

**Abstract.**— An anomalous inability to distinguish certain geographically-separated chinook salmon *Oncorhynchus tshawytscha* populations of the Snake River and the Klamath River from a survey of 18 polymorphic loci led to a prediction that distinction would ultimately be found through sampling of additional polymorphic loci. Recently published studies involving pertinent groups within each of these rivers included data from an additional 15 polymorphic loci, and therefore allow a re-examination of the relationships between these groups. Comparison of results for the new studies shows the formerly indistinguishable groups from two areas to be as distinct from one another as from other major groupings of the species with a mean genetic distance between populations of each river (0.014) that is double that of the maximum within-group genetic distance. Two newly-resolved gene loci (*mMDH-2\** and *sMEP-1\**) are particularly good at distinguishing populations from the two rivers. In addition to resolving the anomalous similarity between populations inhabiting geographically separated areas, the new results illustrate the care that must be used in drawing inferences from negative data.

## Genetic isolation of previously indistinguishable chinook salmon populations of the Snake and Klamath Rivers: Limitations of negative data

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A variety of characteristics can be useful in distinguishing particular groups of organisms from other related groups. In humans, for instance, major ancestral groups can be identified by heritable morphological traits, as well as by characteristic frequencies of alleles detected by molecular or immunological procedures. Conversely, although two groups lacking any distinguishing characteristics may, in fact, be closely related, the possibility of undetected differences often prevents a conclusive determination of the degree of relatedness. For example, two cryptic species of bonefishes in Hawaii were considered members of a common gene pool until biochemical genetic analysis revealed that the two forms diverged perhaps 20 million years ago (Shaklee and Tamaru 1981). Other examples of genetic distinctions between and within species of fishes previously considered to be homogeneous are listed in Allendorf et al. (1987).

The motivation behind our present study was a puzzling instance of apparent genetic similarity between two geographically separated groups of chinook salmon *Oncorhynchus tshawytscha*. Indigenous chinook salmon from the Klamath River and spring- and summer-run chinook salmon from the Snake River are well differentiated from nearby

populations at several protein-coding gene loci (Utter et al. 1989, Bartley and Gall 1990, Waples et al. 1991, Bartley et al. 1992). However, a comparison of the two river groups by Utter et al. (1989) failed to distinguish them despite their substantial geographic separation. The mouths of the Snake and Klamath Rivers are separated by a distance of almost 600 river-ocean miles, and a number of ancestrally distinct groups of populations (Utter et al. 1989) are found in intervening areas.

This apparent genetic similarity was even more puzzling because of substantial life-history differences between chinook salmon from the two rivers. The populations that were not well differentiated in the Utter et al. (1989) study included four spring-run and two summer-run populations from the Snake River and two fall- and one spring-run population from the Klamath River. Utter et al. (1989) also sampled fall-run fish from the Snake River, but this population is genetically quite different both from Snake River spring- and summer-run fish and chinook salmon from the Klamath River. Whereas the fall-run fish migrate to sea as subyearlings, the other populations produce juveniles that spend an additional winter in freshwater and outmigrate as yearlings.

Utter et al. (1989) speculated that the anomalously high degree of genetic similarity between Klamath and Snake River populations was due to coincidentally high frequencies of the same common alleles (possibly a reflection of restricted gene flow among populations and reduced population sizes over an extended time interval) rather than to a recent common ancestral origin. Of the 25 polymorphic loci examined, only 18 were variable in either the Snake or Klamath River groups, and populations from these two areas had the lowest average heterozygosities (0.027–0.045; Utter et al. 1989, App. A) of any populations included in the study. Utter et al. (1989) predicted that additional genetic surveys would ultimately reveal divergent frequencies of alleles in the two areas. If such differences were not found in more extensive studies, alternate explanations for this apparent similarity would be required.

This paper retests and rejects the null hypothesis of no genetic difference between these two groups based on two recently published studies, which sample several new populations and an additional 15 polymorphic loci. Comparison of results for the new studies shows the formerly-indistinguishable chinook salmon populations of the Klamath and Snake River to be quite distinct, with a mean genetic distance between populations of each river (0.014) that is double that of the maximum within-group genetic distance. In addition to resolving the anomalous apparent similarity between these chinook salmon populations of these geographically separated areas, the new results illustrate the care that must be used in drawing inferences from negative data.

