GENETIC ANALYSIS OF SOCKEYE SALMON POPULATIONS FROM THE CHIGNIK WATERSHED

Final Report to Chignik Regional Aquaculture Association pursuant to Cooperative Agreement No. 98-024

by

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INTRODUCTION:

The Chignik watershed on the south Alaska Peninsula is a major producer of sockeye salmon, with annual runs often exceeding 2 million fish (Owen and Sarafin 1999). The watershed covers 1,520 km^2 and consists of two lakes and two rivers (Figure 1). Black Lake is large and shallow (41 km^2, mean depth = 3 m). Major sockeye spawning areas in the Black Lake drainage are found in the Alec River and Fan Creek. Black River connects Black Lake to Chignik Lake and most sockeye salmon spawning between the lakes occurs in West Fork and Chiaktuak Creek, tributaries to Black River. Chignik Lake has a smaller surface area, but is deeper (24 km^2, mean depth = 26m). Its major spawning areas are the Clark River and shoreline spawning at Hatchery Beach (Conrad 1984). Sockeye salmon also spawn in Chignik River, which drains Chignik Lake into Chignik Lagoon. Scale pattern data indicate that the lagoon is an important rearing area (Phinney 1968).

Sockeye salmon enter the Chignik watershed in two runs. The early run fish enter freshwater from June to early July, and typically spawn in August in tributaries feeding into Black Lake. However, early run fish also spawn in Chiaktuak Creek and West Fork, tributaries of Black River. The later run enters freshwater during July, and spawns in September and October in Chiaktuak Creek and tributaries to Chignik Lake. When the early run of adults is large, late run returns to Chignik Lake have often been low. Sockeye salmon spawning in tributaries entering Black Lake often rear in Black Lake for only a portion of their freshwater residency (Conrad 1984). A significant emigration of fry from Black Lake to Chignik Lake occurs during spring and early summer. This emigration is in part related to the annual abundance of juveniles in Black Lake (Ruggerone 1995).

Genetic stock identification (GSI) has been used to describe the population structure of sockeye salmon within drainages and within nursery lakes as well as over broad geographic areas. For example, Seeb et al. (*in press*) detected population subdivision within the Kenai River watershed; Varnavskaya et al. (1994) found genetic differences among sockeye salmon populations spawning within lakes in Russia, Alaska, and British Columbia. Further, these and other researchers have shown that timing of spawning is a significant component of genetic structuring within nursery lakes or rivers (Ramstad 1998, Bear Lake; Seeb et al. *in press*, Russian River; Varnavskaya et al. 1994, Nachiki, Kuril, Karluk, and Babine lakes).

In this project, we investigate the population structure of sockeye salmon spawning in the Chignik watershed. We use protein markers and GSI procedures to determine if population subdivision exists in the Chignik watershed and how the structure is related to the initial nursery lake and/or time of spawning. This project is a cooperative effort between the Chignik Regional Aquaculture Association (CRAA), Natural Resources Consultants, Inc. (NRC) and the Alaska Department of Fish and Game Gene Conservation Laboratory (ADFG).

OBJECTIVE:

To characterize the genetic structure of the major spawning components of sockeye salmon within the Chignik watershed.

METHODS:

Sample collection

Greg Ruggerone (NRC, Suite 100, 4055 21st Avenue West, Seattle, WA 98199, U.S.A) collected baseline samples for allozyme analysis from 14 spawning aggregates of sockeye salmon at 10 locations within the watershed during 1996 and 1997. In August 1998, ADF&G personnel took an additional collection from spawners in the Chignik River (Table 1; Figure 1). The target sample size for adult collections was set at 100 to achieve acceptable precision around the allele frequency estimates (Allendorf and Phelps 1981; Waples 1990).

Samples of muscle, liver, eye, and heart tissues were dissected from freshly killed individuals, and individual sample numbers were assigned to uniquely identify all genetic tissues. Tissues were placed into cryovials, which were stored in liquid nitrogen while in the field and during shipping. Upon return to Anchorage, samples were transferred to freezers and stored at -80°C until laboratory analysis.

Laboratory analysis

A comprehensive examination for variation at allozyme loci was conducted following the protocols described in Seeb et al. (*in press*) and the nomenclature followed the American Fisheries Society standard (Shaklee et al. 1990). The products of 30 enzymes encoded at 68 allozyme loci were resolved (Table 2). A photographic record of each gel was made, and a collection of mobility standards for all scored alleles was constructed and used to verify alleles.

Genotypes were scored from enzyme phenotypes and then summarized into allele frequency estimates. An allele that did not appear more than once in any of the collections was reported, but was not used in the analysis. In these situations, the rare allele was pooled with the common allele. Heterozygosity for each collection was computed using the loci that were scored in every collection (*PGM-1** was excluded) after the rare alleles were pooled.

Data analysis

Only homozygote alternate phenotypes could be scored for null allele variation at *PGM-1** because of difficulty scoring the **100/*null* heterozygote. Hardy-Weinberg expected frequencies were calculated for this locus and were used for the computation of genetic distances and log-likelihood ratio statistics. Frequencies at isoloci (*sAAT-1,2*; mAH-1,2*; G3PDH-1,2*; sMDH-A1,2*; sMDH-B1,2*; GPI-B1,2*; TPI-1,2**) were calculated assuming the variation occurred with equal frequency at both loci. Departure from Hardy-Weinberg equilibrium (HWE) was examined in each population at each single locus using the log-likelihood ratio statistic (Lessios 1992). Statistics and degrees of freedom were then summed across loci to make a single test for random mating within each population ($\alpha = 0.05$). *PGM-1** was excluded from these tests.

Prior to formal analysis and testing procedures, two exploratory data analysis techniques were applied to decode possible sources of genetic structure in the data. First, genetic distance measures (Nei's unbiased genetic distance; Nei 1978) were calculated between all pairs of collections. These values were then used to construct a dendrogram using the unweighted pair-group method with arithmetic mean (UPGMA) to depict similarities between collections in a step-wise manner. Genetic distances were also used to perform a multi-dimensional scaling analysis (MDS, Lessa 1990) to visualize the genetic relationships without the pooling implicit in

the construction of dendrograms.

Homogeneity of allelic frequencies among the various collections was tested using log-likelihood ratios (modified from Weir 1990). This statistic is distributed approximately chi-squared with $(n - 1)(m - 1)$ degrees of freedom, where n is the number of alleles and m is number of populations in the test. The likelihood values can be summed over all loci to obtain a total value at each level of analysis. The total gene frequency dispersion at each locus was subdivided into within- and among-group components in a hierarchical fashion. Hierarchical levels were organized to test for homogeneity (1) among sites within a spawning month, (2) among spawning months within regions, (3) among regions within nursery lakes, and 4) between nursery lakes. Rejection of the null hypothesis of homogeneity indicates presence of discrete spawning populations. This analysis is a conservative test because the degrees of freedom reflect the entire pattern of diversity within the area sampled. Comparison-wise significance levels were adjusted for multiple tests using a sequential Bonferonni adjustment (modified from Milliken & Johnson 1984 and Rice 1989) with the overall experiment-wise significance level set at $\alpha = 0.05$. This procedure first tested for differences at the top hierarchical level, i.e., between and within nursery lakes. Significance within nursery lakes led to a sequentially adjusted test applied at the next level, and testing proceeded similarly through the hierarchy. If a test was not significant, all remaining lower levels were combined, and a final sequentially-adjusted multiple test of significance was performed. We also performed pair-wise comparisons of collections taken at the same location during different months, a comparison not made explicitly in the above analysis.

Simulations

We conducted simulations to evaluate the usefulness of GSI techniques based on the allozyme baseline for distinguishing population groups within the Chignik watershed. Population groups were combined into larger groups for reporting results based on similarities between collections as observed in MDS and the hierarchical analyses. In these simulations, mixtures were composed entirely and equally of populations from each of the defined reporting groups to determine the accuracy of the stock composition estimates. These hypothetical mixtures (N = 400) were generated from the baseline allele frequencies assuming HWE (with the exception of *PGM-1** which was treated as a non-genetic character). The precision of the simulated mixtures was estimated by a parametric bootstrap (500 iterations, Efron and Tibshirani 1986), where the observed multilocus genotype frequencies were assumed to be distributed multinomial, as were the allele frequencies in the baseline. Simulations were performed using the Statistical Package for Analyzing Mixtures (SPAM95, ADF&G 1997).

