the appendix lists the enzymes used, the loci scored, the tissue(s) and buffer(s) used to resolve each locus, and the number of stocks that were polymorphic for each marker.

Data Analysis

The electrophoretic phenotypes visualized on starch gels were interpreted as genotypes according to the guidelines in Utter et al. (1987). Allelic frequencies, genetic distance values, and tests of Hardy–Weinberg genotypic proportions were obtained using the BIOSYS program (Swofford and Selander 1981). We used Fisher's exact probability test for all Hardy–Weinberg tests. At loci for which more than two alleles were expressed in a sample, all but the most common allele were pooled to yield a test involving two alleles and three genotypic classes. The unweighted pair-group method with arithmetic averages was used with Cavalli-Sforza and Edwards' (1967) chord distance and Nei's (1978) unbiased genetic distance values to generate phenograms depicting the genetic affinities among the samples.

In *O. nerka*, as in other salmonids, several pairs of duplicated gene loci occur that form allelic products with identical electrophoretic mobility. These loci are termed "isoloci" (Allendorf and Thorgaard 1984). Isoloci present special problems for interpretation and data analysis because the genotypes of individual fish cannot be determined unambiguously. Also, in sockeye salmon overlapping bands from other gene loci make it difficult to score all phenotypes at *LDH-A1** and *PGM-1**. For these loci, only two phenotypic classes are scored: one class that includes only individuals that are homozygous for the variant allele (genotype denoted by "22") and another class that includes both heterozygotes (genotype "12") and homozygotes for the common allele (genotype "11"). The allele frequency of the variant "2" allele can be estimated as the square root of the frequency of the "22" phenotype, the frequency of the common "1" allele as 1.0 minus the estimated frequency of the "2" allele. In this study, as in Winans et al. (1996), we recorded the observed frequencies of the two phenotypes at these loci and used those frequencies in temporal and geographic comparisons among populations.

RESULTS

Preliminary Analyses

A total of 76 presumptive gene loci were scored in at least 75% (40 or more) of the 53 samples analyzed (Table A.1). Of these, 41 were polymorphic (two or more alleles segregating in at least one sample) and 35 were monomorphic. The allele frequencies for the polymorphic loci are presented in Waples et al. (1997).

Five of the polymorphic loci (*mAH-1,2**; *G3PDH-1,2**; *GPI-B1,2**; *sMDH-A1,2**; and *SMDH-B1,2**) are generally considered to be isoloci in sockeye salmon. However, only *mAH-1,2** was strongly variable in this study, and this was the only isolocus for which any individuals had three or more doses of variant

alleles (indicating that both loci must be variable in that population). Because the variation at the remaining four isoloci was consistent with the patterns expected from variation at a single locus (see also the Hardy–Weinberg results below), we treated each of these pairs of loci as one variable locus and one monomorphic locus.

Four of the collections shown in Table 1 included more than one sample in the same year (the August and September trawl samples from Alturas Lake and Redfish Lake in 1992 and the early and late kokanee samples from Redfish Lake in 1991 and 1992). In each case, contingency chi-square tests indicated that the overall allele frequencies did not differ significantly between pairs of samples; therefore, these samples were combined in later analyses. Because of the small number of individuals involved, we also combined 3 years of samples of adult sockeye salmon from Redfish Lake (total $N = 13$) and 2 years of samples of "residual" sockeye salmon from Redfish Lake (total $N = 14$). These combinations resulted in 46 samples that were considered in the following two types of analyses.

Tests of Genotypic and Phenotypic Proportions

A total of 272 exact probability tests were performed to compare the expected and observed genotypic frequencies at the polymorphic gene loci in these 46 samples; of these, 11 (4.0%) had probabilities less than 0.05 and 2 (0.74%) had probabilities less than 0.01. The significant tests occurred at seven different gene loci, and no population had more than a single locus that failed to conform to expected Hardy–Weinberg genotypic frequencies. We concluded that the genotypic data were consistent with expectations from simple Mendelian inheritance of genetic traits. These results are also consistent with the hypotheses that the gene loci considered here are not strongly affected by selection and that the samples analyzed represented approximately random samples from single populations. It should be noted, however, that the power to detect selection, population admixture, and/or nonrandom mating using this test is typically low.

Nonsignificant results were found for all but 1 of the 29 tests involving isoloci that were treated here as individual gene loci. We concluded that the decision to treat these isoloci as individual gene loci was reasonable and not likely to lead to any serious bias in the results.

Of the 46 samples examined, 43 were polymorphic at the isolocus *mAH-1,2**. In each of these samples, the observed phenotypic distributions agreed with two-locus Hardy–Weinberg expectations based on the test developed by Waples (1988). This result supports the hypothesis that allelic dosages can reliably be scored at this locus in sockeye salmon.

Temporal Comparisons

At nine different locations (Alturas Lake, Redfish Lake, Pettit Lake, Stanley Lake, Warm Lake, Wallowa Lake, Deadwood Reservoir, Payette Lake, and Lake Wenatchee), samples from multiple years were available for comparison. For most of these comparisons, allele frequency differences between years were not statistically significant ($P > 0.05$; combined test) or were marginally significant but within the range that can be expected from normal interannual variability (see Waples and Teel 1990). At three localities, however, the differences between samples were large enough to suggest the existence of multiple populations. The 1990 and 1992 Warm Lake samples were so dramatically different (combined χ^2 over nine loci = 285, df = 14) that it is not plausible they were drawn from the same gene pool. Highly significant ($P < 0.01$; combined test over 11 loci) differences were also found between a 1992 sample from the Wallowa River and a 1993 sample from Wallowa Lake. Heterogeneity was also found among some collections in Stanley Lake (discussed below).

Guided by these results, in some subsequent analyses we combined samples from different years as follows: trawl samples in Alturas, Redfish, Stanley, and Pettit Lakes; collections of kokanee and out-migrants in Redfish Lake; collections of sockeye salmon from Lake Wenatchee; and collections of spawners from Deadwood Reservoir and Payette Lake/River. Temporal samples from Warm and Wallowa lakes were not pooled in any analyses.

Levels of Genetic Variability

Pooling temporal samples as described above yielded a data set with 32 different localities and/or types of collections (see Table 1). A total of 64 gene loci were scored in all 32 collections (these loci can be identified in Table A.1), and 35 (55%) of these were polymorphic in at least one collection. However, the percentage of polymorphic loci within each collection was much lower, ranging from 4% to 6% in some Redfish and Stanley Lake collections to over 23% at Wizard Falls Hatchery—a result that indicates that different populations tended to be polymorphic for at least partially nonoverlapping sets of gene loci.

As is typical for sockeye salmon, average heterozygosities were low (Table 2), ranging from 0.006 in the 1990 Warm Lake sample to 0.041 in the 1994 Stanley Lake spawners. (Note that these values include monomorphic loci, a fact that should be kept in mind in comparisons with other studies.) In general, low heterozygosities were found for collections of Redfish Lake sockeye salmon, out-migrants, and residuals, and relatively high values were found in many of the kokanee collections as well as in the sockeye salmon from the Okanagan River. The polymorphic loci differed considerably in their overall level of variability. A few loci (e.g., *mAH-1,2**, *mAAT-1**, *ALAT**, *MPI**, *PGM-1**, and *PGM-2**) were polymorphic in most or all samples and often had high frequencies of variant alleles, whereas many other loci were variable in only one or a few populations.

The heterozygosity values reported in Table 2 are biased downward somewhat because they do not include data for three polymorphic loci (the isolocus *mAH-1,2** and the phenotypic loci *LDH-A1** and *PGM-1**) for which genotypes cannot be unambiguously assigned. Both *mAH-1,2** and *PGM-1** were highly variable in most of the collections.

