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## Genetic Differences among Populations of Alaskan Sockeye Salmon

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### Abstract

Biochemical genetic variation was found among populations of sockeye salmon *Oncorhynchus nerka* in the Russian and Karluk river systems in Alaska. Significant differences in allele frequencies of lactate dehydrogenase (*Ldh-4*), phosphoglucosmutase (*Pgm-1*), and cis-aconitase (*Aco*) were found between the early and late runs in both the Karluk and Russian rivers, and between fish from the two rivers. The most common allele for *Aco* in the Russian River fish was lacking in fish from the Karluk River. Gene frequencies were stable between years, except for 1 year in Karluk River fish. Within the Karluk system, there were no significant genetic differences between groups of early-run fish, or between groups of late-run fish. Average heterozygosities (*H*) fell within ranges reported for other populations of sockeye salmon. Our data suggest that the two runs of sockeye salmon in each river system are now reproductively isolated as a result of natural events.

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Biochemical genetic studies can be used to separate and characterize stocks of salmonids (Hodgins et al. 1969; Utter et al. 1974; Allendorf and Utter 1979). Available technology permits numerous populations to be screened for protein polymorphism and breeding studies generally show that isoenzyme variation is inherited in a simple Mendelian fashion.

Increasing pressure from commercial fishing on sockeye salmon *Oncorhynchus nerka* in Alaska has produced an urgent need to adjust management criteria to ensure that mixed stock fisheries do not inadvertently harm specific populations within larger runs of these fish. It is known, for example, that both early and late runs of sockeye salmon (late May to early July, and July to early October) enter the Karluk River system (Fig. 1). Early-run fish spawn in tributaries such as Moraine and Canyon creeks and Upper Thumb River, and late-run fish spawn in Lower Thumb River, O'Malley River, Karluk Lake beaches, and the main-stem Karluk River below the lake. The total sockeye salmon run for the Karluk River was estimated to be as high as 5 million fish in the late 1800s (Rounsefell 1958), but had declined to 0.2 to 0.7 million by the early 1970s (Manthey et al. 1980). Because plantings of alvins were planned for this drainage, the first objective of the present study was to determine whether or not the Karluk River sockeye salmon were genetically homogeneous.

Nelson (1980) showed that runs of sockeye

salmon also occur early (mid-June to mid-July) and late (August) in the Russian River system (Fig. 1). Fish in the early run spawn above Upper Russian Lake in the Upper Russian River, and fish in the late run spawn in the main stem between Upper and Lower Russian lakes, and along the beaches of the upper lake. Both runs must migrate past Russian River Falls in the lower main stem, although a few late-run fish (not included in this investigation) spawn below the falls. Other researchers (Grant et al. 1980) examined Russian River sockeye salmon electrophoretically. They reported results for two runs, but based on their sampling times and locations, they sampled only the late run. The second objective of this study was to determine whether or not the early and late runs were genetically distinct populations of sockeye salmon.

### Methods

From the Karluk River system, samples of liver and muscle tissue were obtained from fish captured by the Alaska Department of Fish and Game for artificial spawning during the peak of the early and late runs into Thumb River. Samples of postspawners in Canyon Creek, Moraine Creek, and O'Malley River came from fish seined on the spawning grounds. Russian River samples were taken from fish collected each July and August at a wier at the outlet of Lower Russian Lake. Early and late runs of sockeye salmon from the Russian River, and from Upper Thumb (early