To further test the ability of GSI to provide useable information for fishery management, two more sets of simulations were made. In this analysis, baseline populations were grouped in the first case by nursery lake and in the second case by time of spawning. Hypothetical mixtures were then created entirely from each reporting group as in the previous set of simulations. Ostensibly, sockeye salmon spawned in the Alec River and Fan Creek are the only ones to use Black Lake for rearing, so allocations to all the other groups were pooled into the Chignik Lake Nursery reporting group (Table 1). Under the second set of grouping conditions, all allocations to collections that were taken in August were assumed to have entered the watershed during the June run and were pooled into the Early reporting group (Table 1). The September and October collections formed the Late reporting group, because they were assumed to have arrived during

July and August.

RESULTS:

Laboratory analysis

Of the 68 loci (Table 2), six loci were not resolved in every collection: *mAAT-2**, *ESTD**, *FDHG**, *βGLUA**, *αMAN**, and *sSOD-1**. Of these, only *FDHG** and *βGLUA** exhibited polymorphism, but the variant alleles seen were rare. These loci were not used in the analysis. Of the remaining 62 loci, 30 loci had variant alleles in the collections analyzed (Tables 2 and 3); five of these exhibited rare polymorphism (no more than one observation of the variant allele in any of the collections). Except where indicated, statistical analyses for all populations were based on the remaining set of 25 loci: *mAAT-1**, *mAH-1,2**, *mAH-4**, *ALAT**, *FH**, *GAPDH-2**, *GPI-B1,2**, *GR**, *mIDHP-1**, *sIDHP-2**, *LDH-B1**, *LDH-B2**, *sMDH-A1,2**, *sMDH-B1,2**, *mMEP-1**, *PEPC**, *PEPD-1**, *PEPLT**, *PGM-1**, *PGM-2** and *TPI-4**.

Data analysis

When tested across loci within a collection, allele frequencies observed were not significantly different from HWE expected values. Heterozygosity values, calculated from the full set of 62 loci, ranged from 0.029 in the Clark River September collection to 0.036 in the Broad Creek collection with a mean of 0.033 (Table 3).

A UPGMA dendrogram (Figure 2) and MDS plot (Figure 3) were generated using the Nei's unbiased genetic distances computed between all pairs of collections (Table 4). Both techniques show a similar pattern of genetic relationships. Collections from spawning groups sampled in Black Lake tributaries (Alec River and Fan Creek drainages) are all very similar relative to the entire set of collections. Collections from Hatchery Beach and Clark River show greater similarities based on the sampling date than on the location of the collection. In the MDS, the West Fork collection is separate from all other collections. Chiaktuak Creek and Chignik River collections appear genetically more similar to the Black Lake collections than to the Chignik Lake collections.

Systematic testing for genetic differences between collections was accomplished using the hierarchical log-likelihood analysis (Table 5). The hierarchy was defined based on geography, biological assumptions and the relationships depicted in the dendrograms and the MDS, which show the presence of four groups of genetically similar populations. The top level of the hierarchy split the collections by nursery lake. The collections from the Alec River drainage and Fan Creek are from populations that use Black Lake as their initial nursery lake; all other collections are from populations that only rear in Chignik Lake. The next level segregated collections by regional association within the nursery lake. The Alec River partially drains into Fan Creek, so all of the Black Lake Nursery collections were combined at this level. The Chignik Lake Nursery collections were separated into three regions: Black River (West Fork and Chiaktuak Creek collections), Chignik Lake (Hatchery Beach and Clark River collections), and Chignik River. The lowest level of the hierarchy combined collections by month within regions, because exploratory analyses showed temporal association between collections within regions. All Black Lake Nursery collections were taken in August, so no comparison could be made, but within the Chignik Lake Nursery, collections were taken from August to October. Comparisons

were made when multiple collections were taken from a region during the same month.

The hierarchical log-likelihood analysis shows that a significant amount of genetic structure exists within the sockeye populations spawning within the Chignik watershed. There are significant differences between populations using the two nursery lakes, and among and within the populations rearing in Chignik Lake when grouped by regions. The time of spawning is an important barrier to gene flow within the Chignik Lake region as shown by the highly significant differences between months and almost complete identity within months. The same does not hold true for the Black River collections where there are large differences between the two August collections (West Fork and Chiaktuak Creek). No heterogeneity was detected within collections from the Alec River drainage.

Pair-wise comparisons between collections taken at different months from Hatchery Beach, Clark River and Chiaktuak Creek were not made in the previous analysis. Log-likelihood ratio statistics show that there are significant differences between collections taken at different times from Hatchery Beach ($G = 56.7$; $DF = 18$; $P < 0.001$) and Clark River ($G = 39.3$; $DF = 16$; $P = 0.001$). Comparisons between the Chiaktuak Creek collections were as follows: August/ September ($G = 27.5$; $DF = 17$; $P = 0.050$), September/October ($G = 29.0$; $DF = 17$; $P = 0.034$), and August/October ($G = 32.3$; $DF = 15$; $P = 0.006$).

The baseline for the stock identification simulations was prepared by pooling populations that were not significantly different from each other using the log-likelihood ratio statistics. Under these conditions, all the Black Lake Nursery collections were pooled, and the Hatchery Beach and Clark River collections were pooled by collection month to form the Chignik Lake September and Chignik Lake October population groups. Genetic relationships and the effects of pooling into the eight populations in the baseline were examined using Nei's genetic distance measure and MDS (Figure 4). The original structure appears to be unchanged by pooling.

Simulations

Baseline populations were combined into three reporting groups based on the patterns observed in the previous analyses (Figure 4) and management objectives. Populations were grouped as follows: 1) Alec/Chiaktuak/Chignik River comprising Black Lake tributaries, Chignik River and the Chiaktuak Creek collections, 2) West Fork, and 3) Chignik Lake comprising both the September and October collections from Hatchery Beach and Clark River. These reporting groups reflect the tradeoff between genetically identifiable sets of populations and distinctions important for resource management. The Clark River and Hatchery Beach populations from September and October can easily be distinguished, but this separation is not considered necessary under current management objectives which combine September- and October-spawning populations into the same escapement goal. Conversely, in order for fishery managers to meet lake-specific escapement goals, they must distinguish between populations that use Black Lake and those that do not. This is difficult to do, because the Chignik River and Chiaktuak Creek populations are genetically similar to the Alec River populations and splitting them will increase the chance for misallocation between these populations.

The correct mean allocation to each reporting group in the simulations was 89% for Alec/Chiaktuak/Chignik River, 94% for West Fork, and 86% for Chignik Lake (Table 6).

Misallocation from hypothetical Alec/Chiaktuak/Chignik River mixtures was approximately evenly distributed between Chignik Lake and West Fork. From Chignik Lake mixtures, there was a larger misallocation to the Alec/Chiaktuak/Chignik River (12%) than to West Fork (2%). Examination of baseline population allocations shows that most of the 12% misallocation to Alec/Chiaktuak/Chignik River was to Chiaktuak Creek and Chignik River collections (10%). In the West Fork simulation, half of the 6% misallocation to Alec/Chiaktuak/Chignik River was also attributed to these non-Alec River collections.

Alternate grouping of these populations may be meaningful for management or ecological and life history studies. Therefore, two other sets of simulations were performed examining the potential of the baseline to identify stock components based on 1) nursery lake and 2) timing of spawning (Table 7). Mixtures composed of collections that use Black Lake for part of their rearing had a mean allocation of 83% to the Black Lake Nursery reporting region. Mixtures composed of collections from below Black Lake performed slightly better, with a correct mean estimate of 89% for this Chignik Lake-only nursery group. When reporting groups (and mixtures) were defined by time of spawning, correct allocation to the Early group was 88% and 81% for the Late group.

DISCUSSION:

Population structure

Highly significant genetic structure exists within sockeye populations in the Chignik watershed, demonstrated by the MDS and confirmed by the hierarchical log-likelihood analyses. Both geography and timing are important factors. Within the early run (populations spawning in August), geography plays an important role. While no significant differences were found between the collections from Alec River and Fan Creek, the West Fork collection is widely divergent from all other collections. Chiaktuak Creek August and Chignik River collections also show some segregation from the Alec River/Fan Creek collections. Within the late run (populations spawning in September and October) there is a clear distinction between the Chiaktuak Creek collections and the collections from Clark River and Hatchery Beach. Between the Clark River and Hatchery Beach collections there was no significant difference between samples taken from each location during the same month.

Time of spawning also segregates collections within the Chignik watershed. While the September and October collections from Clark River and Hatchery Beach show no differences between locations within months, between months there is significant divergence. The September spawners were different from the October spawners at each site. Likewise, within Chiaktuak Creek there are differences between the August collection and the September and October collections.