TABLE 2. Levels of genetic variability in 32 populations of *O. nerka*. The values for sample size and percent polymorphic loci are based on 64 gene loci, including 29 that were monomorphic in all samples. In computing heterozygosities, data for the isolocus *mAH-1,2** and the phenotypic loci *LDH-A1** and *PGM-1** were not used. Abbreviations are as follows: H_o = observed heterozygosity, H_e = expected heterozygosity.

Population	Year(s)	Mean sample size	Percent loci polymorphic	Mean heterozygosity	
				H_o	H_e
Alturas Lake out-migrants	1991	26.5	10.9	.018	.015
Alturas Lake spawners	1992	29.9	12.5	.019	.020
Alturas Lake trawl	1990, 1992	135.0	15.6	.023	.022
Redfish Lake kokanee	1990–1992	208.5	15.6	.021	.021
Redfish Lake trawl	1990–1994	114.7	15.6	.022	.022
Redfish Lake out-migrants	1991–1993	172.5	12.5	.011	.012
Redfish Lake sockeye	1991–1993	12.7	4.7	.010	.010
Redfish Lake residuals	1992–1993	13.8	6.3	.013	.011
Stanley Lake spawners	1992	58.5	6.3	.012	.012
Stanley Lake trawl	1992–1994	36.4	10.9	.015	.016
Stanley Lake spawners	1994	7.4	15.6	.041	.038
Pettit Lake	1992, 1994	60.0	9.4	.015	.018
Lake Whatcom	1990	59.0	18.8	.023	.021
Coeur d'Alene Lake	1990	49.3	10.9	.021	.021
Lake Pend Oreille	1990	59.1	14.1	.020	.020
Anderson Ranch Reservoir	1990	11.6	10.9	.029	.028
Deadwood Reservoir	1990, 1992	138.1	18.8	.026	.027
Dworshak Reservoir	1990	56.2	15.6	.025	.027
Payette Lake/River	1990, 1992	115.9	14.1	.031	.032
Lower Granite Dam	1992	17.7	10.9	.022	.028
Warm Lake	1990	57.7	9.4	.006	.006
Warm Lake	1992	59.7	14.1	.029	.029
Wallowa River	1992	59.4	17.2	.029	.027
Wallowa Lake	1993	38.3	15.6	.023	.022
Lake Billy Chinook	1992	47.2	14.1	.027	.028
Link Creek	1992	48.0	14.1	.024	.028
Odell Lake	1992	59.1	17.2	.025	.025
Wizard Falls Hatchery	1993	79.9	23.4	.033	.035
Lake Wenatchee	1987–1988	256.0	20.3	.019	.020
Okanagan River	1990	61.7	17.2	.034	.032
Babine Lake	1990	57.6	14.1	.015	.016
Fish Creek	1992	39.9	12.5	.027	.028

Variation between Life History Forms and Collection Types

Multiple types of collections from Redfish, Alturas, and Stanley lakes provided the opportunity to compare data for what might represent different life history forms within a geographic location. In Alturas Lake, no significant differences were found between samples of out-migrants, spawners, and trawled fish. In Redfish Lake, pooled kokanee samples did not differ significantly from pooled trawl samples ($\chi^2 = 24.86$, df = 17, $P > 0.05$). The pooled sockeye salmon, pooled out-migrant, and pooled residual samples were also statistically homogenous. However, the latter three forms had highly significant ($P < 0.01$) differences compared with the kokanee and trawled samples. Samples of sockeye salmon, out-migrants, and residuals were characterized by a higher mean frequency (over both loci) of the "75" allele at *mAH-1,2** (about 0.28, compared with approximately 0.08 for the kokanee and trawl samples), a lower frequency of the "100" allele at *mAAT-1** (~0.1 versus ~0.5), a lower frequency of the "91" allele at *ALAT** (rare or missing versus ~0.15), the presence of the "88" allele at *PEPLT**, and absence of (or very low levels of) variation at *ADH**, *ADA-1**, *sMDH-B2**, *MPI**, and *PGM-2**.

In Stanley Lake, no individual loci showed significant frequency differences when comparing the 1992 spawners with the combined 1992–1994 trawl samples, but the overall test was marginally significant ($\chi^2 = 18.57$, df = 9, $P < 0.05$). The 1994

sample of spawners ($N = 8$) was very divergent from the other two collections ($\chi^2 = 145$ and 76, df = 12 and 11 for the 1992 spawner and combined trawl samples, respectively). Assuming that the 1994 sample was random, these differences are much too large to attribute to the small size of the sample. The 1994 spawner sample was distinguished by unusually high frequencies of variant alleles at *mIDHP-2**, *LDH-A1**, *PGM-1**, and *PGM-2**.

Geographic Variation

Considerable genetic diversity among populations was found, as is evident from an examination of Table A.2. The F_{ST} values at nine loci (*ADA-1**, *mAAT-1**, *ALAT**, *G3PDH-2**, *mIDHP-1**, *mIDHP-2**, *PEPLT**, *MPI**, and *PGM-2**) were greater than 0.1, and the overall value (0.244) is larger than has been reported in any study of anadromous Pacific salmonids. At three loci (*mAAT-1**, *ALAT**, and *PGM-1**), alleles that were rare or absent in some populations were common or fixed in other populations.

Two major genetic groups of *O. nerka* can be identified (Figure 2), as well as a number of individual populations that are genetic outliers. Group I includes all of the *O. nerka* samples from Redfish, Alturas, and Stanley lakes, with the exception of the 1994 sample of spawners from Stanley Lake. Three subgroups can be identified within this area: Redfish and Alturas Lake kokanee and trawl samples and Alturas Lake out-migrants (IA); Redfish Lake sockeye salmon, out-migrants, and residuals (IB); and Stanley Lake trawl samples and 1992 spawners (IC).

Group II includes all the samples of Idaho kokanee from outside the Sawtooth Valley area. Two subgroups can be identified: a northern-Idaho (Columbia River drainage) kokanee group (IIA); and a Deadwood Reservoir (Snake River drainage) kokanee group (IIB). Group IIA also includes samples from Lake Whatcom and Pettit Lake and the 1993 sample from Wallowa Lake. Group IIB includes samples from the Deadwood, Dworshak, Anderson Ranch, and Lower Granite Dam reservoirs, Payette Lake/River, the 1992 samples from Warm Lake and the Wallowa River, and the sample from Odell Lake.

Also apparent in Figure 2 is a third, loosely affiliated group that includes Lake Wenatchee and Okanagan River sockeye salmon, the 1994 Stanley Lake spawners, the 1990 Warm Lake sample, and three samples of kokanee from the Deschutes River drainage in Oregon. The samples from the British Columbia coast (Babine Lake) and Alaska (Fish Creek) were genetic outliers. A cluster analysis of Cavalli-Sforza and Edwards' (1967) chord genetic distance (not shown) revealed most of the same major features, including two major genetic groups and two to three subgroups within each of the major groups.