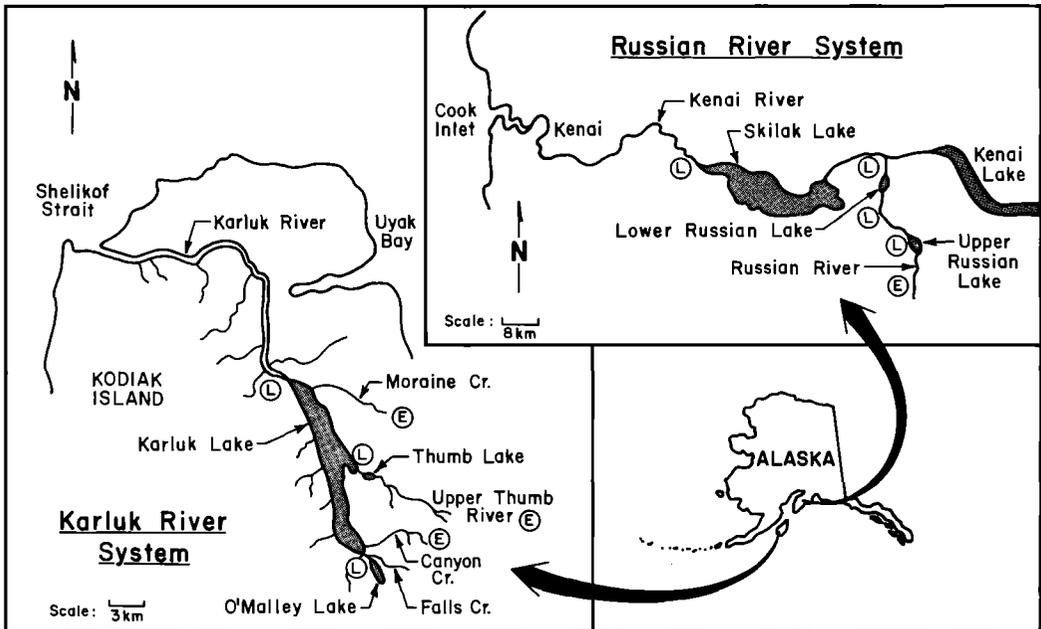


FIGURE 1.—Locations of study areas in the Karluk River and Russian River systems, Alaska. Spawning areas of early- and late-run sockeye salmon are marked E and L, respectively.

run) and Lower Thumb (late run) rivers of the Karluk River system were sampled in four consecutive years (1978–1981). All samples were placed on ice and sent to Anchorage for electrophoretic analyses.

Horizontal starch gel electrophoresis (Utter et

al. 1974) was used to analyze protein differences. Four buffer systems were used (Table 1). Staining procedures described by Harris and Hopkinson (1976) were used, except that the amount of  $MgCl_2$  in the ACO stain (used only in 1981) was doubled. Gels were made with 11% starch (Sigma

TABLE 1.—Enzymes screened for variation in this study, and the tissues and buffer systems used. (Enzyme abbreviations are in parentheses; locus abbreviations are similar but italic with lower-case letters.)

Enzyme	Enzyme commission number	Tissue (locus)	Buffer <sup>a</sup>
Cis-aconitase (ACO)	4.2.1.3	Muscle ( <i>I</i> )	4
Alpha-glycerol phosphate dehydrogenase (AGP)	1.1.1.8	Muscle ( <i>I, 2</i> )	2
Creatine kinase (CK)	2.7.3.2	Muscle ( <i>I, 2</i> )	1
Glutamate pyruvate transaminase (GPT)	2.6.1.2	Muscle ( <i>I, 2</i> )	3
Glutamate-oxalacetate transaminase (GOT)	2.6.1.1	Muscle ( <i>I, 2</i> )	1
Lactate dehydrogenase (LDH)	1.1.1.27	Muscle ( <i>I, 2, 3, 4</i> ) Liver ( <i>4</i> )	1 1
Malate dehydrogenase (MDH)	1.1.1.37	Muscle ( <i>I, 2, 3, 4</i> )	2
Peptidase (PEP) GL	3.4.13.9	Muscle ( <i>I</i> )	2
Phosphoglucisomerase (PGI)	5.3.1.9	Muscle ( <i>I, 2, 3</i> )	1
Phosphoglucomutase (PGM)	2.7.5.1	Muscle ( <i>I, 2</i> )	1
6-Phosphogluconate dehydrogenase (6PG)	1.1.1.47	Muscle ( <i>I</i> )	2
Phosphomannoisomerase (PMI)	5.3.1.8	Muscle ( <i>I</i> )	3
Superoxide dismutase (SOD)	1.15.1.1	Liver ( <i>I</i> )	1