It is surprising that the Chignik River collection should appear so similar to the Alec River collections for two reasons. First, they are at the extreme ends of the watershed. Second, they are downstream and upstream spawners respectively. This may act as a barrier to gene flow due to the necessity for correct orientation and migration after emergence (Burgner 1991 and citations therein). Juveniles from the Alec River populations need to swim downstream to find a lake to rear in, while juveniles from Chignik River must swim upstream to the lake or be swept into the

ocean. While a difference might be expected, a similar lack of difference has been noted before; Seeb et al. (*in press*) found few differences between sockeye spawning in the Kenai River above and below Skilak Lake. One possible explanation might be that the sample from the Chignik River inadvertently included spawners bound for the Black Lake tributaries. While an attempt was made to ensure that samples were taken from adults actively spawning in the Chignik River, all salmon entering the watershed must pass through this spot and some individuals collected may have been destined for spawning grounds further up the system.

Mixture analysis

Identifiable genetic units in mixture analyses occurring within the Chignik watershed include: 1) Chignik Lake; 2) West Fork; and 3) Alec River, Chignik River, and Chiaktuak Creek. The differences between these three units were confirmed both visually (Figure 2) and with formal tests (Table 5). Substructure exists within the Alec/Chiaktuak/ Chignik River unit and analyses involving the Alec/Chiaktuak/Chignik River unit may be confounded by the ambiguity of the association between the Alec River collections and the Chiaktuak Creek and Chignik River collections. The September and October collections from Chiaktuak Creek show a close affinity to the Alec River collections, while the Chiaktuak Creek August and Chignik River collections show some separation from this group in the MDS.

When these three genetic units were used as reporting regions for the simulations, the results were promising. Only the West Fork genetic unit was correctly recognized better than the 90% of the time, but the Alec/Chiaktuak/Chignik River and Chignik Lake units had correct allocations of better than 86%. There were consistent misallocations from the Chignik Lake and West Fork units to the Alec/Chiaktuak/Chignik River unit due to the presence of the Chiaktuak Creek and Chignik River collections into this reporting region. When the reporting groups are rearranged by nursery lake it becomes apparent that very little of the misallocation from these groups was attributed to the Black Lake baseline population group. The Chignik River population may be sufficiently different to be considered separately, but the Chiaktuak Creek populations appear to be intermediate to Chignik Lake and Black Lake populations; not really belonging to either group, but not different enough to be a separate group.

An important assumption of genetic stock identification is that all stocks potentially contributing to a mixture are represented in the baseline (Pella and Milner 1987). We used simulated mixtures and baselines created from the data available for the Chignik watershed and the Tustumena watershed in Cook Inlet (reported in Seeb et al. *in press*) to illustrate the potential of mixed stock analysis of south Alaska Peninsula fisheries and the necessity for a complete baseline. The analysis was limited to loci and alleles that were standardized between these sets of data. First, the genetic structure of these populations was evaluated with an UPGMA dendrogram (Figure 5) using Nei's unbiased genetic distances. Three simulated mixtures were created and analyzed as follows: 1) mixture – Tustumena, baseline – Tustumena and Chignik (500 resamples of mixture and baseline); 2) mixture – Chignik, baseline – Tustumena and Chignik (500 resamples of mixture and baseline); 3) mixture – Tustumena, baseline – Chignik (estimate).

Both the UPGMA dendrogram (Figure 5) and simulated mixes 1 and 2 clearly show the genetic distinctness of these two watersheds. Mixtures comprising Tustumena populations had a correct

mean allocation of 97% and mixtures comprising Chignik populations had a correct mean allocation of 98% using a baseline composed of both Tustumena and Chignik populations. This shows that when the baseline contains the populations represented in the fishery sample, we can accurately distinguish between these populations groups. However, when the baseline does not contain populations represented in the fishery sample, results are much poorer as shown in the third simulation. When the mixture is composed entirely of Tustumena salmon and the baseline has only Chignik populations, 87% of the mixture was attributed to Chignik and only 13% could not be attributed to a population in the Chignik baseline.

Genetic stock identification of sockeye salmon collections from the Chignik watershed shows that genetic information can be a useful tool to answer both life history and fishery management questions. Currently, these questions can only be answered within the context of the Chignik watershed. A more comprehensive baseline could be built with the existing Upper Cook Inlet data and with the addition of Bristol Bay, South Alaska Peninsula and Kodiak Island stocks. This comprehensive baseline may be sufficient to allow genetic stock identification of fisheries harvesting sockeye salmon from these regions.

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Table 1. Collections received by the Alaska Department of Fish and Game (ADFG) Gene Conservation Laboratory for analysis from the Chignik watershed. The identification number is unique and corresponds to the numbers on Figure 1. Collections have been segregated based on use of rearing lakes and spawning time. The Chignik River collection was taken by ADFG personnel, all other collections were taken by Greg Ruggerone of Natural Resources Consultants, Inc. The juvenile collections were taken by trap under the ice on Chignik Lake and are mixtures of young salmon of unknown origin. They were not analyzed in this project.

ID Number	Sample Location	Sample Size	Collection Date	Nursery Lake[1]	Spawning Time[2]
	Adult Collections				
1	Chignik River	100	22-Aug-98	Chignik	Early
2	Hatchery Beach	100	15-Sep-97	Chignik	Late
3		100	18-Oct-96	Chignik	Late
4	Clark River	100	16-Sep-97	Chignik	Late
5		100	19-Oct-96	Chignik	Late
6	Chiaktuak Creek	100	04-Aug-97	Chignik	Early
7		94	18-Sep-97	Chignik	Late
8		50	23-Oct-96	Chignik	Late
9	West Fork	100	05-Aug-97	Chignik	Early
10	Fan Creek	100	07-Aug-97	Black	Early
11	Alec River	100	10-Aug-97	Black	Early
12	Boulevard Creek	100	06-Aug-97	Black	Early
13	Broad Creek	100	09-Aug-97	Black	Early
14	Big Spring	100	08-Aug-97	Black	Early
	Juvenile Collections				
	Lower Chignik Lake	224	07-Feb-97		
	Upper Chignik Lake	62	07-Feb-97		
	Chignik Lake	200	Jan-98		

[1] Populations that use Black Lake at anytime as juveniles are part of the Black Lake Nursery group, all others form the Chignik Lake Nursery group.

[2] Populations spawning in August were considered to be early spawners; all others were considered late spawners.

Table 2. Enzymes or proteins screened in sockeye salmon from Chignik Lake and Black Lake drainages. Enzyme nomenclature follows Shaklee et al. (1990), and tissue/buffer systems used to detect the enzymes are given. An M (monomorphic) indicates the detection of only one form of the enzyme and a P (polymorphic) indicates the detection of at least one variant. Loci with incomplete data (i) and loci excluded from the statistical analysis due to rare polymorphism (r) are indicated.

Enzyme or Protein	Enzyme Number	Locus	Tissue	Buffer [1]	Presence of Variation
Aspartate aminotransferase	2.6.1.1	*sAAT-1,2**	Heart	ACE 7.2	M
		*sAAT-3**	Eye	TBCL	M
		*mAAT-1**	Heart	ACE 7.2	P
		*mAAT-2**	Liver	ACE 7.0	M [i]
Adenosine deaminase	3.5.4.4	*ADA-1**	Muscle	KG	M
Aconitate hydratase	4.2.1.3	*mAH-1,2**	Heart	ACE 7.2	P
		*mAH-3**	Heart	ACE 7.2	M
		*mAH-4**	Heart	ACE 7.2	P
		*sAH**	Liver	ACE 7.0	M
Alanine aminotransferase	2.6.1.2	*ALAT**	Muscle	KG	P
Creatine kinase	2.7.3.2	*CK-A1**	Muscle	TBCLE	M
		*CK-A2**	Muscle	TBCLE	M
		*CK-B**	Eye	ACE 7.0	M
		*CK-C1**	Eye	ACE 7.0	M
		*CK-C2**	Eye	ACE 7.0	M
Esterase-D	3.1.-.-	*ESTD**	Muscle	TBCLE	M [i]
Fructose-bisphosphate aldolase	4.1.2.13	*FBALD-3**	Eye	ACE 7.0	M
		*FBALD-4**	Eye	ACE 7.0	M
Formalin dehydrogenase (glutathione)	1.2.1.1	*FDHG**	Liver	TBE	P [i]
Fumarate hydratase	4.2.1.2	*FH**	Muscle	ACN 7.0	P
β-N-Acetylgalactosaminidase	3.2.1.53	*βGALA**	Liver	ACE 7.0	M
N-Acetyl-beta-glucosaminidase	3.2.1.30	*βGLUA**	Liver	TC4	P [i]
Glyceraldehyde-3-phosphate	1.2.1.12	*GAPDH-2**	Heart	ACN 7.0	P
		*GAPDH-4**	Eye	ACE 7.0	M
		*GAPDH-5**	Eye	ACE 7.0	M
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1,2**	Muscle	ACN 7.0	M
		*G3PDH-3**	Heart	ACN 7.0	M
		*G3PDH-4**	Heart	ACN 7.0	M
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B1,2**	Muscle	TBCLE	P
		*GPI-A**	Muscle	TBCLE	M