## Materials and methods

Our analyses used the data from Bartley et al. (1992) for Klamath River populations and Waples et al. (1991) for Snake River populations; comparisons also were made with earlier data from Utter et al. (1989). Sampling locations included 10 areas from the Klamath River and 11 from the Snake River drainages (Table 1, Fig. 1). Samples of juvenile fish from hatcheries and naturally-spawning populations were collected between 1986 and 1989 for the Klamath River, and 1989 and 1990 for the Snake River. Starch gel electrophoresis for all three studies followed procedures described by Aebersold et al. (1987). The data used in these analyses were part of a larger baseline dataset used by management agencies to help determine natal origins of chinook salmon harvested in mixed-stock fisheries (Shaklee and Phelps 1990).

Genetic nomenclature and abbreviations followed a system suggested by Shaklee et al. (1989). Data were collected from 21 enzyme systems and 30 presumptive gene loci that were polymorphic in at least one of the

**Table 1**

Collection data for samples of chinook salmon *Oncorhynchus tshawytscha* from the Klamath (K1–K10; Bartley et al. 1992) and Snake (S1–S11; Waples et al. 1991) Rivers. Samples from hatchery stocks are marked by a dagger (†); other samples were from naturally spawning populations. Locations included in the study of Utter et al. (1989) are indicated by an asterisk (\*). Run timing indicates the season of entry of adults into freshwater.

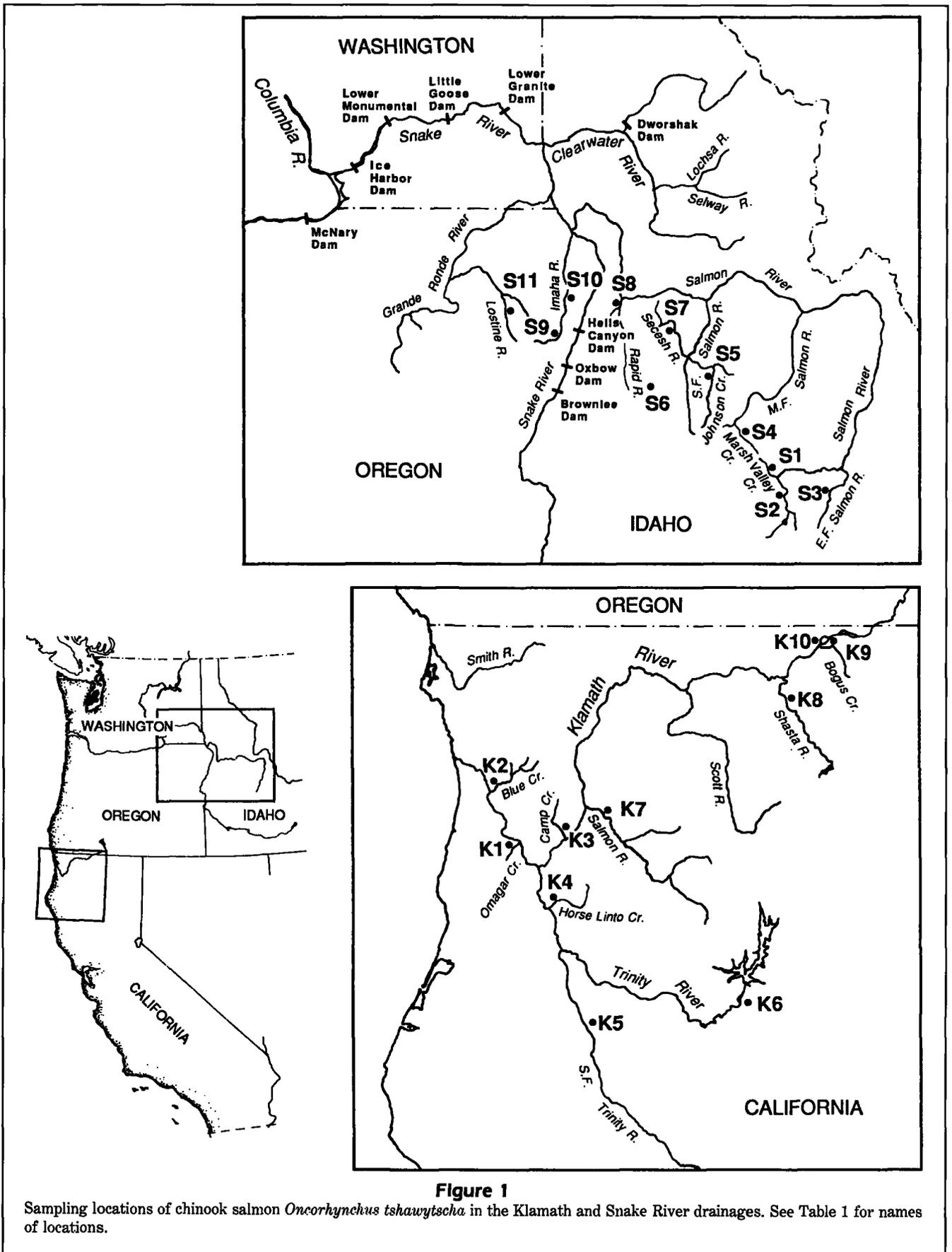
Map code	Location	Run timing	Sample size
<b>Klamath River</b>			
K1	Omagar Creek	Fall	100
K2	Blue Creek	Fall	100
K3	Camp Creek	Fall	106
K4	Horse Linto Creek	Fall	100
K5	S. Fork Trinity River	Fall	100
*K6	Trinity River†	Fall	120
K7	Upper Salmon River	Fall	98
K8	Shasta River	Fall	100
K9	Bogus Creek	Fall	128
K10	Iron Gate Hatchery†	Fall	99
<b>Snake River</b>			
*S1	Valley Creek	Spring	99
*S2	Sawtooth Hatchery†	Spring	100
S3	Salmon River	Spring	99
S4	Marsh Creek	Spring	100
*S5	Johnson Creek	Summer	97
*S6	McCall Hatchery†	Summer	100
S7	Secesh River	Summer	92
*S8	Rapid River Hatchery†	Spring	100
S9	Imnaha River	Summer	100
S10	Imnaha Hatchery†	Summer	100
S11	Lostine River	Spring	100