To provide a more focused look at the genetic relationships within the Sawtooth Valley, we repeated these analyses using only Sawtooth Valley samples as well as samples from two exogenous hatchery populations that are the presumed sources of the populations sampled in Pettit and Stanley lakes (Figure 3). Four separate genetic groups of presumably native *O. nerka* are evident: Redfish Lake kokanee; Alturas Lake kokanee and out-migrants; Redfish Lake sockeye salmon–residuals–out-migrants; and Stanley Lake kokanee (except the spawners sampled in 1994). Of these groups, the most similar pair were Redfish Lake kokanee and Alturas Lake *O. nerka*, and the most divergent were Stanley Lake kokanee. This figure also shows

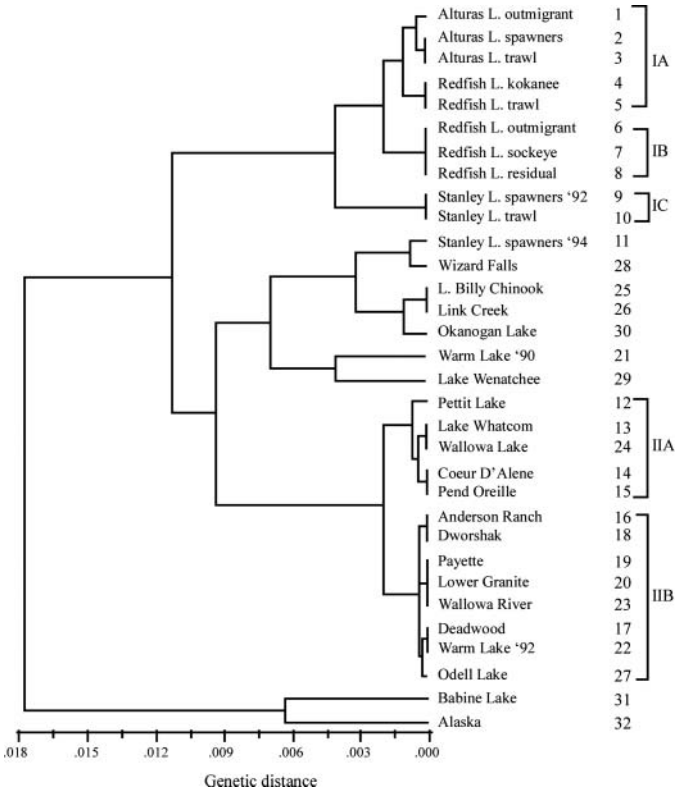

FIGURE 2. Dendrogram, based on Nei (1978) genetic distance, showing the genetic relationships among 32 populations of *O. nerka* from the Pacific Northwest based on the variation at 64 gene loci. The population numbers correspond to those in Table 1.

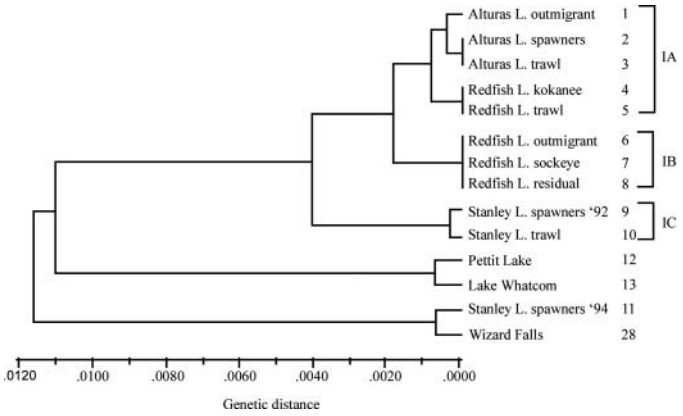

FIGURE 3. Dendrogram, based on Nei (1978) genetic distance, showing the genetic relationships among 12 populations of *O. nerka* from the Sawtooth Valley, Idaho, and two exogenous populations.

the intermediate position of the 1991 out-migrant sample from Alturas Lake, which exhibited some genetic affinity to the Redfish Lake sockeye salmon group as well as to the other samples of *O. nerka* from Alturas Lake. The Pettit Lake and 1994 Stanley Lake spawner samples were quite divergent from all other *O. nerka* in the Sawtooth Valley but were quite similar to the Lake Whatcom and Wizard Falls Hatchery stocks, respectively. We therefore conclude that these Pettit and Stanley samples did not represent native gene pools.

The heterogeneity chi-square tests provided an opportunity to evaluate more fine-scale patterns of genetic differentiation within several geographic regions and genetic clusters. Here we highlight some important points; more details can be found in Waples et al. (1997).

1. All Alturas Lake samples considered together differed significantly from all other samples in the Sawtooth Valley lakes.
2. All Redfish Lake *O. nerka* samples also differed significantly from Stanley Lake samples.
3. None of the pairwise comparisons of Lake Pend Oreille, Coeur d'Alene Lake, and Lake Whatcom were statistically significant.
4. The combined Pettit Lake samples differed significantly from the Lake Whatcom, Coeur d'Alene, and Pend Oreille samples ($P < 0.01$ for overall test; three individual loci with significant differences in each comparison). However, the allele frequency differences were not large, and the Pettit Lake samples shared some of the genetic traits that characterize the late-spawning kokanee populations from Lake Whatcom and northern Idaho (e.g., the high frequency of the "100" allele at *mAAT-1**, the absence of variation at *ADA-1**, and the moderately high frequency of the "136" allele at *PGM-2**). The 1993 Wallowa Lake sample also shared this genetic profile.
5. The second genetic group of Idaho kokanee showed a high degree of homogeneity among populations. Most pairwise comparisons among samples from Anderson Ranch, Deadwood, and Dworshak reservoirs and Payette River/Lake were not statistically significant. Three other samples (Lower Granite Dam, Warm Lake [1992], and Wallowa River [1992]) also had nonsignificant tests in comparison with some or all of the above samples. The sample from Odell Lake was more loosely affiliated with this group
6. The Wizard Falls Hatchery population shared with the 1994 sample of Stanley Lake spawners unusual allele frequencies at a number of loci, including *ALAT**, *mIDHP-2**, *LDH-A1**, *LDH-C**, *PGM-1**, and *PGM-2**.
7. The 1990 Warm Lake sample was a genetic outlier; it differed markedly from the 1992 Warm Lake sample and showed no clear affinity with any other sampled population.

DISCUSSION

Our results both confirm and expand those of previous studies and provide new biological insights that can help inform conservation planning for the remarkable Snake River populations of *O. nerka*.

Patterns of Genetic Variability

The low levels of heterozygosity reported in this study (range, 0.006–0.041) are consistent with the findings of previous allozyme studies (e.g., Utter et al. 1984; Wood 1995; Winans et al. 1996). We found no consistent pattern in the levels of genetic variability between resident and anadromous forms. In contrast to the low levels of within-population genetic variability, the *O. nerka* samples we examined were characterized by unusually large differences between populations. At several loci (*mAAT-1**, *ALAT**, and *PGM-1**), nearly fixed allelic differences were found between some populations. The mean F_{ST} (0.244) is larger than has been reported for any other study of anadromous Pacific salmonids. This result can be attributed at least in part to the unusually broad geographic coverage of the samples (from inland Snake and Columbia River basins to Alaska) as well as to the inclusion of samples from resident populations, which tend to be more strongly differentiated. Nevertheless, it emphasizes the tendency of sockeye salmon to form discrete, isolated populations that apparently only rarely experience gene flow from other populations. Our results also expand those of Winans et al. (1996) in demonstrating that native Snake River populations of *O. nerka* as a group are well differentiated genetically from all other *O. nerka* populations that have been sampled in North America.

Conservation planning is challenging for a unit like Snake River sockeye salmon, which is currently represented by a single anadromous population. It is widely recognized that multiple populations generally help reduce overall extinction risk, and for this reason the original Snake River Recovery Team (Bevan et al. 1994) recommended that delisting of Snake River sockeye salmon should require viable populations in at least two different lakes. More broadly, according to the Viable Salmonid Populations document (McElhany et al. 2000), which has formed the basis for ESA recovery planning of Pacific salmon and steelhead over the last decade, guidelines for the viability of ESUs include the following:

1. ESUs should contain multiple populations, some of which should be geographically widespread;
2. Populations within an ESU should not all share common risks of catastrophic failure;
3. Populations should display diverse phenotypes and life history traits.