Enzyme or Protein	Enzyme Number	Locus	Tissue	Buffer [1]	Presence of Variation
Glutathione reductase	1.6.4.2	*GR**	Eye	TBCL	P
Isocitrate dehydrogenase (NADP+)	1.1.1.42	*mIDHP-1**	Heart	ACN 7.0	P
		*mIDHP-2**	Heart	ACN 7.0	M
		*sIDHP-1**	Liver	ACE 7.0	P [r]
		*sIDHP-2**	Liver	ACE 7.0	P
L-Lactate dehydrogenase	1.1.1.27	*LDH-A1**	Muscle	ACN 7.0	M
		*LDH-A2**	Muscle	ACN 7.0	M
		*LDH-B1**	Muscle	TBCLE	P
		*LDH-B2**	Liver	TBE	P
		*LDH-C**	Eye	KG	P [r]
αMannosidase	3.2.1.24	*αMAN**	Liver	TC4	M [i]
Malate dehydrogenase	1.1.1.37	*sMDH-A1,2**	Heart	ACN 7.0	P
		*sMDH-B1,2**	Heart	ACN 7.0	P
		*mMDH-1**	Heart	ACN 7.0	M
		*mMDH-2**	Muscle	ACN 7.0	M
		*mMDH-3**	Muscle	ACN 7.0	M
Malic enzyme (NADP+)	1.1.1.40	*sMEP-1**	Liver	TC4	P [r]
		*mMEP-1**	Muscle	ACN 7.0	P
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	Liver	TBE	M
Dipeptidase	3.4.-.-	*PEPA**	Muscle	TBCLE	M
Tripeptide aminopeptidase	3.4.-.-	*PEPB-1**	Heart	TBE	P [r]
Peptidase-C	3.4.-.-	*PEPC**	Eye	KG	P
Proline dipeptidase	3.4.13.9	*PEPD-1**	Heart	TBE	P
Peptidase-LT	3.4.-.-	*PEPLT**	Muscle	TBCLE	P
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	Liver	ACE 7.0	P [r]
Phosphoglucomutase	5.4.2.2	*PGM-1**	Heart	ACE 7.2	P
		*PGM-2**	Muscle	TBCLE	P
Superoxide dismutase	1.15.1.1	*sSOD-1**	Liver	TBE	M [i]
Triose-phosphate isomerase	5.3.1.1	*TPI-1,2**	Eye	KG	M
		*TPI-3**	Eye	KG	M
		*TPI-4**	Eye	KG	P

[1] Buffer system abbreviations and descriptions are listed in Seeb et al. *in press*.

Table 3. Allele frequency estimates of polymorphic allozyme loci for sockeye salmon collected from the Chignik watershed, Alaska between 1996 and 1998. Only variant alleles are included and they are identified by their mobility relative to the standard form of the allele (relative mobility = 100). The month in which the sample was taken is included.

	*mAAT-1**		*mAH-1,2**			*mAH-4**		*ALAT**			*FH**		*GAPDH-2**			*GPI-B1,2**	
Population	N	-83	N	75	133	N	114	N	91	95	N	73	N	50	208	N	-100
Chignik River - Aug	100	0.325	100	0.010	0.003	100	0.030	98	0.388	0.082	100	0.000	100	0.015	0.000	100	0.005
Hatchery Beach - Sep	98	0.209	99	0.003	0.000	99	0.000	100	0.385	0.105	100	0.005	99	0.010	0.000	100	0.005
Hatchery Beach - Oct	99	0.187	97	0.028	0.010	98	0.000	100	0.220	0.100	100	0.010	99	0.000	0.000	100	0.005
Clark River - Sep	100	0.210	99	0.010	0.000	100	0.000	100	0.355	0.080	100	0.005	100	0.000	0.000	100	0.000
Clark River - Oct	99	0.212	100	0.020	0.008	100	0.000	100	0.215	0.120	99	0.005	100	0.000	0.010	99	0.008
Chiaktuak Creek - Aug	100	0.290	100	0.003	0.005	100	0.000	98	0.372	0.133	98	0.000	100	0.000	0.005	100	0.008
Chiaktuak Creek - Sep	94	0.266	94	0.008	0.000	94	0.000	93	0.317	0.065	91	0.000	94	0.000	0.011	94	0.003
Chiaktuak Creek - Oct	50	0.300	49	0.026	0.000	50	0.000	50	0.260	0.150	50	0.000	49	0.010	0.000	50	0.000
West Fork - Aug	99	0.237	100	0.000	0.000	100	0.000	100	0.250	0.060	100	0.000	99	0.000	0.000	100	0.000
Fan Creek - Aug	100	0.355	100	0.015	0.000	100	0.005	100	0.290	0.070	100	0.000	100	0.000	0.000	100	0.005
Alec River - Aug	98	0.337	99	0.020	0.003	100	0.000	98	0.342	0.092	96	0.000	100	0.000	0.000	100	0.003
Boulevard Creek - Aug	99	0.354	100	0.013	0.000	100	0.000	99	0.293	0.066	98	0.005	96	0.000	0.000	100	0.005
Broad Creek - Aug	98	0.281	96	0.016	0.003	96	0.000	100	0.305	0.070	96	0.000	99	0.000	0.000	100	0.005
Big Spring - Aug	100	0.285	99	0.013	0.003	100	0.000	100	0.370	0.080	99	0.000	100	0.000	0.005	99	0.003

	*GR**		*mIDHP-1**		*sIDHP-1**		*sIDHP-2**		*LDH-B1**			*LDH-B2**		*LDH-C**			*sMDH-A1,2**	
Population	N	60	N	33	N	162	N	115	N	123	80	N	110	N	108	89	N	147
Chignik River - Aug	100	0.000	100	0.010	100	0.000	100	0.000	99	0.000	0.010	100	0.160	100	0.000	0.000	100	0.000
Hatchery Beach - Sep	96	0.000	99	0.000	100	0.000	100	0.000	100	0.000	0.000	100	0.160	98	0.000	0.000	100	0.000
Hatchery Beach - Oct	100	0.000	99	0.000	99	0.000	99	0.000	100	0.010	0.000	100	0.160	100	0.000	0.000	100	0.000
Clark River - Sep	100	0.000	100	0.000	100	0.000	100	0.000	100	0.000	0.000	100	0.110	100	0.000	0.000	100	0.000
Clark River - Oct	99	0.000	93	0.000	100	0.000	100	0.000	100	0.000	0.000	100	0.190	100	0.000	0.000	100	0.000
Chiaktuak Creek - Aug	100	0.000	100	0.000	98	0.000	97	0.000	100	0.000	0.000	100	0.170	100	0.000	0.000	100	0.003
Chiaktuak Creek - Sep	94	0.005	94	0.000	94	0.000	94	0.000	93	0.005	0.000	94	0.165	94	0.005	0.000	94	0.000
Chiaktuak Creek - Oct	47	0.000	50	0.000	50	0.000	50	0.000	50	0.010	0.000	50	0.170	50	0.000	0.000	50	0.005
West Fork - Aug	100	0.000	91	0.000	100	0.000	100	0.005	100	0.000	0.000	100	0.265	99	0.000	0.000	100	0.000
Fan Creek - Aug	100	0.000	97	0.000	100	0.005	99	0.000	100	0.000	0.000	100	0.200	95	0.000	0.000	100	0.000
Alec River - Aug	100	0.015	99	0.000	100	0.005	100	0.000	100	0.005	0.000	99	0.187	100	0.000	0.000	100	0.000
Boulevard Creek - Aug	100	0.010	100	0.000	100	0.000	100	0.000	100	0.005	0.000	100	0.185	100	0.000	0.005	100	0.000
Broad Creek - Aug	97	0.016	99	0.000	100	0.000	100	0.000	50	0.000	0.000	99	0.182	95	0.000	0.000	100	0.000
Big Spring - Aug	98	0.010	100	0.000	100	0.000	100	0.015	100	0.000	0.000	100	0.175	100	0.000	0.005	100	0.000