populations (Tables 2, 3). The observed polymorphisms were attributed to 26 disomic loci and 2 isolocus pairs (*sAAT-1.2\** and *sMDH-B1.2\**; see Allendorf and Thorgaard 1984). A single, average allele frequency was computed for each isolocus pair for purposes of comparing populations.

Genetic data were analyzed using the BIOSYS program of Swofford and Selander (1981). Analyses included calculation of unbiased pairwise genetic distances between populations (Nei 1978), unweighted pair group method (UPGM) projection of a matrix of these distances (Sneath and Sokal 1973), average heterozygosities, and the number of alleles per locus.

## Results and discussion

Our analyses focused on a comparison of genetic characteristics between chinook salmon from the Klamath and Snake Rivers. Discussion of population structure within these two areas appears elsewhere, as do more



**Figure 1**

Sampling locations of chinook salmon *Oncorhynchus tshawytscha* in the Klamath and Snake River drainages. See Table 1 for names of locations.

**Table 2**  
Enzymes and loci examined (enzyme nos. in parentheses) of chinook salmon *Oncorhynchus tshawytscha*.

Enzyme	Locus	Enzyme	Locus
Aspartate aminotransferase (2.6.1.1)	<i>sAAT-1,2*</i>	Tripeptide aminopeptidase (3.4.11.4)	<i>PEPB-1*</i>
	<i>sAAT-3*</i>	Leucine-tyrosine dipeptidase (3.4.-.-)	<i>PEP-LT*</i>
	<i>sAAT-4*</i>	Malate dehydrogenase (1.1.1.37)	<i>sMDH-B1,2*</i>
Adenosine deaminase (3.5.4.4)	<i>ADA-1*</i>		<i>mMDH-1*</i>
Alcohol dehydrogenase (1.1.1.1)	<i>ADH-4</i>		<i>mMDH-2*</i>
Aconitate hydratase (4.2.1.3)	<i>sAH-1*</i>	Malic enzyme (1.1.1.40)	<i>sMEP-1*</i>
	<i>mAH-4*</i>	Mannose-6-phosphate isomerase (5.3.1.8)	<i>MPI*</i>
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	<i>GAPDH-3*</i>	Phosphogluconate dehydrogenase (1.1.1.44)	<i>PGDH*</i>
Dipeptidase (3.4.13.11)	<i>PEPA*</i>	Phosphoglycerate kinase (2.7.2.3)	<i>PGK-2*</i>
Glutathione reductase (1.6.4.2)	<i>GR*</i>	Phosphoglucomutase (2.7.5.1)	<i>PGM-2*</i>
Hydroxyacylglutathione hydrolase (3.1.2.6)	<i>HAGH*</i>	L-Iditol dehydrogenase (1.1.1.14)	<i>IDDH-1*</i>
Isocitrate dehydrogenase (1.1.1.42)	<i>sIDHP-1*</i>	Superoxide dismutase (1.15.1.1)	<i>sSOD-1*</i>
	<i>sIDHP-2*</i>	Triose-phosphate isomerase (5.3.1.1)	<i>TPI-4*</i>
Lactate dehydrogenase (1.1.1.27)	<i>LDH-B2*</i>		
	<i>LDH-C*</i>		