As summarized below, information from this study can help direct choices about the most suitable populations and locations to consider in long-term recovery planning activities.

Redfish Lake *O. nerka*

Our results also support Cummings et al. (1997) in clearly demonstrating that there are two distinct gene pools of *O. nerka* in Redfish Lake: one consisting of Redfish Lake kokanee, the

other of anadromous and "residual" fish from the lake. Outmigrants collected in 1991–1993 appear to be mostly (if not entirely) from the anadromous–residual gene pool, while the 1992–1994 trawls appear to have taken almost entirely fish from the kokanee gene pool. The genetic similarity of the trawl and kokanee spawner samples is reasonable, given that no anadromous fish spawned in the lake from 1989 to the time of sampling and that the Fishhook Creek kokanee population is believed to be many times larger than any other resident population in the lake. With the small samples of anadromous and residual fish available ($N = 13$ and 12, respectively), it is not possible to draw definitive conclusions about their relationship, except to say that no significant genetic differences were observed between the two forms. One possible scenario is that there is some regular or intermittent exchange between the life history forms, with anadromous fish occasionally producing offspring that remain in the lake until maturity and/or resident fish occasionally producing offspring that migrate to sea and back. This hypothesis is consistent with microchemistry analysis of otoliths from residuals and returning adults (P. Kline, Idaho Department of Fish and Game, personal communication).

Genetic information regarding the relationships between the different forms of *O. nerka* in Redfish Lake has been instrumental in helping to direct implementation of the captive broodstock program—in particular, the decision to include residual and out-migrant forms but exclude Fishhook Creek kokanee. More recently, highly variable genetic markers have been used to estimate the relatedness of potential captive spawners and to create spawning matrices that maximize genetic diversity in the offspring and minimize matings among close relatives (Kozfkay et al. 2008). S. Kalinowski, Montana State University, D. Van Doornik, National Oceanic and Atmospheric Administration—Fisheries, and R. Waples, unpublished data, have used pedigree information to estimate that, although the population experienced a severe bottleneck, the captive broodstock program generally has been effective in minimizing additional levels of inbreeding in the captive–wild system.

We have used the term "residual" to describe resident *O. nerka* in Redfish Lake that are genetically similar to the sockeye salmon. These resident fish have many of the features typically associated with "residual" sockeye salmon: they spawn at the same place and approximately the same time (October–November) as anadromous *O. nerka* in Redfish Lake, and they are similar in size to kokanee but have a much more drab (greenish) spawning coloration than Fishhook Creek kokanee. However, Redfish Lake "residuals" differ in one important respect from the profile of "residual" sockeye salmon as originally defined by Ricker (1940): whereas residual sockeye salmon are almost exclusively male, the limited information available for the Redfish Lake population indicates that females are present (some were included among the fish we analyzed), and the sex ratio may be approximately equal. In any case, it appears that the situation involving life history forms of *O. nerka* in Redfish Lake is unusually complex for the species. Although a number of lake–river systems support both sockeye salmon and kokanee and others have both sockeye salmon and residuals, the only other system that we are aware of that supports all three forms is the Sammamish River system in Puget Sound (Young et al. 2004).

Native *O. nerka* in the Sawtooth Valley

Given that single, isolated populations are particularly vulnerable to extinction and that the Sawtooth Valley historically supported multiple populations of sockeye salmon, long-term recovery plans for Snake River sockeye salmon call for restoring or establishing viable anadromous populations in multiple lakes within the Sawtooth Valley. However, informed decisions are complicated by uncertainties associated with a long history of fish eradication efforts compounded with introductions of exogenous *O. nerka*.

The spatial and temporal scale of our collections provided an opportunity for a fairly comprehensive assessment of the effects of stock transfers (summarized in Table 3) on extant Snake River *O. nerka* populations. Although efforts have been made to include all known stock transfers into historic sockeye salmon–bearing lakes in the Snake River basin, the list in Table 3 is not necessarily comprehensive. Our results reaffirm a conclusion by Winans et al. (1996) that there is no evidence for lasting effects of 1980–1983 releases of sockeye salmon fry from Babine Lake into Alturas and Stanley lakes. For example, the "100" allele at *mAAT-1** was nearly fixed (frequency, 0.942) in the Babine Lake sample but rare or uncommon in all of the samples from Stanley Lake (range, 0.05–0.192). Similarly, at *ALAT** the "91" allele occurred at high frequency (0.650) in Babine Lake but was rare in each of the samples from Alturas Lake (range, 0.033–0.069).

We also found no evidence that stock transfers of kokanee into Redfish and Alturas lakes have had a substantial genetic impact on the extant populations and therefore conclude that these represent essentially native populations. However, the strength of this conclusion is limited somewhat by two factors. First, the power to detect the genetic effects of stock transfers is greatest when the donor population is known and has been characterized, which was not always the case. Second, we lack historical data on the genetic composition of *O. nerka* in Alturas or Redfish Lake, so we do not know whether or how much those characteristics have changed over time. Although relatively large and highly significant allele frequency differences were found between the Redfish and Alturas Lake samples and both the early-spawning Anderson Ranch–Payette–Deadwood–Dworshak kokanee complex and the late-spawning northern Idaho kokanee complex, it is possible that the *O. nerka* in Redfish and Alturas lakes were even more distinctive prior to those introductions. Along those lines, Faler and Powell (2003) suggested that the relatively high mtDNA haplotype diversity of Redfish Lake kokanee might reflect some residual effects from these introductions.

In contrast, the data for the Pettit Lake trawl samples from 1992 and 1994 showed a strong genetic affinity between those

TABLE 3. Records of transplants of sockeye salmon and kokanee into selected Snake River populations. These records are not necessarily complete, particularly prior to 1968. Releases of local stocks are not included.