Table 3. Continued

Population	*sMDH-B1,2** N	*sMDH-B1,2** 120	*mMEP-1** N	*mMEP-1** 80	*sMEP-1** N	*sMEP-1** 106	*PEPB-1** N	*PEPB-1** 113	*PEPC** N	*PEPC** 90	*PEPD-1** N	*PEPD-1** 130	*PEPLT** N	*PEPLT** 105
Chignik River - Aug	100	0.000	100	0.000	99	0.000	100	0.000	100	0.000	100	0.005	100	0.045
Hatchery Beach - Sep	100	0.018	100	0.005	99	0.000	99	0.000	100	0.000	99	0.000	92	0.011
Hatchery Beach - Oct	100	0.000	100	0.010	96	0.000	98	0.005	100	0.005	99	0.000	100	0.025
Clark River - Sep	100	0.010	100	0.000	100	0.000	99	0.005	100	0.000	100	0.000	99	0.015
Clark River - Oct	100	0.005	94	0.000	100	0.000	100	0.000	100	0.000	100	0.000	100	0.045
Chiaktuak Creek - Aug	100	0.028	100	0.000	100	0.000	100	0.000	100	0.000	100	0.000	88	0.011
Chiaktuak Creek - Sep	94	0.024	92	0.000	94	0.000	94	0.011	94	0.005	94	0.000	93	0.032
Chiaktuak Creek - Oct	50	0.000	50	0.000	50	0.000	49	0.000	50	0.000	44	0.000	47	0.032
West Fork - Aug	100	0.000	99	0.000	97	0.000	100	0.010	100	0.000	100	0.000	98	0.031
Fan Creek - Aug	100	0.010	97	0.000	100	0.000	100	0.000	100	0.000	100	0.000	99	0.035
Alec River - Aug	100	0.010	89	0.000	100	0.000	95	0.000	100	0.000	100	0.005	99	0.081
Boulevard Creek - Aug	100	0.013	98	0.000	99	0.000	97	0.000	100	0.000	100	0.000	100	0.025
Broad Creek - Aug	100	0.008	100	0.000	100	0.000	98	0.000	100	0.000	100	0.005	98	0.046
Big Spring - Aug	100	0.018	99	0.000	98	0.005	96	0.000	100	0.000	100	0.000	100	0.040

Population	*PGDH** N	*PGDH** 88	*PGM-1** N	*PGM-1** null	*PGM-2** N	*PGM-2** 136	*TPI-4** N	*TPI-4** 106	Observed Heterozygosity[1]
Chignik River - Aug	100	0.000	100	0.938	99	0.242	100	0.010	0.034
Hatchery Beach - Sep	100	0.010	99	0.948	99	0.192	99	0.005	0.032
Hatchery Beach - Oct	100	0.000	99	0.954	100	0.185	100	0.035	0.031
Clark River - Sep	99	0.005	100	0.959	100	0.180	99	0.020	0.029
Clark River - Oct	99	0.000	100	0.943	100	0.170	100	0.060	0.033
Chiaktuak Creek - Aug	100	0.000	100	0.933	100	0.225	100	0.000	0.034
Chiaktuak Creek - Sep	92	0.000	94	0.957	94	0.186	94	0.011	0.032
Chiaktuak Creek - Oct	50	0.000	50	0.970	50	0.240	50	0.000	0.033
West Fork - Aug	100	0.000	100	0.964	100	0.295	100	0.000	0.031
Fan Creek - Aug	100	0.000	100	0.943	100	0.170	100	0.010	0.033
Alec River - Aug	100	0.000	100	0.959	100	0.215	99	0.010	0.034
Boulevard Creek - Aug	100	0.005	100	0.949	100	0.175	100	0.010	0.034
Broad Creek - Aug	100	0.000	97	0.919	100	0.240	100	0.000	0.036
Big Spring - Aug	99	0.000	100	0.927	100	0.240	100	0.000	0.033

[1] Excludes *PGM-1**.

Table 4. Nei's unbiased genetic distances (Nei 1978) between all collections from the Chignik watershed, Alaska, 1996-1998.

	Chignik River	Hatchery Bch-Sep	Hatchery Bch-Oct	Clark River-Sep	Clark River-Oct	Chiaktuak Crk-Aug	Chiaktuak Crk-Sep	Chiaktuak Crk-Oct	West Fork	Fan Creek	Alec River	Boulevard Creek	Broad Creek
Chignik River	–												
Hatchery Bch - Sep	0.00050	–											
Hatchery Bch - Oct	0.00216	0.00119	–										
Clark River – Sep	0.00070	-0.00014	0.00062	–									
Clark River - Oct	0.00198	0.00126	-0.00027	0.00085	–								
Chiaktuak Crk-Aug	-0.00015	-0.00001	0.00190	0.00044	0.00173	–							
Chiaktuak Crk-Sep	0.00029	0.00022	0.00036	0.00002	0.00032	0.00029	–						
Chiaktuak Crk-Oct	0.00006	0.00058	0.00055	0.00054	0.00044	0.00003	-0.00014	–					
West Fork	0.00192	0.00215	0.00110	0.00227	0.00108	0.00204	0.00101	0.00065	–				
Fan Creek	0.00053	0.00152	0.00139	0.00136	0.00098	0.00084	0.00008	0.00007	0.00145	–			
Alec River	-0.00017	0.00085	0.00172	0.00095	0.00135	0.00017	0.00007	-0.00019	0.00150	-0.00001	–		
Boulevard Creek	0.00047	0.00141	0.00132	0.00119	0.00100	0.00077	0.00001	0.00001	0.00148	-0.00044	0.00000	–	
Broad Creek	0.00014	0.00062	0.00065	0.00056	0.00058	0.00031	-0.00019	-0.00028	0.00048	0.00014	-0.00002	0.00010	–
Big Spring	-0.00029	0.00011	0.00141	0.00034	0.00131	-0.00026	-0.00005	-0.00009	0.00122	0.00048	-0.00014	0.00042	-0.00021

Table 5. Hierarchical log-likelihood analysis of population structure within the Chignik watershed, Alaska, 1996-1998.

	DF	*mAAT-1**	DF	*mAH-1,2**	DF	*mAH-4**	DF	*ALAT**	DF	*FH**	DF	*GAPDH-2**	DF	*GPI-B1,2**	DF	*GR**
Total	13	41.6	26	53.9	13	30.7	26	63.7	13	12.4	26	35.9	13	11.2	13	23.4
Between Nursery Lakes	1	18.2	2	2.8	1	1.8	2	3.5	1	1.2	2	6.8	1	0.0	1	14.1
Within Nursery Lakes	12	23.4	24	51.0	12	28.9	24	60.1	12	11.2	24	29.1	12	11.2	12	9.3
Black Lake [3]	4	4.9	8	4.1	4	3.2	8	6.6	4	3.2	8	3.2	4	0.8	4	5.0
Chignik Lake	8	18.5	16	46.9	8	25.7	16	53.6	8	8.0	16	25.9	8	10.4	8	4.4
Among Regions [1]	2	16.0	4	7.6	2	25.7	4	6.5	2	7.4	4	7.1	2	0.6	2	1.8
Within Regions	6	2.5	12	39.3	6	0.0	12	47.0	6	0.5	12	18.8	6	9.8	6	2.6
Chignik Lake	3	0.5	6	21.5	3	0.0	6	24.5	3	0.5	6	11.1	3	4.3	3	0.0
Between Months	1	0.1	2	18.8	1	0.0	2	22.7	1	0.2	2	5.5	1	1.3	1	0.0
Within Months	2	0.4	4	2.7	2	0.0	4	1.9	2	0.3	4	5.6	2	3.0	2	0.0
September	1	0.0	2	1.9	1	0.0	2	1.5	1	0.0	2	2.8	1	2.8	1	0.0
October	1	0.4	2	0.8	1	0.0	2	0.4	1	0.3	2	2.8	1	0.2	1	0.0
Black River	3	2.0	6	17.8	3	0.0	6	22.5	3	0.0	6	7.7	3	5.5	3	2.6
Between Months [2]	2	0.5	4	13.7	2	0.0	4	5.7	2	0.0	4	6.3	2	1.4	2	2.6
Within Months	1	1.4	2	4.2	1	0.0	2	16.8	1	0.0	2	1.4	1	4.2	1	0.0
August	1	1.4	2	4.2	1	0.0	2	16.8	1	0.0	2	1.4	1	4.2	1	0.0