**Table 3**

Range of common allele frequencies in samples of chinook salmon *Oncorhynchus tshawytscha* from the Snake and Klamath Rivers reported in three investigations. Parenthetical entries summarize data from studies (2) and (3), respectively, for those populations studied in (1). Subset (A) are loci common to all studies; subset (B) are isocus pairs unique to study (1); subset (C) are loci newly resolved in studies (2) and (3).

Locus	(1) Utter et al. 1989		(2) Waples et al. 1991		(3) Bartley et al. 1992	
	Snake	Klamath	Snake	Klamath	Snake	Klamath
(A) <i>sAAT-1,2*</i>	0.981-1.000	0.995-1.000	0.957-1.000 (0.957-1.000)		1.000	(1.000)
<i>sAAT-3*</i>	0.994-1.000	0.995-1.000	0.965-1.000 (0.980-1.000)		0.985-1.000	(0.985-1.000)
<i>ADA-1*</i>	0.953-0.969	1.000	0.846-1.000 (0.894-1.000)		0.995-1.000	(1.000)
<i>sAH-1*</i>	0.994-1.000	0.995-1.000	0.985-1.000 (0.990-1.000)		0.940-1.000	(0.940-1.000)
<i>PEPA*</i>	0.994-1.000	0.990-1.000	0.995-1.000 (0.995-1.000)		0.770-1.000	(0.930-1.000)
<i>GR*</i>	1.000	0.995-1.000	0.995-1.000 (0.985-1.000)		0.995-1.000	(1.000)
<i>LDH-B2*</i>	0.972-1.000	1.000	0.970-1.000 (0.970-0.995)		1.000	(1.000)
<i>LDH-C*</i>	0.976-1.000	1.000	0.920-1.000 (0.920-1.000)		0.890-1.000	(0.980-1.000)
<i>PEPB-1*</i>	0.944-0.976	0.949-0.990	0.904-0.985 (0.904-0.985)		0.860-1.000	(0.980-1.000)
<i>sMDHB-1,2*</i>	0.995-0.998	0.997-1.000	0.942-0.997 (0.944-0.990)		0.993-1.000	(0.997-1.000)
<i>MPI*</i>	0.910-0.953	0.975-0.990	0.770-0.990 (0.884-0.990)		0.860-1.000	(0.970-0.992)
<i>PGK-2*</i>	0.062-0.139	0.146-0.350	0.065-0.187 (0.065-0.187)		0.148-0.400	(0.148-0.320)
<i>sSOD-1*</i>	0.944-0.976	0.895-0.990	0.885-0.980 (0.939-0.980)		0.755-0.992	(0.845-0.992)
(B) <i>sIDHP-1,2*</i>	0.913-0.937	1.000	—		—	
<i>PGM-1,2*</i>	1.000	0.942-0.990	—		—	
(C) <i>TPI-4*</i>	—	—	0.825-0.955		0.995-1.000	
<i>sAAT-4*</i>	—	—	0.919-1.000		0.985-1.000	
<i>ADH*</i>	—	—	0.985-1.000		1.000	
<i>mAH-4*</i>	—	—	0.985-1.000		0.775-1.000	
<i>GAPDH-3*</i>	—	—	1.000		0.871-1.000†	
<i>HAGH*</i>	—	—	0.902-1.000		1.000	
<i>sIDHP-1*</i>	—	—	0.783-0.950		0.992-1.000	
<i>sIDHP-2*</i>	—	—	0.945-1.000		0.900-1.000	
<i>PEP-LT*</i>	—	—	0.870-0.985		0.985-1.000	
<i>mMDH-1*</i>	—	—	0.995-1.000		0.795-1.000	
<i>mMDH-2*</i>	—	—	0.490-0.800		0.905-1.000	
<i>sMEP-1*</i>	—	—	0.010-0.079		0.150-0.465	
<i>PGDH*</i>	—	—	1.000		0.910-1.000	
<i>PGM-2*</i>	—	—	1.000		0.860-1.000	
<i>IDDH-1*</i>	—	—	0.897-1.000		0.990-1.000	

† Data from Gall et al. 1989

complete details of the individual studies. (Bartley et al. 1992, Waples et al. 1991).