Year	Source	Number	Life stage	Type	Source[a]
		Alturas Lake			
1921	Unknown	40,300	Yearling	Sockeye[b]	d
1930–1952	Unknown	655,500	Fry, yearling	Kokanee	a
1941	Bull River, Montana	$>10^6$	Eggs	Kokanee	f
1966	Anderson Ranch Reservoir	59,332	Fry	Kokanee	d
1968	Anderson Ranch Reservoir	196,000	Fry	Kokanee[c]	d
1983	Babine Lake	480,000	Fry	Sockeye	b
1984	Babine Lake	63,000	Fry	Sockeye	b
		Payette Lake			
1940–1947	Unknown	1,480,066	Fry	Sockeye	h
1946[d]	Unknown	102,000	Fry	Sockeye	h
1968–1971	Eagle Hatchery	618,485	Fry, fingerling	Kokanee[c]	k
1970	Hayspur Hatchery	89,577	Fry	Kokanee[c]	k
1972[e]	Eagle Hatchery	119,880	Fry	Kokanee[c]	k
1972[e]	Hayspur Hatchery	84,000	Fry	Kokanee[c]	k
1975[e]	McCall Hatchery	82,800	Fry	Kokanee[c]	k
1975	McCall Hatchery	138,000	Fry	Kokanee[c]	k
1976[e]	American Falls Hatchery	87,500	Fry	Kokanee[c]	k
1976	American Falls Hatchery	87,500	Fry	Kokanee[c]	k
1988	Eagle Hatchery	300,266	Fingerling	Kokanee[f]	k
1989–1993	Deadwood Reservoir	1,068,500	Fingerling	Kokanee[f]	k
		Pettit Lake			
1932–1933	Unknown	18,400	Yearling	Kokanee	a
1965	Unknown	29,600	Fingerling		c
1968	North Idaho	79,100	Fry	Kokanee[c]	a
1995	Redfish Lake	8,572	Fingerling	Sockeye	k
		Redfish Lake			
1930	Kootenay Lake?	17,500		Kokanee	e
1930–1945	Unknown	225,900	Fry, yearling	Kokanee	a
1940–1947	Unknown	325,320	Fingerling	Sockeye	h
1941	Bull River, Montana	$>10^6$	Eggs	Kokanee	f
1962	Anderson Ranch Reservoir	43,251	Fry	Kokanee	d
1968[g]	Unknown[h]	10,440	Fingerling	Sockeye	k
1971[g]	Anderson Ranch Reservoir	50,344	Fry	Kokanee[c]	d
1971	Anderson Ranch Reservoir	45,900	Fry	Kokanee[c]	d
1972	Anderson Ranch Reservoir	51,435	Yearling	Kokanee[c]	d
		Stanley Lake			
1923	Unknown	1,000		Kokanee?	d
pre-1935	Unknown	Numerous		Kokanee	d
1946	Unknown	379,000		Sockeye	h
1981	Babine Lake	173,880	Fry	Sockeye	b
1982	Babine Lake	260,393	Fry	Sockeye	b
1983	Babine Lake	150,015	Fry	Sockeye	b
1984	Babine Lake	147,000	Fry	Sockeye	b
1988	Deadwood Reservoir	49,926	Yearling[i]	Kokanee[f]	a
1989	Deadwood Reservoir	60,000	Yearling[i]	kokanee[f]	a
1990	Deadwood Reservoir	52,800	Fingerling	Kokanee[f]	k

(Continued on next page)

TABLE 3. Continued.

Year	Source	Number	Life stage	Type	Source[a]
1991	Roaring Judy Hatchery	56,250	Fingerling	Kokanee[c]	k
1991	Deadwood Reservoir	34,500	Fingerling	Kokanee[f]	k
	Streams of Sawtooth Mountains				
1921	Hayspur Hatchery	15,000	Yearling	Kokanee	d
	Wallowa Lake				
1914	Alaska	380,500		Sockeye	h
1916–1919	Unknown	5,144,300		Sockeye	h
1922–1937	Unknown	21,784,521	Fry, fingerling	Sockeye	h
1925–1926[j]	Unknown	2,443,600	Fry, fingerling	Kokanee	g
1926–1950	Unknown	1,041,200		Kokanee	g
1953–1954	Unknown	147,910		Kokanee	g
1955–1970	Montana	2,588,513	Fry, fingerling	Kokanee	g
1962–1963	Washington	304,269	Fry, fingerling	Kokanee	g
1964–1966	British Columbia	615,550	Fry, fingerling	Kokanee	g
1981–1994	Wizard Falls Hatchery	136,000	Fry, fingerling	Kokanee	i
	Warm Lake				
1938	Evergreen Hatchery	25,000		Sockeye	d
1940–1952	McCall Hatchery	248,490	Fry	Kokanee?[k]	k
1946	McCall Hatchery	118,000	Fry, fingerling	Sockeye	k
1948	North Idaho	20,000	Fry	Kokanee?[k]	k
1950–1962	McCall Hatchery	831,000	Fry	Kokanee	j
1990	Deadwood Reservoir	49,980	Fingerling	Kokanee[f]	j

[a]Sources: a = Bowler (1990); b = Howell et al. (1985); c = Corley (1966); d = Hall-Griswold (1990); e = Welsh (1991); f = Chapman et al. (1990); g = Cramer (1990); h = NRC (1995); i = Kostow (1996); j = D. Anderson, Idaho Department of Fish and Game, personal communication; and k = IDFG (1997).
[b]Recorded as kokanee by Bowler (1990).
[c]Recorded as "October spawner" by IDFG (1997).
[d]Released into Payette River.
[e]Released into Little Payette Lake.
[f]Recorded as "early spawner" by IDFG (1997).
[g]Released into Fishhook Creek, a tributary of Redfish Lake.
[h]Source may have been Redfish Lake stock.
[i]Recorded as fingerlings by IDFG (1997).
[j]Released into the Wallowa River.
[k]Recorded as "blueback salmon."

populations and the late-spawning kokanee populations from northern Idaho. Presumably, the current population in Pettit Lake is derived from northern Idaho kokanee obtained from Anderson Ranch Reservoir that were planted in the lake in 1968 (Table 3). If any *O. nerka* native to Pettit Lake survived overharvesting, the effects of Sunbeam Dam (Jones 1991) and other barriers to migration, and poisoning of the lake in 1960 (Hall-Griswold 1990), they have yet to be found.

The situation regarding stock transfers and extant populations of *O. nerka* in Stanley Lake is more complex, as this lake apparently supports (or at least did in the mid-1990s) both indigenous and introduced populations. Four of the five samples from Stanley Lake (the 1992 spawners and 1992, 1993, and 1994 trawled fish) appear to be from a common gene pool that is more similar to the *O. nerka* from Redfish and Alturas lakes than it is to any other population we examined. We believe that the most likely explanation is that this gene pool is native to Stanley Lake. Again, we cannot rule out some effects on this gene pool from stock transfers, but it appears that at least substantial native components remain. In contrast, the gene pool represented by the eight spawners collected in 1994 is radically different from that of other Sawtooth Valley *O. nerka*. These fish spawn somewhat later than the spawners sampled in 1992, and the most plausible explanation is that they are the result of an introduction (either direct or indirect) from the Wizard Falls Hatchery stock. The close similarities in allele frequencies to the Wizard Falls population at several key gene loci are too striking to be explained by chance. Table 3 shows a release into Stanley Lake of 56,250 October-spawning kokanee fingerlings from Roaring Judy Hatchery in Colorado, and it is possible that this was the source of the spawners sampled in 1994. However, the Roaring Judy Hatchery stock was initiated with an egg take in 1950 from Flathead Lake in Montana, and there is no record of use of Wizard Falls stock at the hatchery

(B. Weiler, Colorado Division of Wildlife, personal communication).

Other Snake River *O. nerka*

Historically, Payette Lake may have supported the largest run of sockeye salmon in the Snake River basin, but access for anadromous fish was blocked by impassable dams early in the 20th century (Chapman et al. 1990). The recent samples from Payette Lake and River were genetically similar to samples of introduced kokanee from reservoirs throughout Idaho. This close genetic similarity suggests that all these populations have a common heritage, but it is not clear whether this has resulted from (1) the planting of Payette Lake with the same stock used in the reservoirs, or (2) the use of native Payette Lake stock in forming the early-spawning kokanee stock that has been widely spread throughout Idaho. A late-December, beach-spawning population of kokanee has been observed in Payette Lake (D. Anderson, Idaho Department of Fish and Game, personal communication). This may be a remnant native population of *O. nerka*, but it has not been sampled or genetically characterized.