<sup>a</sup> Buffer 1: tris, citric acid gel buffer, pH 8.2; boric acid, lithium hydroxide tray buffer, pH 8.0 (Ridgeway et al. 1970);

Buffer 2: amine citrate, pH 6.5 (Clayton and Tretiak 1972);

Buffer 3: tris, boric acid, EDTA, pH 8.5 (Markert and Faulhaber 1965);

Buffer 4: tris, citric acid, pH 7.0 (Shaw and Prasad 1970).

TABLE 2.—Allele frequencies of enzyme variants of sockeye salmon from the Russian River and Karluk River. Asterisks (\*) denote significant deviations from Hardy-Weinberg distributions ( $\chi^2$  goodness of fit,  $P < 0.05$ ).

Run and location	Year	<i>Ldh-4</i>			<i>Pgm-1</i>			<i>Aco</i>		
		N	100	106	N	100	120	N	100	110
<b>Russian River</b>										
Early run	1978	50	0.550	0.450	50	0.860	0.140			
	1979	94	0.489	0.511	72	0.917	0.083			
	1980	104	0.490	0.510	77	0.922	0.078			
	1981	100	0.560	0.440	100	0.850	0.150	96	0.292*	0.708*
	1978-1981	348	0.519	0.481	299	0.886	0.114	96	0.292	0.708
Late run	1978	50	0.730	0.270	50	0.850	0.150			
	1979	100	0.750	0.250	99	0.909	0.091			
	1980	103	0.709	0.291	—	—	—			
	1981	100	0.655	0.345	100	0.885*	0.115*	82	0.427	0.573
	1978-1981	353	0.708	0.292	249	0.888	0.112	82	0.427	0.573
<b>Karluk River</b>										
Early run										
Upper Thumb River	1978	60	0.908	0.092	59	0.839*	0.161*			
	1979	110	0.900	0.100	110	0.736*	0.264*			
	1980	86	0.913	0.087	32	0.875	0.125			
	1981	103	0.893	0.107	103	0.728	0.272	103	1.000	
	1978-1981	359	0.903	0.097	304	0.768	0.232	103	1.000	
Canyon Creek	1981	105	0.900	0.100	105	0.767	0.233	105	1.000	
Moraine Creek	1981	96	0.911	0.089	96	0.719	0.281	96	1.000	
All early run		560	0.904	0.096	505	0.758	0.242	304	1.000	
Late run										
Lower Thumb River	1978	60	0.833	0.167	59	0.720	0.280			
	1979	100	0.840	0.160	100	0.765	0.235			
	1980	75	0.940	0.060	75	0.813	0.197			
	1981	102	0.804	0.196	101	0.777	0.223	102	1.000	
	1978-1981	337	0.850	0.150	335	0.772	0.228	102	1.000	
O'Malley River	1981	100	0.830	0.170	100	0.735	0.265	100	1.000	
All late run		437	0.846	0.154	435	0.788	0.212	202	1.000	

Chemical Company, Saint Louis, Missouri). With one exception (ACO), the enzyme systems surveyed for variation (Table 1) were those identified in Alaskan sockeye salmon by Grant et al. (1980). The system of enzyme nomenclature used was suggested by Allendorf and Utter (1979). The most common allele is scored as 100, and the remaining alleles are given a number based on the migration distance relative to the common allele. The decrease in average heterozygosities resulting from population subdivision was evaluated with Nei's (1973, 1975) gene diversity analysis. The gene diversity at a single locus within each population is

$$h = 1 - \sum X_i^2,$$

where  $X_i$  is the frequency of the  $i$ th allele. The average gene diversity of a population ( $H_s$ ) is the average of  $h$  over all loci. The total gene diversity over all populations ( $H_t$ ) is the unweighted mean allele frequencies averaged over all populations.