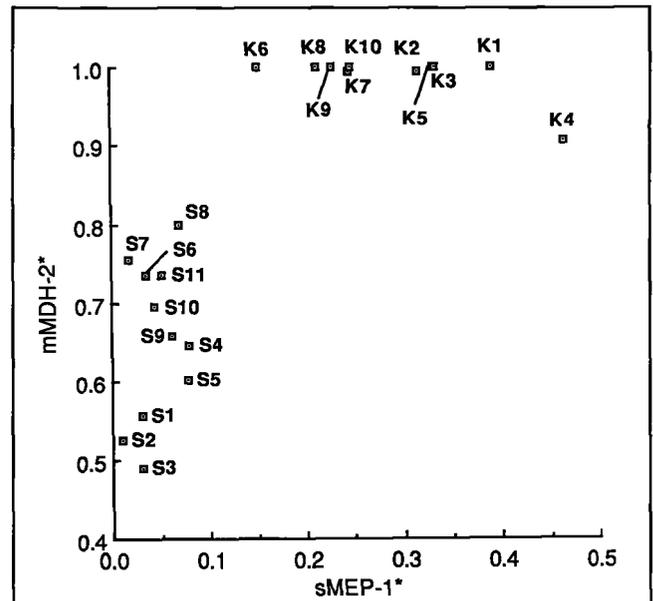
### Variability within populations

The levels of genetic variation within populations were evaluated using only the loci found to be polymorphic. Because this restriction does not represent a random sample of gene loci, values reported here are applicable only for comparisons among populations included in this study or with other studies using the same set of loci. Indices of genetic variability were consistently slightly higher in the Snake River samples; the average number of alleles per locus was 1.63 vs. 1.51 for the Klamath River, and the average heterozygosity was 0.079 vs. 0.065 ( $0.05 > p > 0.01$  in both instances, based on Mann-Whitney tests). Heterozygosities ranged from 0.058 to 0.090 in the Snake River populations and were less uniform in the Klamath River groups, where both the lowest (0.039 in Shasta River) and the highest (0.126 in Omagar Creek) values were found. Neither of these latter two populations were represented in the initial study of the Klamath River by Utter et al. (1989). The actual heterozygosity values reported here are higher than those reported by Utter et al. (1989), primarily because a number of new, very polymorphic systems are included in the more recent analyses. Nevertheless, Utter et al. (1989) also found a slightly higher average heterozygosity in Snake River spring-run and summer-run chinook salmon (0.035–0.045) than in those from the Klamath River (0.027–0.032). Based on the new data, Waples et al. (1991) concluded that, in comparison with other Columbia River populations, Snake River spring-run and summer-run chinook salmon have somewhat reduced levels of genetic variability, but that the difference is apparently not as large as suggested by earlier studies (Utter et al. 1989, Winans 1989).

### Variability between regions

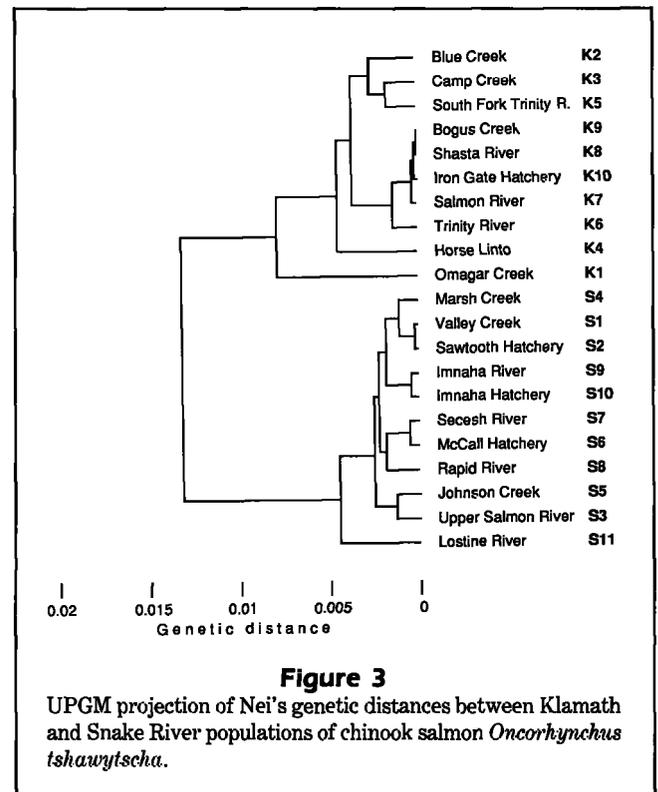
Allele frequency distributions differed substantially between the two regions at a number of gene loci. Although three or more alleles were found at some of these loci, most of the important differences were reflected in differing frequencies of the common allele (Table 3). Particularly large differences were found at *mMDH-2\** and *sMEP-1\** (Fig. 2); for these loci, the range of allele frequencies was nonoverlapping between regions, with substantially higher frequencies of the common (i.e., 100\*) allele found in the Klamath River samples at both loci.