The genetic data also provided considerable insight into the effects of stock transfers into two other Snake River lakes that historically supported populations of sockeye salmon: Warm Lake and Wallowa Lake. The 1990 sample from Warm Lake was quite distinctive, bearing little genetic similarity to any of the stocks known or likely to have been planted there. The distinctiveness and the low level of genetic variability found in this sample are consistent with the hypothesis that it represents a native gene pool that has been isolated and that has experienced severe and/or prolonged bottlenecks in the past. In contrast, Warm Lake spawners sampled in 1992 appear to be derived from the stocking in 1990 of fingerlings from Deadwood Reservoir (Table 3). Survivors from that release would have been 3 years old in 1992, a typical age for maturity in kokanee. It is not clear, however, whether these spawners will have a permanent genetic impact on the population. The presumably native fish sampled in 1990 are part of a beach spawning population, whereas the Deadwood Reservoir stock spawns in tributaries. There is little suitable habitat in Warm Lake tributaries for stream-spawning kokanee (D. Anderson, personal communication), which may help explain why we found no genetic evidence for the survival of fish transfers into the lake prior to 1990.

The situation is also complex in Wallowa Lake, where we found evidence for two separate gene pools, one spawning in the river and one in the lake. The stream spawners were genetically similar to the Deadwood–Dworshak–Anderson Ranch–Payette group of stream-spawning kokanee, and the lake spawners were genetically similar to late-spawning kokanee from northern Idaho. These genetic affinities suggest that neither of these populations is native to Wallowa Lake. However, these results do not prove that a native gene pool does not persist in the lake; the results for Stanley Lake indicate that native and introduced gene pools of *O. nerka* can coexist in Snake River lakes, at least in the short term. Furthermore, the failure of either of the samples from Wallowa Lake to show an affinity with the Wizard Falls stock that has been planted there in recent years is interesting and suggests that the population-genetic structure in Wallowa Lake is complex, such that additional sampling might yield more information.

The population in Odell Lake, which is isolated from anadromous fish by a lava dam 5,000–6,000 years old (USFS 1994), appears to be the result of an introduction of kokanee from the Deadwood–Dworshak–Anderson Ranch–Payette complex, perhaps with some influence from other stocks as well.

It is notable that all the genetic evidence for successful stock transfers of *O. nerka* found in this study involve kokanee. We found no evidence for genetic effects from transfers of anadromous fish, including several million sockeye salmon from British Columbia that were released into Sawtooth Valley lakes in the 1980s. This result is consistent with Wood's (1995) report of finding many records of successful transplants of kokanee but very few for sockeye salmon and Utter's (2004) generalization of this pattern to other salmonids with both anadromous and resident forms. Presumably this reflects the more complicated life history of anadromous *O. nerka* and the much greater opportunity for local adaptations to develop.

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REFERENCES

Aebersold, P. B., G. A. Winans, D. J. Teel, G. B. Milner, and F. M. Utter. 1987. Manual for starch gel electrophoresis: a method for the detection of genetic variation. NOAA Technical Report NMFS 61.

Allendorf, F. W., and G. H. Thorgaard. 1984. Tetraploidy and the evolution of salmonid fishes. Pages 1–53 *in* B. Turner, editor. Evolutionary genetics of fishes. Plenum, New York.

Bevan, D., J. Harville, P. Bergmann, T. Bjornn, J. Crutchfield, P. Klingeman, and J. Litchfield. 1994. Snake River Salmon Recovery Team: final recommendations to the National Marine Fisheries Service. National Marine Fisheries Service, Portland, Oregon.

Bjornn, T. C., D. R. Craddock, and D. R. Corley. 1968. Migration and survival of Redfish Lake, Idaho, sockeye salmon, *Oncorhynchus nerka*. Transactions of the American Fisheries Society 97:360–373.

Bowler, B. 1990. Additional information on the status of Snake River sockeye salmon. Report submitted to ESA Administrative Record for sockeye salmon, Idaho Department of Fish and Game, Boise.

Brannon, E., A. Setter, T. Welsh, R. Danner, K. Collins, M. Casten, G. Thorgaard, K. Adams, and S. Cummings. 1994. Genetic analysis of Oncorhynchus nerka: life history and genetic analysis of Redfish Lake Oncorhynchus nerka. 1992–1993 completion report to the Bonneville Power Administratration. Available: pisces.bpa.gov/release/documents/documentviewer.aspx?doc=12885-2. (June 2010).

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. Evolution 21:550–570.

Chapman, D. W., W. S. Platts, D. Park, and M. Hill. 1990. Status of Snake River sockeye salmon. Pacific Northwest Utilities Conference Committee, Final Report, Portland, Oregon.

Corley, D. C. 1966. Redfish, Stanley, Yellow Belly, Pettit, Perkins and Little Redfish lake fisheries investigations, May 15 to September 30, 1966. Idaho Department of Fish and Game, Boise.

Cramer, S. P. 1990. The feasibility for reintroducing sockeye and coho salmon in the Grande Ronde River and coho and chum salmon in the Walla Walla River. S. P. Cramer and Associates, Report submitted to the Nez Perce Tribal Executive Committee and Nez Perce Fisheries Resource Management, Gresham, Oregon.

Cummings, S. A., E. L. Brannon, K. J. Adams, and G. H. Thorgaard. 1997. Genetic analyses to establish captive breeding priorities for endangered Snake River sockeye salmon. Conservation Biology 11:662–669.

Faler, J., and M. Powell. 2003. Genetic analysis of Snake River sockeye salmon (*Oncorhynchus nerka*). Technical Report to the Bonneville Power Administration, Project 90–93, BPA Report DOE/BP-12885-3, Portland, Oregon.

Flagg, T. A. 1993. Redfish Lake sockeye salmon captive broodstock rearing and research. Annual research report to the Bonneville Power Administration, Portland, Oregon.

Flagg, T. A., C. V. W. Mahnken, and K. A. Johnson. 1995. Captive broodstocks for recovery of Snake River sockeye salmon. Pages 81–90 *in* H. L. Schramm Jr. and R. G. Pipers, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Flagg, T. A., W. C. McAuley, P. A. Kline, M. S. Powell, D. Taki, and J. C. Gislason. 2004. Application of captive broodstocks to preservation of ESA-listed stocks of Pacific salmon: Redfish Lake sockeye salmon case example. Pages 387–400 *in* M. Nickum, P. Mazik, J. Nickum, and D. MacKinley, editors. Propagated fish in resource management. American Fisheries Society, Symposium 44, Bethesda, Maryland.

Gustafson, R., R. S. Waples, J. M. Myers, J. J. Hard, G. J. Bryant, O. W. Johnson, and L. A. Weitkamp. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Hall-Griswold, J. A. 1990. Sockeye of Stanley basin: summary. Report submitted to the ESA Administrative Record for sockeye salmon, July 1990. Idaho Department of Fish and Game, Boise.

Howell, P., K. Jones, D. Scarnecchia, L. Lavoy, W. Kendra, and D. Ortmann. 1985. Stock assessment of Columbia River anadromous salmonids, volume I: Chinook, coho, chum, and sockeye salmon stock summaries. Final Report to the Bonneville Power Administration, Project 83–33, Portland, Oregon.

IDFG (Idaho Department of Fish and Game). 1997. Computer database of historic stocking records: 1968–present. IDFG, Boise.

Johnson, K. A. 1993. Research and recovery of Snake River sockeye salmon. Annual research report to the Bonneville Power Administration, Portland, Oregon.

Jones, R. 1991. The effect of Sunbeam Dam on sockeye salmon in the Salmon River, Idaho. Technical Memorandum to ESA Administrative Record for sockeye salmon, National Marine Fisheries Service, Environmental and Technical Services Division, Portland, Oregon.

Kostow, K. 1996. ODFW *O. nerka* hatchery records in Wallowa and Metolius subbasins. Oregon Department of Fish and Wildlife Memorandum to, West Coast Sockeye Salmon Administrative Record, National Marine Fisheries Service, Environmental and Technical Services Division, Portland, Oregon.