The total gene diversity is

$$H_t = H_s + D_{st},$$

where  $D_{st}$  is the gene diversity due to differences between populations. The  $D_{st}$  is further divided to correspond to different levels of the population structure. The various  $D$  values are divided by  $H_t$  to express their relative importances (relative gene diversities) as percentages of the total gene diversity. In our analysis, the *Aco* locus was not used because we had data for it in only 1 year.

### Results

Twenty-six enzyme systems were screened by electrophoresis. Four displayed genetic variation and 22 were monomorphic. The four systems displaying variation were lactate dehydrogenase (*Ldh-4*), phosphoglucomutase (*Pgm-1*), cis-aconitase (*Aco*), and glutamate pyruvate transaminase (*Gpt-2*). Results for *Gpt-2* were inconsistent and not included in the analysis. Genotypic

TABLE 3.—Log-likelihood ratio analysis of variation for *Ldh-4* and *Pgm-1* by year in Russian River and Karluk River sockeye salmon (1978–1981) and between all Karluk River early- and late-run tributaries. Values with asterisks indicate significant allele frequency differences of \* $P < 0.05$  or \*\* $P < 0.01$ .

Source of variation	<i>Ldh-4</i>		<i>Pgm-1</i>		Total	
	df	G	df	G	df	G
Russian River						
Early run	3	3.079	3	6.658	6	9.737
Late run	3	4.629	2 <sup>a</sup>	2.285	5	6.914
Karluk River						
Upper Thumb River (early-run)	3	0.473	3	11.307*	6	11.780
Lower Thumb River (late-run)	3	15.445**	3	3.316	6	18.762**
All early-run tributaries	2	0.180	2	1.984	4	2.165
All late-run tributaries	1	0.471	1	1.124	2	1.595

<sup>a</sup> Data missing for 1980.

frequencies of all groups of Karluk River and Russian River fish were tested for departure from Hardy–Weinberg proportions, and gene or allelic frequencies were calculated from genotypic frequencies (Table 2). Of the 19  $\chi^2$  goodness-of-fit tests, four were significant: *Pgm-1* for Upper Thumb River in 1978 and 1979 ( $P = 0.02$  and  $P = 0.03$ ), *Pgm-1* for the Russian River late run in 1981 ( $P = 0.01$ ), and *Aco* for Russian River early run in 1981 ( $P < 0.01$ ).

Two loci have been discovered for ACO in humans, *Aco<sub>s</sub>* and *Aco<sub>m</sub>*, and seven alleles have been identified for the *Aco<sub>s</sub>* locus (Harris and Hopkinson 1976). McGregor (1982) found two loci, each with two allele variants, in white muscle of pink salmon *Oncorhynchus gorbuscha*. However, we detected only one locus in sockeye salmon white muscle and liver tissue; it had the typical monomeric banding pattern. Other variations that we could clearly identify were for *Ldh-4* and *Pgm-1* (Tables 1 and 2). We found variability in *Gpt-2* but our results were too inconsistent for reliable analysis.

The frequency of *Pgm-1* for fish from Upper Thumb River in 1981, and the frequency of *Ldh-4* for fish from Lower Thumb River in 1980 (Table 2) were both significantly different from frequencies of these alleles in other years (Table 3). The total log-likelihood ratio analysis over both loci (Sokal and Rohlf 1981) showed only fish from Lower Thumb River to have significant yearly differences ( $P < 0.01$ ).

In 1981, fish from three additional tributaries in the Karluk River system were sampled for analysis. The log-likelihood ratio analysis of all

the Karluk tributaries (Table 3) showed no significant differences for *Ldh-4*, *Pgm-1*, or *Aco* between early-run fish in different tributaries (Upper Thumb River, Canyon Creek, and Moraine Creek), or between late-run fish in different tributaries (Lower Thumb River and O'Malley River).