Genetic differences between the two regions based on data for all 30 loci are summarized in a phenogram resulting from clustering of pairwise genetic distances



**Figure 2**

Plot of frequencies of common alleles of Klamath (K) and Snake (S) River populations of chinook salmon *Oncorhynchus tshawytscha* at the *mMDH-2\** and *sMEP-1\** loci.



**Figure 3**

UPGM projection of Nei's genetic distances between Klamath and Snake River populations of chinook salmon *Oncorhynchus tshawytscha*.

(Fig. 3). The Snake and Klamath River populations are separated by a mean genetic distance of 0.014, whereas the within-river separations average 0.004 and 0.007,

respectively. The present data, then, clearly identify two genetically-distinct groups on the basis of the 30 polymorphic loci that were examined.

This genetic distinction clearly rejects a hypothesis of a recent common ancestry for populations of these regions. The topography of the clustering within Klamath and Snake River groups and the relative genetic distance between them are very similar to those distinguishing Klamath River populations from other genetically-distinct population groups of California and the Oregon Coast based on a similar set of polymorphic loci (Bartley et al. 1992).

### Comparison with previous information

Because the clear separation of Snake and Klamath River populations reported here contrasts sharply with the minimal differences detected between these groups by Utter et al. (1989), an examination of results from that earlier study is warranted. A direct comparison of the original study with the two more recent studies is complicated by (1) the addition of a number of new gene loci in the more recent studies, (2) the greater discriminatory capabilities for some loci used in the newer studies, and (3) the more extensive sampling of populations in the newer studies. A comparison of the 15 loci common to both the original and more recent studies was made for the five Snake River sampling sites (S1, S2, S5, S6, S8) and two Klamath River sites (K6, K10) that were sampled in both investigations. In general, very similar allele frequencies were found at most loci in the two sets of samples (Table 3). None of the allele frequency differences between the original and the more recent studies exceeded 0.06 (at *PEPA*\* in the Klamath River comparisons). Thus, the more recent samples confirm the minimal differences between the two regions reported by Utter et al. (1989) based on the loci and populations originally examined.

The improved resolution in the more recent studies, therefore, can be attributed to an increase in the number and type of usable genetic characters. Particularly important was the addition of 15 gene loci not included in the earlier study (Table 3). Although regional differences are strongest at *mMDH-2*\* and *sMEP-1*\*, clear contrasts between the regions are also seen at five other loci (*mAH-4*\*, *GAPDH-3*\*, *HAGH*\*, *PEP-LT*\*, and *TPI-4*\*). In addition, the more recent studies resolve individual loci that had previously been considered isolocus pairs, which further enhanced the discriminating power of two genetic systems. This effect was most apparent for the enzyme IDH. Utter et al. (1989), as have other previous studies (e.g., Utter et al. 1987), reported variation for the isolocus pair *sIDHP-1,2*\*; subsequently, Shaklee et al. (1990) showed that it is possible to resolve the two loci individually.

Whereas the most extreme frequency difference between the two regions at *sIDHP-1,2*\* was 0.087 (1.0–0.913; Table 3) in the original study, the maximum difference at *sIDHP-1*\* in the newer studies was 0.217 (1.0–0.783). Similarly, the protocol of Gall et al. (1989) for partitioning variation at the *PGM-1,2*\* isolocus increased the discriminatory power of this genetic system.