	DF	*mIDHP-1**	DF	*sIDHP-2**	DF	*LDH-B1**	DF	*LDH-B2**	DF	*sMDH-A1,2**	DF	*sMDH-B1,2**	DF	*mMEP-1**	DF	*PEPC**
Total	13	10.3	13	16.3	26	23.8	13	19.1	13	9.0	13	47.2	13	11.7	13	23.5
Between Nursery Lakes	1	1.9	1	2.4	2	1.7	1	0.8	1	1.9	1	0.4	1	2.7	1	5.8
Within Nursery Lakes	12	8.5	12	13.9	24	22.1	12	18.4	12	7.1	12	46.8	12	8.9	12	17.8
Black Lake [3]	4	0.0	4	9.7	8	3.2	4	0.4	4	0.0	4	1.9	4	0.0	4	7.6
Chignik Lake	8	8.5	8	4.2	16	18.8	8	17.9	8	7.1	8	44.9	8	8.9	8	10.2
Among Regions [1]	2	8.5	2	1.8	4	9.6	2	4.6	2	3.6	2	11.1	2	4.5	2	2.3
Within Regions	6	0.0	6	2.4	12	9.2	6	13.3	6	3.6	6	33.8	6	4.4	6	7.9
Chignik Lake	3	0.0	3	0.0	6	5.6	3	5.2	3	0.0	3	10.5	3	4.4	3	5.5
Between Months	1	0.0	1	0.0	2	2.8	1	2.4	1	0.0	1	6.9	1	0.4	1	4.1
Within Months	2	0.0	2	0.0	4	2.8	2	2.8	2	0.0	2	3.6	2	4.0	2	1.3
September	1	0.0	1	0.0	2	0.0	1	2.2	1	0.0	1	0.8	1	1.4	1	0.1
October	1	0.0	1	0.0	2	2.8	1	0.6	1	0.0	1	2.8	1	2.7	1	1.2
Black River	3	0.0	3	2.4	6	3.7	3	8.1	3	3.6	3	23.2	3	0.0	3	2.4
Between Months [2]	2	0.0	2	1.1	4	3.7	2	2.8	2	2.2	2	7.8	2	0.0	2	0.7
Within Months	1	0.0	1	1.4	2	0.0	1	5.3	1	1.4	1	15.4	1	0.0	1	1.7
August	1	0.0	1	1.4	2	0.0	1	5.3	1	1.4	1	15.4	1	0.0	1	1.7

Table 5. Continued.

	DF	*PEPD-1**	DF	*PEPLT**	DF	*PGM-1**	DF	*PGM-2**	DF	*TPI-4**	DF	Overall	P
Total	13	15.4	13	12.5	13	9.4	13	20.7	13	49.7	325	541.7	0.000
Between Nursery Lakes	1	5.5	1	0.3	1	1.4	1	0.0	1	6.3	25	79.4	0.000
Within Nursery Lakes	12	9.9	12	12.2	12	8.0	12	20.6	12	43.4	300	462.2	0.000
Black Lake [1]	4	0.0	4	3.2	4	3.6	4	5.7	4	6.2	100	72.6	0.982
Chignik Lake	8	9.9	8	9.0	8	4.3	8	15.0	8	37.2	200	389.6	0.000
Among Regions [2]	2	2.5	2	4.5	2	0.8	2	8.1	2	19.9	50	154.5	0.000
Within Regions	6	7.4	6	4.5	6	3.6	6	6.9	6	17.4	150	235.1	0.000
Chignik Lake	3	2.8	3	4.5	3	0.6	3	0.3	3	12.2	75	114.2	0.002
Between Months	1	0.0	1	4.2	1	0.1	1	0.1	1	8.8	25	78.5	0.000
Within Months	2	2.8	2	0.3	2	0.5	2	0.2	2	3.3	50	35.7	0.937
September	1	1.4	1	0.3	1	0.3	1	0.1	1	2.0	25	17.6	0.860
October	1	1.4	1	0.0	1	0.2	1	0.2	1	1.4	25	18.1	0.838
Black River	3	4.6	3	0.0	3	3.0	3	6.5	3	5.2	75	120.9	0.001
Between Months [3]	2	1.8	2	0.0	2	0.9	2	4.0	2	5.2	50	60.4	0.149
Within Months	1	2.8	1	0.0	1	2.1	1	2.6	1	0.0	25	60.5	0.000
August	1	2.8	1	0.0	1	2.1	1	2.6	1	0.0	25	60.5	0.000

[1] Includes Fan, Boulevard and Broad creeks, Alec River and Big Springs.
[2] Includes Chignik River.
[3] Includes Chiaktuak Creek September and October collections.

Table 6. Results of simulated mixtures of sockeye salmon from the Chignik watershed, Alaska, using allozyme data for 25 polymorphic loci. Each region comprises 100% of the mixture, simulation sample size is 400, and 500 bootstrap resamples were conducted. Reporting groups correspond to three genetically similar population groups reported in the analysis. The standard deviation of the estimate is in parentheses. Results may not sum to 1.0 due to rounding errors.

	Mixture		
Regional Allocation	Alec/ Chiaktuak/ Chignik R.[1]	Chignik Lake[2]	West Fork
Reporting Groups			
Alec/ Chiaktuak/ Chignik R.	**0.89**	0.12	0.06
	(0.080)	(0.081)	(0.066)
Chignik Lake	0.05	**0.86**	0.01
	(0.066)	**(0.081)**	(0.026)
West Fork	0.03	0.02	**0.94**
	(0.040)	(0.033)	**(0.068)**

[1] This mixture is composed of equal parts of the Alec River, Chignik River and the Chiaktuak Creek August, September and October baseline population groups.

[2] This mixture is composed of equal parts of the Hatchery Beach/Clark River September and October collections.

Table 7. Results of simulated mixtures of sockeye salmon from the Chignik watershed, Alaska, using allozyme data for 25 polymorphic loci. Each mixture is composed of randomly generated genotypes based on the allele frequencies in each population group. The simulation sample size is 400, and 500 bootstrap resamples were conducted. Nursery lake groups combine the baseline population allocations based on lake-use by juveniles. Run timing groups combine the baseline population allocations based on month of return: Early is August and Late is September and October. The standard deviation of the estimate is in parentheses. Results may not sum to 1.0 due to rounding errors.

	Mixture			
Allocation	Black Lake[1]	Chignik Lake[2]	Early Run[3]	Late Run[4]
Nursery Lake				
Black Lake	**0.83**	0.10		
	(0.089)	(0.096)		
Chignik Lake	0.17	**0.89**		
	(0.089)	**(0.096)**		
Spawning Time				
Early			**0.88**	0.19
			(0.083)	(0.105)
Late			0.12	**0.81**
			(0.083)	**(0.105)**

[1] Includes the Alec River baseline populations.
[2] Includes all non-Alec River baseline populations.
[3] Includes the Alec River, West Fork, Chignik River and Chiaktuak Creek – August baseline populations.
[4] Includes the Chignik Lake and the September and October collections from Chiaktuak Creek.