The log-likelihood ratio analysis of the two river systems (Table 4) was derived by pooling the four years of data for the Russian River early-run fish and for the Russian River late-run fish. The four years of data for Upper Thumb River were pooled with Canyon Creek and Moraine Creek, and the four years of data for Lower Thumb River were pooled with O'Malley River. The differences between Russian River early-run fish and Russian River late-run fish were significant for *Ldh-4* ( $P < 0.001$ ) and *Aco* ( $P < 0.05$ ), and for the analysis over all loci ( $P < 0.001$ ). The *Ldh-4* locus was significantly different between the Karluk River early-run fish and late-run fish ( $P < 0.001$ ), and over all loci ( $P < 0.001$ ). The *Aco* locus was fixed for one allele in Karluk River fish, but highly variable in fish from the Russian River. The most common *Aco* allele (*I10*) in fish from the Russian River was lacking in fish from the Karluk River (Table 2).

An *F*-ratio of variation between rivers to that within rivers was significant ( $P < 0.05$ ) indicating that the difference between rivers was much greater than the differences within rivers (Table 4). The differences between fish from the two river systems were significant ( $P < 0.001$ ) for total samples and for early runs and late runs.

Average heterozygosities (*H*) were calculated

TABLE 4.—Log-likelihood ratio analysis of variation at three loci and pooled over all loci for sockeye salmon spawning in the Russian and Karluk rivers. Asterisks indicate significant allele-frequency differences at \* $P < 0.05$  or \*\*\* $P < 0.001$ .

Source of variation	df	<i>Ldh-4</i>	<i>Pgm-1</i>	<i>Aco</i>	<i>G</i>	<i>F</i>
Between drainages	1	321.855***	75.537***	785.292***		
Within drainages	2	68.842***	0.063	6.466*		
Russian River	1	53.525***	0.004	6.466*		
Karluk River	1	15.317***	0.059	0.000		
Total	3	390.697***	75.600***	791.758***		
Between rivers	3				1,182.684***	15.691 (3,6 df)*
Within rivers	6				75.371***	
Russian River	3				59.995***	
Karluk River	3				15.376***	
Total	9				1,258.055***	

as described by Nei (1977) for each river. The  $H$  values were 0.047 for Russian River sockeye salmon and 0.024 for Karluk River sockeye salmon. Grant et al. (1980) reported values of 0.041 and 0.042 for Russian River fish. The gene diversity analysis (Table 5) reveals that 91.77% of the gene diversity is found within populations, 0.53% between years within populations, 0.10% between populations, 1.47% between runs within populations and 6.12% between drainages. Run timing constituted the largest portion of the remaining diversity. The *Pgm-1* locus was the major contributor to the diversity within populations and between years and populations, and *Ldh-4* was the major contributor between run timing and rivers.

Standard genetic distance (Nei 1972; Nei and Roychoudhury 1974) was calculated between all possible pairs of spawning areas. Values for genetic distance ranged from zero for fish spawning in Upper Thumb River and Moraine Creek and in Lower Thumb River and O'Malley River, to a high of  $0.298 \pm 0.232$  (SE) between fish spawning in Moraine Creek and the Russian River early-run fish. A dendrogram based on the unweighted pair-group method of cluster analysis (Sneath

and Sokal 1973) displays the genetic relationship between fish from all spawning areas (Fig. 2).

### Discussion

Of the 26 loci screened by enzyme electrophoresis in sockeye salmon from the Russian and Karluk rivers, three were usable for genetic separation. A fourth system, *Gpt*, displayed much polymorphism, but our results were too inconsistent to enable us to use *Gpt* in the analysis. Four of the  $\chi^2$  goodness-of-fit tests for Hardy-Weinberg equilibrium conditions were significant ( $P < 0.05$ ). It is not possible to assign a specific reason to these four cases of nonequilibrium, but at least one of the 19 tests could be expected to deviate due to random chance.

A note of caution is in order concerning the use of *Aco* in the analysis. No breeding studies have been performed in sockeye salmon to confirm simple Mendelian inheritance. McGregor (1982), who made a single mating of pink salmon from southeastern Alaska, found that phenotypic ratios of the progeny did not differ from the expected Mendelian model.