Kozfkay, C. C., M. R. Campbell, J. A. Heindel, D. J. Baker, P. Kline, M. S. Powell, and T. Flagg. 2008. A genetic evaluation of relatedness for broodstock management of captive, endangered Snake River sockeye salmon, *Oncorhynchus nerka*. Conservation Genetics 9:1421–1430.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMF/S-NWFSC 42.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

NRC (Natural Resources Consultants). 1995. Artificial propagation of anadromous Pacific salmonids: West Coast sockeye salmon. Electronic database submitted to Coastal Zone and Estuarine Studies Division, Northwest Fisheries Science Center, contract 50ABNF400128. Available: ftp.streamnet.org/pub/streamnet/nmfs_data. (June 2010).

Ricker, W. E. 1940. On the origin of kokanee, a freshwater type of sockeye salmon. Transactions of the Royal Society of Canada 34:121–135.

Shaklee, J. B., F. W. Allendorf, D. C. Morizot, and G. S. Whitt. 1990. Gene nomenclature for protein-coding loci in fish. Transactions of the American Fishery Society 119:2–15.

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

Thorgaard, G. H., P. Spruell, S. A. Cummings, A. S. Peek, and E. L. Brannon. 1995. Mixed DNA fingerprint analysis differentiates sockeye salmon populations. Pages 295–303 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

USACE (U.S. Army Corps of Engineers). 1993. 1992 Reservoir drawdown test: Lower Granite and Little Goose dams. USACE, Final Report, Walla Walla, Washington.

USFS (U.S. Forest Service). 1994. Odell pilot watershed analysis. USFS, Deschutes National Forest, Bend, Oregon.

U.S. Office of the Federal Register. 1991. Endangered and threatened species: endangered status for Snake River sockeye salmon, Final Rule. Federal Register 56:224(20 November 1991):58619–58624.

Utter, F. 2004. Population genetics, conservation, and evolution in salmonids and other widely cultured fishes: some perspectives over six decades. Reviews in Fish Biology and Fisheries 14:125–144.

Utter, F., P. Aebersold, and G. Winans. 1987. Interpreting genetic variation detected by electrophoresis. Pages 21–45 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Utter, F. M., P. B. Aebersold, J. Helle, and G. A. Winans. 1984. Genetic characteristics of populations on the southeastern range of sockeye salmon. Pages 17–32 *in* J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic wild fish conference. Peninsula College, Port Angeles, Washington.

Waples, R. S. 1988. Estimation of allele frequencies at isoloci. Genetics 118:371–384.

Waples, R. S. 1995. Genetic effects of stock transfers of fish. Pages 51–69 *in* D. Philipp, J. M. Epifanio, J. E. Marsden, J. E. Claussen, and R. J. Wolotira Jr., editors. Protection of aquatic biodiversity: proceedings of the world fisheries congress, theme 3. Oxford and IBH Publishing, New Delhi.

Waples, R. S., P. B. Aebersold, and G. A. Winans. 1997. Population genetic structure and life history variability in *Oncorhynchus nerka* from the Snake River basin. Final Research Report to the Bonneville Power Administration, Portland, Oregon.

Waples, R. S., O. W. Johnson, and R. P. Jones Jr. 1991a. Status review for Snake River sockeye salmon. NOAA Technical Memorandum NMFS F/NWC-195.

Waples, R. S., and D. J. Teel. 1990. Conservation genetics of Pacific salmon, I. Temporal changes in allele frequency. Conservation Biology 4:144–156.

Waples, R. S., D. J. Teel, and P. B. Aebersold. 1991b. A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River basin. Annual research report to the Bonneville Power Administration, Portland, Oregon.

Welsh, T. L. 1991. Stanley Basin sockeye salmon lakes, upper Salmon River drainage, Idaho: fish stocking history; fish eradication projects;

present status of the kokanee salmon stocks. University of Idaho, Moscow.

Winans, G. A., P. B. Aebersold, and R. S. Waples. 1996. Allozyme variability of *Oncorhynchus nerka* in the Pacific Northwest, with special consideration to populations of Redfish Lake, Idaho. Transactions of the American Fishery Society 125:645–663.

Wood, C. C. 1995. Life history variation and population structure of sockeye salmon. Pages 195–216 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Wright, S. 1978. Evolution and the genetics of populations, volume 4. Variability within and among natural populations. University of Chicago Press, Chicago.

Young, S. F., M. R. Downen, and J. B. Shaklee. 2004. Microsatellite DNA data indicate distinct native populations of kokanee, *Oncorhynchus nerka*, persist in the Lake Sammamish basin, Washington. Environmental Biology of Fishes 69:63–79.

Appendix: Enzymes Surveyed

TABLE A.1. List of enzymes surveyed, enzyme numbers, new and old abbreviations for each presumptive gene locus, tissues sampled (M = muscle, L = liver, H = heart, and E = eye), and buffers used. All loci scored in at least 40 of the 53 total samples (75%) are included. The numbers of samples shown (with data and polymorphic) are based on the 32-population data set obtained by pooling the temporal samples (see Table 1). Locus names and abbreviations follow the guidelines provided by Shaklee et al. (1990). Descriptions of the buffer systems are found in Aebersold et al. (1987), with modifications described by Waples et al. (1991).

						Number of samples	
Enzyme name	Number	Locus	Previous abbreviation	Tissue	Buffer	With data	Polymorphic
Aspartate aminotransferase	2.6.1.1	*sAAT-2**	GOT-2	MH	TBCLE	32	6
		*sAAT-3**	GOT-3, AAT-3	E	TBE	32	0
		*sAAT-4**	AAT-4	L	TBE	32	0
		*mAAT-1**		HME	ACE7	32	31
		*mAAT-2**		HME	ACE7	32	1
Acid phosphatase	3.1.3.2	*ACP-1**		L	TBE	31	0
Adenosine deaminase	3.5.4.4	*ADA-1**		E	TBE	32	20
		*ADA-2**		E	TBE	32	3
Alcohol dehydrogenase	1.1.1.1	*ADH**		L	ACE7	27	1
Aconitate hydratase	4.2.1.3	*sAH**	ACON-2, AH	L	ACE7	32	2
		*mAH-1,2**		HME	ACE7	32	31
		*mAH-3**		HME	ACE7	32	1
		*mAH-4**		HME	ACE7	32	0
Adenylate kinase	2.7.4.3	*AK**		ME	ACE7	32	0
Alanine aminotransferase	2.6.1.2	*ALAT**	GPT	M	TBE	32	32
Creatine kinase	2.7.3.2	*CK-A1**	CK-1	M	TBCLE	32	1
		*CK-A2**	CK-2	M	TBCLE	32	1
		*CK-B**	CK-5	E	TBCLE	32	5
		*CK-C1**	CK-3	E	TBCLE	32	0
		*CK-C2**	CK-4	E	TBCLE	32	2
Esterase-D	3.1.-.-	*ESTD**		M	TBCLE	32	0
Fructose-bisphosphate aldolase	4.1.2.13	*FBALD-3**	ALD-3	E	ACEN7	32	0
		*FBALD-4**	ALD-4	E	ACEN7	29	4
Formaldehyde dehydrogenase (glutathione)	1.2.1.1	*FDHG**	HAGH	L	TBE	31	2
Fumarate hydratase	4.2.1.2	*FH**	FUM	M	ACEN7	32	0
β-*N*-Acetylgalactosaminidase	3.2.1.53	*βGALA**		L	ACE7	32	1
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	GAP-1	M	ACEN7	32	0
		*GAPDH-2**	GAP-3	H	ACEN7	32	0
		*GAPDH-3**	GAP-4	MH	ACEN7	32	0
		*GAPDH-4**	GAP-5	E	ACEN7	28	1
		*GAPDH-5**	GAP-6	E	ACEN7	28	0

(Continued on next page)

TABLE A.1. Continued.