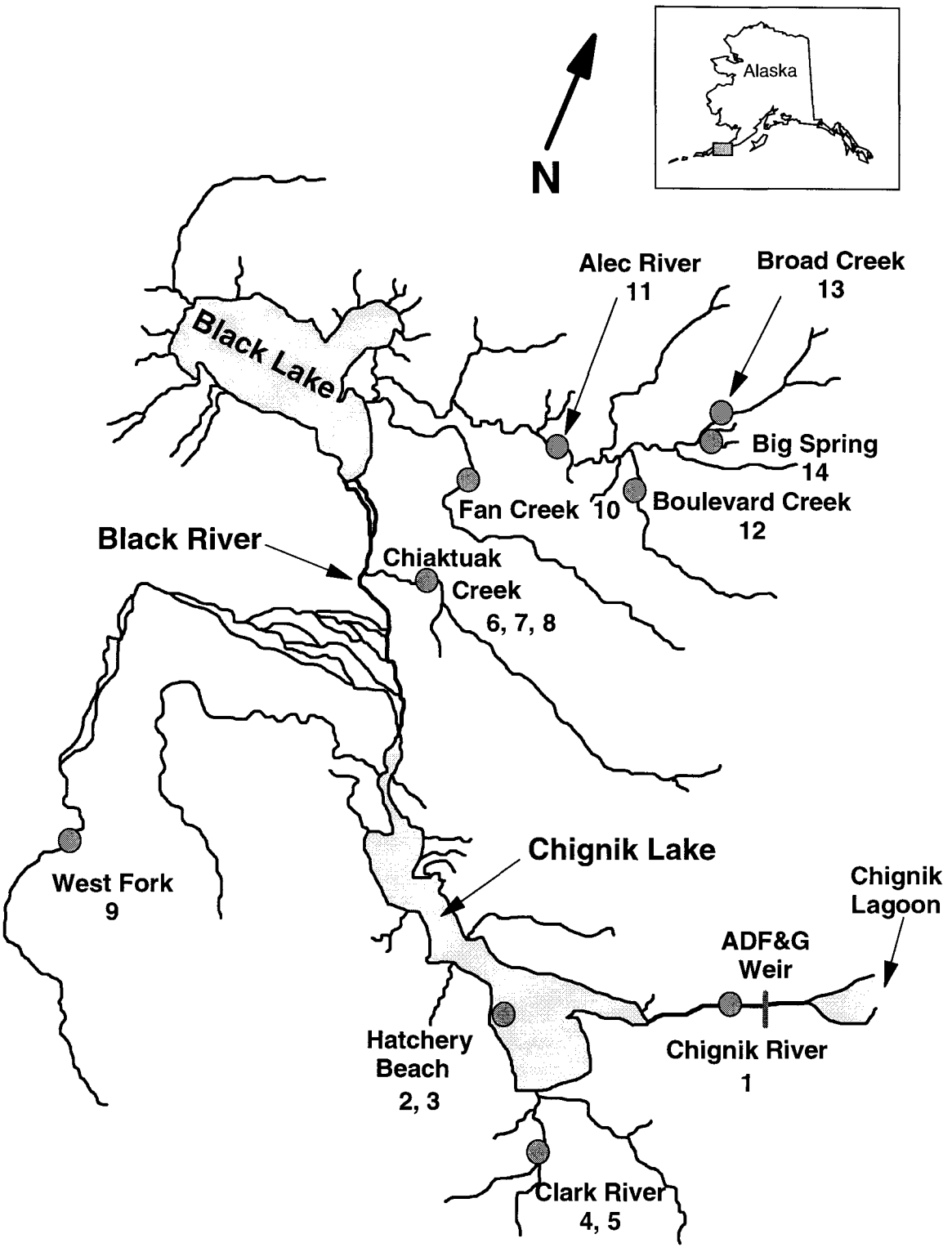

Figure 1. Map of the Chignik watershed in southwest Alaska with collection sites indicated. Numbers refer to the collection identification numbers assigned in Table 1.

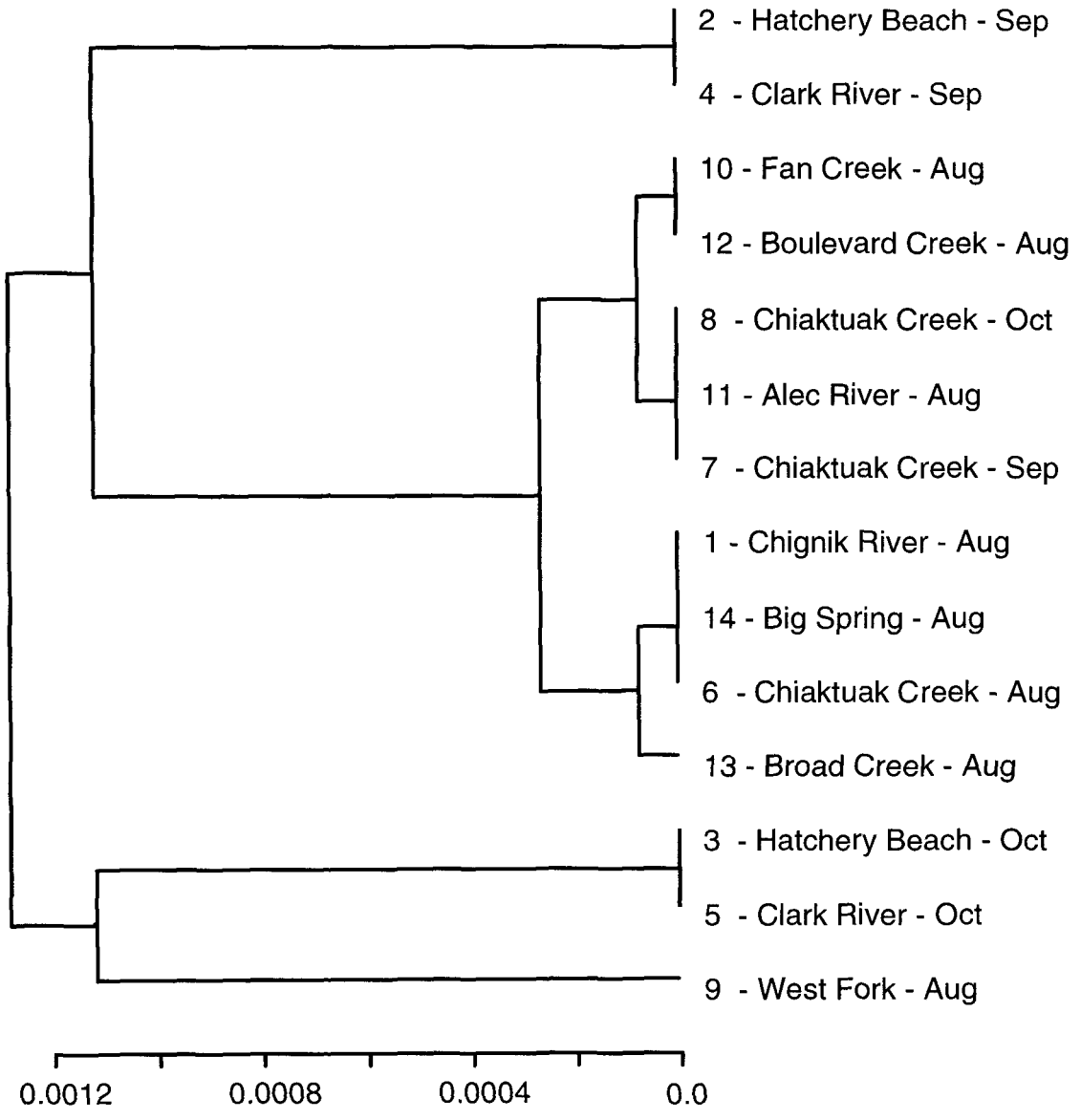

Figure 2. An unweighted pair-group method with arithmetic mean (UPGMA) dendrogram of Nei's unbiased genetic distances (Nei 1987) between collections.

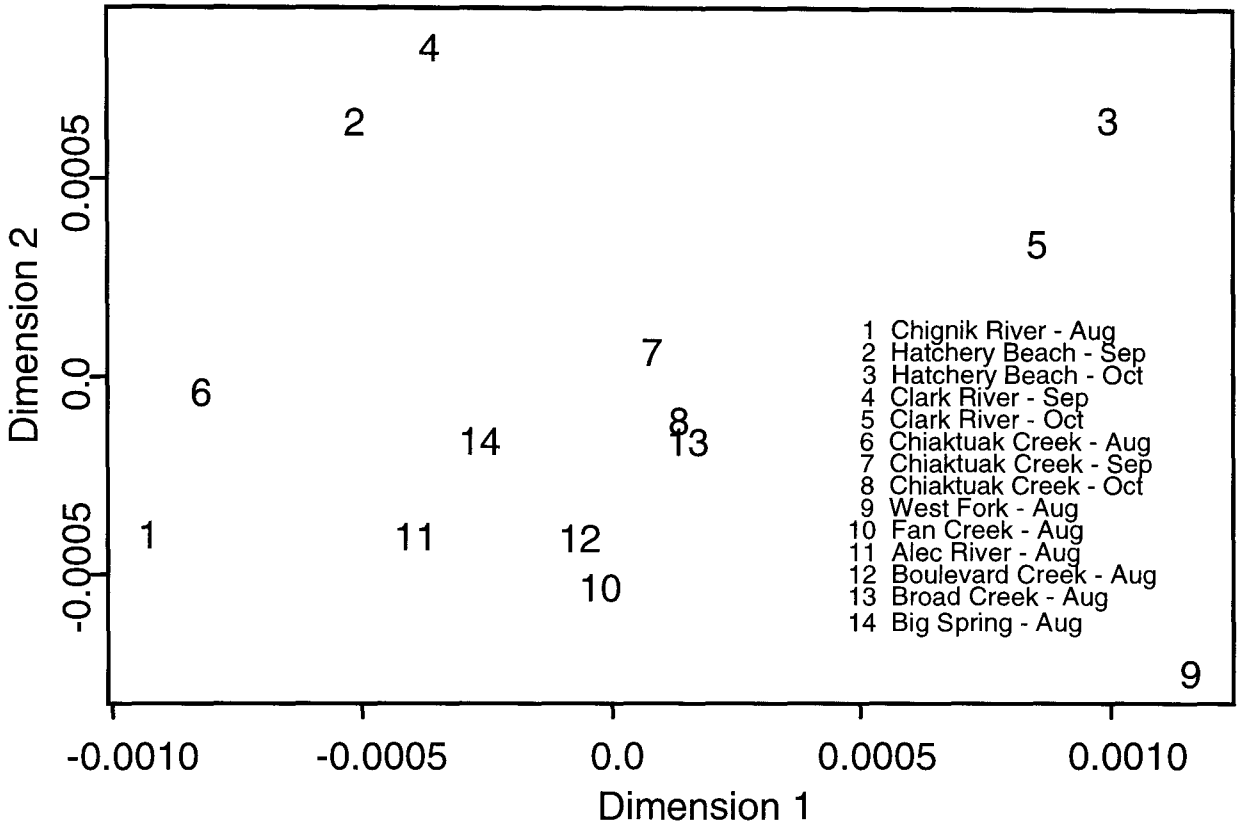

Figure 3. Plot of the first two dimensions of the multidimensional scaling analysis of Nei's unbiased genetic distances (Nei 1987) between collections from Chignik Lake and Black Lake drainages, Alaska.