We are aware of only two other populations of sockeye salmon for which *Aco* has been ana-

TABLE 5.—Distribution of detectable gene diversity among sockeye salmon from the Russian River and Karluk River. Averages are based on 2 polymorphic and 22 monomorphic loci.

Locus	Absolute gene diversity		Relative gene diversity (%)				
	Total ( $H_t$ )	Within populations ( $H_s$ )	Within populations	Between years	Between populations	Between timing	Between rivers
<i>Ldh-4</i>	0.380	0.335	88.21	0.48	0.02	2.60	8.69
<i>Pgm-1</i>	0.295	0.284	96.38	0.59	0.21	0.01	2.81
Average	0.028	0.026	91.77	0.53	0.10	1.47	6.12

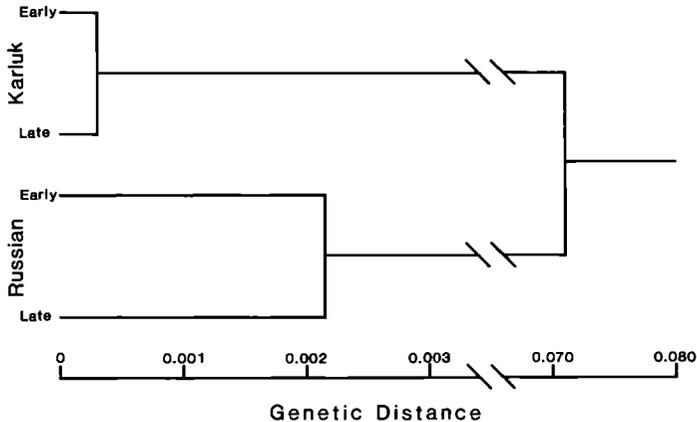


FIGURE 2.—Dendrogram of standard genetic distances among early- and late-spawning sockeye salmon in the Russian River and Karluk River systems. Early Karluk River spawning areas are Upper Thumb River, Moraine Creek, and Canyon Creek; genetic distances between these are  $-0.00001$  to  $-0.00007$  (considered zero). Late Karluk River spawning areas are Lower Thumb and O'Malley rivers (genetic distance,  $-0.00002$ , or zero).

lyzed. One occurs in the Gulkana River (part of the Copper River system flowing into Prince William Sound), and the other in Hidden Lake, which enters the Kenai River about 16 km below the confluence of the Russian and Kenai rivers. Both populations were identical to the Karluk River fish and fixed for the *100* allele (Robert Davis, Alaska Department of Fish and Game, personal communication). The significant difference in the frequency of the *100* allele for *Aco* between Russian River fish and the other populations of sockeye salmon (0.292 and 0.427 versus 1.0) was unexpected—particularly so for the Russian and Hidden Lake populations because they spawn in the same drainage. The major environmental difference between the two systems is the presence of a waterfall on the Lower Russian River that presents a serious block to migration in high-water years. The *110* allele of *Aco* possibly provides some selective advantage in order to maintain the observed difference from other sockeye salmon populations.

Our gene frequency results compared to those of Grant et al. (1980) for *Ldh-4* in early-run Russian River fish were 0.519 versus 0.683, respectively, and 0.708 versus 0.619 for late-run fish. At the *Pgm-1* locus our results were 0.886 versus 0.800 for early-run fish, and 0.888 versus 0.919 for late-run fish.

The lack of any significant change in gene frequencies from year to year in the Russian River populations was expected. The annual differences shown for *Pgm-1* in the 1980 Upper Thumb

River population, and in *Ldh-4* for the 1980 Lower Thumb River population are most likely due to sampling error. Fish from Upper and Lower Thumb rivers were collected at a single time, rather than over the total period of the spawning run.

Thompson and Bevan (1954) and Van Cleve and Bevan (1973) concluded that the sockeye salmon run in the Karluk River originally had a single peak in early August that was destroyed by an intense commercial fishery. They believed that the annual run was made up of distinct genetic races and that the midseason races were most adversely affected by the fishery. Rounsefell (1958) rejected the idea of separate races based on a correlation between the number of fish of the same brood year running at different seasons and in different years. He concluded that timing was a result of the age of the fish and not a result of genetic differences between races.