### General implications of the results

During the 1960s, the newly found capability to resolve numerous genetic systems exhibiting Mendelian inheritance led to a flood of studies that continues to this day (see Lewontin 1991). Protein electrophoresis has been used extensively in fishery research and management (Utter 1991); such data have proven particularly useful in modifying previously held assumptions about the genetic structure of fish species (Allendorf et al. 1987). The results discussed here are instructive with regard to both the power and the limitations of such information.

The power of Mendelian data lies in the identification of genetic differences among individuals, populations and species. The regional differences among populations of North American chinook salmon originally described by Utter et al. (1989) have also been apparent in subsequent studies (Bartley and Gall 1990, Waples et al. 1991, Bartley et al. 1992). These differences have generally been interpreted to reflect more recent ancestries of populations within a particular genetically-defined region than between populations of different regions.

However, in spite of the power of electrophoretic data to detect genetic differences when present, there are limits to the conclusions that one can draw from the failure to detect such differences. That is, although a finding of a statistically-significant allele frequency difference may provide evidence that gene flow is restricted (or that some other evolutionary force is operating), the inability to identify such differences does not prove that genetic differences do not exist. The present example, in which genetically divergent groups were not well distinguished in a previous study, emphasizes the potential significance of this limitation. Although Utter et al. (1989) hypothesized that the apparent similarity between Klamath and Snake River chinook salmon was a coincidence that did not reflect a common ancestral origin, the distinctness of the two groups could not be demonstrated until new data became available. The situation is analogous to a classical genetic comparison between populations of *Drosophila pseudoobscura* from Berkeley, California and Bogata, Colombia, in which an initial apparent genetic similarity was puzzling in view of the exten-

sive geographic separation of the two regions (Lewontin and Hubby 1966). A subsequent study that found previously-unknown genetic variants (Singh et al. 1976) demonstrated clear genetic differences between populations of each region.

The important message here is to beware of the danger of drawing positive conclusions from negative data. It should also be emphasized that problems of this nature are not confined to genetic data; rather, the limitations of nondiscriminatory information (i.e., the power to reject the null hypothesis) should be considered in evaluating any kind of comparative data for two or more samples.

Similar allele frequencies among samples, then, support but do not confirm hypotheses that the samples are drawn from a common breeding group. This well-established principle requires restatement from time to time (e.g., Utter 1981, Waples 1991). Such awareness serves to safeguard against a premature conclusion of identity for groups that are distinct and thus may be subject to different management criteria.

In these instances it is important to recognize the power of Mendelian data involving multiple polymorphic loci to detect differences between populations when they do exist. For example, assuming that most allozyme variation is neutral, it will take populations that are divided into large units a considerable amount of time before significant divergence will occur. Thus, Atlantic herring *Clupea harengus* populations of the eastern and western Atlantic Ocean that have likely been isolated for thousands of years could not be distinguished because of similar allele frequencies at a number of polymorphic loci (Grant 1984). The observed value for Wright's (1943) fixation index ( $F_{st}$ ) of 0.0042 approximates an  $F_{st}$  value of 0.003 expected for neutral markers among populations of effective size of 1 million individuals separated over 3000 generations (Nei and Chakravarti 1977). Such dynamics preclude genetic distinction of these herring populations through neutral genetic markers (and thus rejection of the null hypothesis) even with very large samples of loci and individuals. Under such circumstances, other criteria (e.g., tagging data) are needed to determine whether one or more populations is being sampled.

Finally, we note the complementary nature of relationships among populations indicated by many phenotypic traits on one hand and by most molecular genetic markers on the other hand. A strong selective component appears to be involved in the maintenance of phenotypic traits such as timings of spawning and migration (e.g., Ricker 1972, Helle 1981); consequently, relationships inferred from such traits tend to reflect relative similarities in adaptations among populations. Conversely, the apparent absence of strong selection at most electrophoretically detectable loci

permits the estimation of relative degrees of gene flow within and among regions (e.g., Chakraborty et al. 1978, Allendorf and Phelps 1981), and such estimations provide useful insights about ancestral relationships. In view of the complementary nature of these different categories of genetic information, adequate sets of both molecular markers (for clarifying ancestral relationships) and phenotypic traits (for identifying adaptive differences within lineages) should be included in genetic surveys of a particular species whenever possible. Such adaptive differences have been noted within a number of apparent ancestral groupings of chinook salmon, including both spring- and fall-spawning migrations within the Klamath River populations of the species (Utter et al. 1989).

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