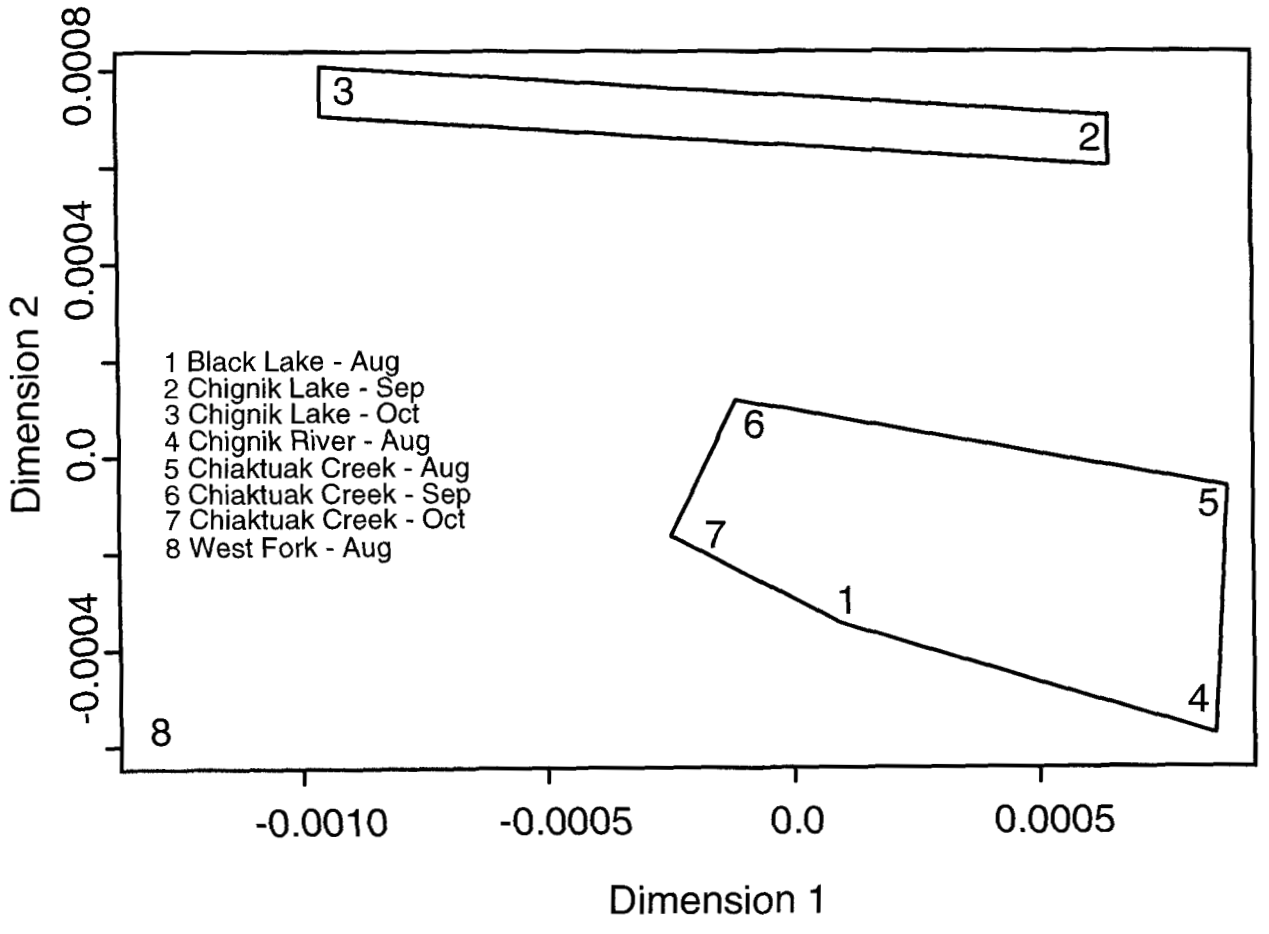

Figure 4. Plot of the first two dimensions of the multidimensional scaling analysis of Nei's unbiased genetic distances between baseline populations from Chignik Lake and Black Lake drainages, Alaska. Polygons indicate the baseline population groups reported in the simulations.

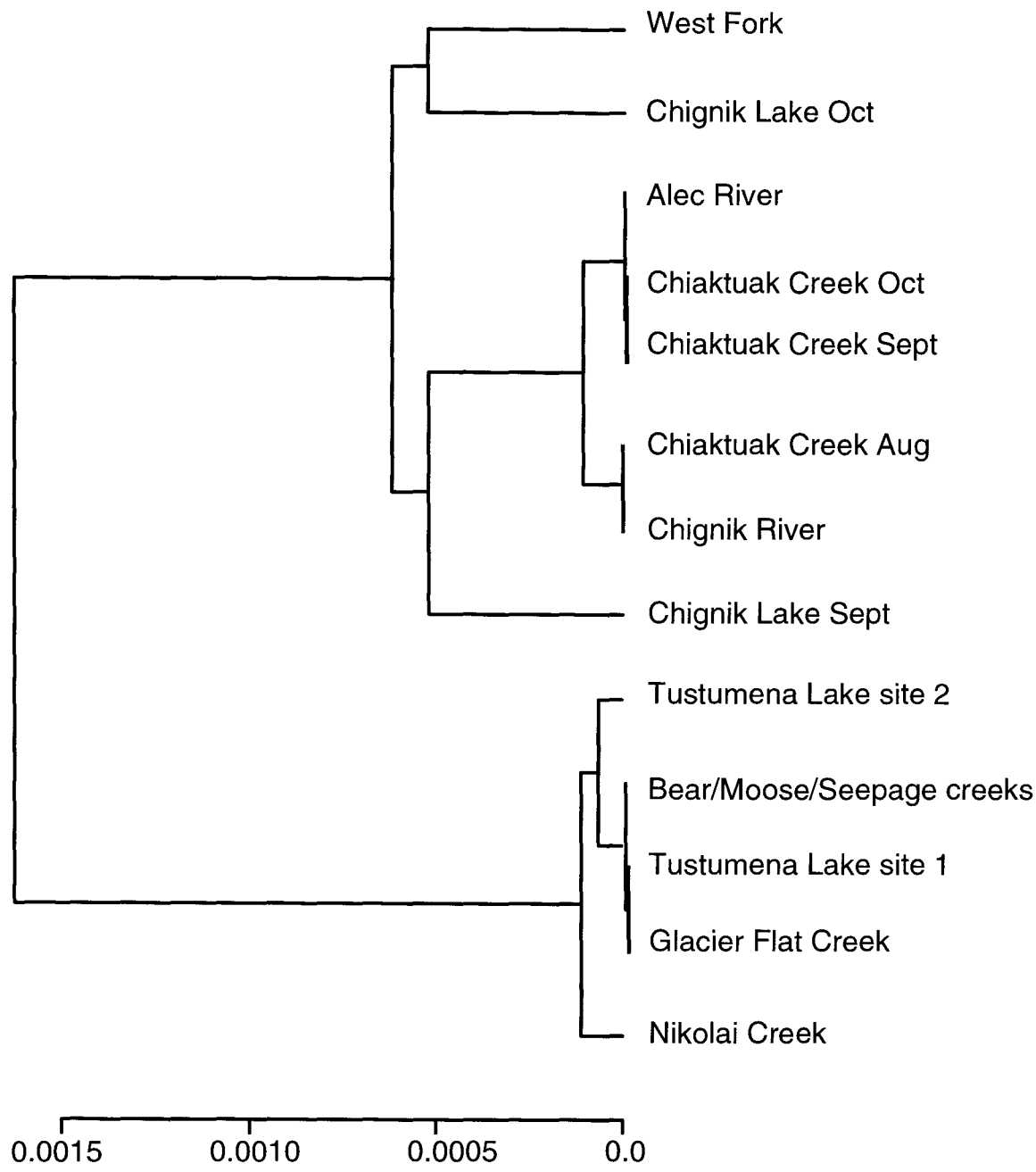

Figure 5. A dendrogram depicting the genetic relationship between populations from the Chignik and Tustumena watersheds using Nei's unbiased genetic distances (Nei 1987) and the UPGMA clustering algorithm. The Tustumena data are reported in Seeb et al. (*in press*).

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