Raleigh (1967) hatched eggs from Karluk fish spawning in the tributaries, the outlet, and on the lake beaches and released the young into a central pool from which they could migrate upstream or downstream. Alevins from fish spawning in tributaries and on the beaches tended to migrate downstream, whereas those from outlet spawners migrated upstream. His study provides evidence that there are at least two genetically distinct populations in the Karluk system.

We found no significant genetic differences between early-run fish spawning in Upper Thumb River, Canyon Creek, and Moraine Creek, or

between late-run fish spawning in Lower Thumb River and O'Malley River. This result indicates sufficient straying and interbreeding among fish using these spawning areas to prevent genetic differentiation. Our results do show a significant difference between the early-run fish and late-run fish, indicating spatial or temporal separation. Although our information demonstrates that two distinct populations now exist within the Karluk system, it is not possible to determine if only one run of sockeye salmon with a single mid-season peak existed prior to the intense commercial fishery. The only real evidence to support a single peak in run timing is historic data that show a single peak in the number of cases of canned fish produced by canneries. It is not known if all fish brought to these canneries were Karluk River fish. Our data and those of Raleigh (1967) support the hypothesis of at least two genetically distinct populations in the Karluk system that are more likely to be of natural origin than the result of overfishing on the center portion of the run.

Catch and escapement data for Russian River sockeye salmon have been available only since 1963 (Nelson 1980). There is no information to suggest whether or not this run was ever other than bimodal. The early run is composed of predominately 6-year-old fish (68%) versus 5-year-olds in the late run (66%) (Nelson 1980). The genetic differences between the early and late runs in the Russian River are striking, especially for *Aco*. As in the Karluk River, early-run fish spawn in a small stream above a lake.

Our estimate of average heterozygosity ( $H$ ) for the Russian River fish (0.047) is similar to values found by Grant et al. (1980). Our estimates do not include *Gpt*, and have added *Aco*. The  $H$  value for the Karluk fish (0.024), however, is lower than their range of values for Cook Inlet sockeye salmon (0.036 to 0.053), and significantly below values for Alaskan populations of pink salmon, which ranged from 0.071 to 0.103 (McGregor 1982).

Results of the gene diversity analysis are similar to those of other studies in that the largest component of diversity is found within populations. Ryman's (1983) analysis of data from Grant et al. (1980) for Cook Inlet sockeye salmon showed that 95.8% of the diversity was found within populations and the remaining 4.2% was about equally distributed among years, locations, and drainages. Our results displayed a substan-

tially higher amount of diversity between the Russian and Karluk rivers (6.12%) than Ryman (1983) found between rivers in Cook Inlet (2.5%). As with Ryman's (1983) analysis, *Ldh-4* was the largest contributor to the diversity between rivers and was also the largest factor in run timing. Ryman (1983) found the phosphoglucosomerase locus (*Pmi*) to be the greatest contributor to diversity within populations whereas we found *Pmi* to be monomorphic in the Russian and Karluk rivers. Our results show *Pgm-1* was responsible for the largest amount of diversity within populations.

The degree of genetic distance between spawning areas of the Russian and Karluk rivers displayed in the dendrogram (Fig. 2) fits well with the likelihood ratio analysis. Early-spawning fish from Karluk form a nearly homogeneous group as do Karluk late-spawning fish.

As judged by comparisons with sockeye salmon spawning in other areas in Alaska, the Russian River fish are unique. In their estimates of the percentage of fish from three major spawning areas of Cook Inlet caught in the commercial fishery, Grant et al. (1980) had difficulty in correctly separating Kenai River fish (predominately Russian River fish) from sockeye salmon destined for other spawning areas. The uniqueness of the frequency for *Aco* in Russian River sockeye salmon should facilitate use of enzyme electrophoresis for distinguishing these fish.

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