Enzyme name	Number	Locus	Previous abbreviation	Tissue	Buffer	Number of samples: With data	Number of samples: Polymorphic
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**	AGP-1	MH	ACEN7	32	0
		*G3PDH-2**	AGP-2	MH	ACEN7	32	2
		*G3PDH-3**	AGP-3	H	ACEN7	30	0
		*G3PDH-4**	AGP-4	H	ACEN7	32	0
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B1**	GPI-1	M	TBCLE	32	0
		*GPI-B2**	GPI-2	M	TBCLE	32	7
		*GPI-A**	GPI-3	M	TBCLE	32	9
Glutathione reductase	1.6.4.2	*GR**		E	TBCLE	32	0
β-*N*-Acetylhexosaminidase	3.2.1.52	*βHEX**	βGLUA, bGA	L	TC4	32	1
L-Iditol 2-dehydrogenase	1.1.1.14	*IDDH-1**	SDH-1	L	TBCL	32	0
		*IDDH-2**	SDH-2	L	TBCL	32	0
Isocitrate dehydrogenase ($NADP^+$)	1.1.1.42	*mIDHP-1**	IDH-1	MH	ACE7	32	3
		*mIDHP-2**	IDH-2	MH	ACE7	32	6
		*sIDHP-1**	IDH-3	LE	ACE7	32	1
		*sIDHP-2**	IDH-4	LE	ACE7	32	0
L-Lactate dehydrogenase	1.1.1.27	*LDH-A1**	LDH-1	M	TBCLE	32	2
		*LDH-A2**	LDH-2	M	TBCLE	32	0
		*LDH-B1**	LDH-3	MEH	TBCLE	32	4
		*LDH-B2**	LDH-4	LMEH	TBCLE	32	4
		*LDH-C**	LDH-5	E	TC4	32	8
Lactoylglutathione lyase	4.4.1.5	*LGL**	GLO-I	M	TBCLE	30	0
α-Mannosidase	3.2.1.24	*αMAN**		L	TC4	31	0
Malate dehydrogenase	1.1.1.37	*sMDH-A1**	MDH-1	LH	ACE7	32	0
		*sMDH-A2**	MDH-2	LH	ACE7	32	4
		*sMDH-B1**	MDH-3	MH	ACE7	32	0
		sMDH-B2	MDH-4	MH	ACE7	32	9
		*mMDH-2**		HM	ACEN7	32	0
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**		EHL	TBE	32	18
Nucleoside-triphosphate pyrophosphatase	3.6.1.19	*NTP**	ITP	M	TBCLE	32	0
Cytosol nonspecific dipeptidase	3.4.13.18	*PEPA**	DPEP-1, GL-1	ME	TBE	32	1
Tripeptide aminopeptidase	3.4.11.4	*PEPB-1**	PEP-3, PEP-LGG	ME	TBCLE	32	0
			TAPEP-1		TC4		
Peptidase-C	3.4.-.-	*PEPC**	DPEP-2, GL-2	E	TBE	32	6
X-Pro dipeptidase	3.4.13.9	*PEPD-1**	PDPEP-1, PHAP-1	M	TBE	32	0
Leucyl-tyrosine peptidase	3.4.-.-	*PEPLT**		ML	TBE	32	5
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	6PG	ME	ACE7	32	2
Phosphoglycerate kinase	2.7.2.3	*PGK-1**		EM	ACE7	30	0
		*PGK-2**		EM	ACE7	31	2
Phosphoglucomutase	5.4.2.2	*PGM-1**		MEH	ACE7	32	28
		*PGM-2**		MEH	ACE7	32	27
Pyruvate kinase	2.7.1.40	*PK-2**		H	ACE7	31	2
Purine-nucleoside phosphorylase	2.4.2.1	*PNP-1**	NP-1	E	ACE7	32	0

TABLE A.1. Continued.

Enzyme name	Number	Locus	Previous abbreviation	Tissue	Buffer	Number of samples: With data	Number of samples: Poly-morphic
Superoxide dismutase	1.15.1.1	*sSOD-1**	SOD-1	L	TBE	32	2
Triose-phosphate isomerase	5.3.1.1	*TPI-1**	TPI-1.1	EM	TBCLE	32	0
		*TPI-2**	TPI-1.2	EM	TBCLE	32	0
		*TPI-3**	TPI-2.1	EM	TG	32	0
		*TPI-4**	TPI-2.2	EM	TG	32	1

TABLE A.2. Summary of genetic variability indices at 35 polymorphic gene loci that were scored in all 32 of the populations in Table 1; F_{IS}, F_{IT}, and F_{ST} are Wright's (1978) fixation indices.

Locus	Number of alleles	F_{IS}	F_{IT}	F_{ST}	Frequency range of common allele
*mAAT-1**	2	0.002	0.483	0.483	0.039–1.0
*mAAT-2**	2	−0.006	0.000	0.006	0.994–1.0
*ADA-1**	3	−0.073	0.054	0.119	0.763–1.0
*ADA-2**	2	−0.020	−0.001	0.018	0.975–1.0
*mAH-3**	2	−0.013	0.000	0.012	0.987–1.0
*sAH**	2	−0.007	0.000	0.006	0.992–1.0
*ALAT**	5	0.011	0.203	0.194	0.103–0.950
*CK-A1**	2	−0.001	0.001	0.002	0.998–1.0
*CK-A2**	2	−0.013	0.000	0.012	0.987–1.0
*CK-B**	2	−0.044	−0.005	0.038	0.949–1.0
*CK-C2**	2	−0.008	0.000	0.007	0.991–1.0
*βGALA**	2	−0.006	0.000	0.006	0.994–1.0
*G3PDH-2**	2	−0.126	−0.004	0.108	0.875–1.0
*GPI-B2**	3	−0.033	−0.003	0.029	0.937–1.0
*GPI-A**	3	−0.033	−0.007	0.025	0.950–1.0
*βHEX**	2	−0.006	0.000	0.006	0.994–1.0
*mIDHP-1**	2	−0.094	0.018	0.103	0.873–1.0
*mIDHP-2**	2	0.183	0.356	0.212	0.688–1.0
*sIDHP-1**	2	0.658	0.666	0.024	0.975–1.0
*LDH-B1**	3	−0.021	−0.002	0.019	0.970–1.0
*LDH-B2**	2	−0.065	−0.004	0.057	0.913–1.0
*LDH-C**	3	0.096	0.130	0.037	0.929–1.0
*sMDH-A2**	3	−0.023	−0.001	0.021	0.969–1.0
*sMDH-B2**	3	0.133	0.175	0.049	0.905–1.0
*MPI**	3	0.014	0.128	0.115	0.667–1.0
*PEPA**	2	−0.010	0.000	0.010	0.990–1.0
*PEPC**	2	−0.080	−0.004	0.070	0.900–1.0
*PEPLT**	2	−0.059	0.090	0.141	0.813–1.0
*PGDH**	2	−0.022	−0.001	0.020	0.975–1.0
*PGM-2**	2	−0.016	0.108	0.122	0.512–1.0
*sSOD-1**	3	−0.015	−0.001	0.014	0.980–1.0
*TPI-4**	2	−0.009	0.000	0.008	0.991–1.0
Means		0.001	0.244	0.244	
Other loci:					
*mAH-1,2**	4				0.552–1.0
*LDH-A1**	2				0.875–1.0
*PGM-1**	2				0.025–1.0