Proc. Mont. Acad. Sci. 48 (1988): Bio. Sci. 57

POPULATION GENETIC STRUCTURE OF WESTSLOPE CUTTHROAT TROUT: GENETIC VARIATION WITHIN AND AMONG POPULATIONS

Robb F. Leary, Fred W. Allendorf, Stevan R. Phelps
and Kathy L. Knudsen
University of Montana
Missoula, Montana, 59801

Abstract: Electrophoretic data indicate that populations of westslope cutthroat trout have low amounts of genetic variation. Most of the allelic variants were detected in only one or two of the populations sampled, resulting in substantial genetic divergence among populations. Populations within the South Saskatchewan drainage appear to be genetically the most divergent, both among themselves and in comparison to those in the upper Missouri and Columbia River Drainages. There appears to be little or no more genetic divergence between populations from these latter two drainages than there is among populations in the Columbia drainage. Within the Columbia drainage, there is as much genetic divergence among populations in the major river systems as there is between the river systems. Preservation of the genetic variation and the biological resource represented by the remaining populations of westslope cutthroat trout requires the continued existence of many populations throughout its range.

INTRODUCTION

Genetic variation is the primary biological resource of a species. This variability is important for the continued existence of the species since it allows populations to respond to changing environmental conditions by the process of natural selection. The total amount of genetic variation in a species consists of both genetic differences between individuals within populations and genetic differences between populations. The genetic differences between populations arise from limited genetic exchange, that is gene flow, among them. This allows allele frequencies to diverge because of selective differences in different environments and genetic drift (random changes in allele frequencies due to finite population size). Unless populations receive an average of one or more migrants per generation from most other populations then it is unlikely that a single population will contain all the allelic variation of the species, and thus, will represent the entire evolutionary potential of the species (21).

An understanding of how the genetic variability of a species is partitioned into within and between population differences will facilitate the biologically sound management and effective use of the resource. This knowledge is especially important when considering preservation of a species. When a large proportion of the genetic variation is due to genetic differences between populations, preservation requires the continued existence of many populations. Furthermore, genetic material from a number of populations will have to be incorporated into domestic populations in order for these to serve as a representative source of the genetic variation of the species.

The westslope cutthroat trout (Salmo clarki lewisi) is in danger of extinction. Many populations have been lost due to alteration of the environment by land use practices (6, 16). Furthermore, rainbow trout (Salmo gairdneri) and Yellowstone cutthroat trout (Salmo clarki bouvieri) have been introduced throughout the range of the westslope cutthroat trout. These introductions have resulted in widespread introgression between the native and introduced trouts causing the irrevocable loss of many populations of westslope cutthroat trout (2, 10, 15, unpublished data). Preservation of this fish is now a goal of management programs.

In this paper, we use electrophoretic data from populations of westslope cutthroat trout collected throughout much of its natural range to obtain an understanding of how the genetic variation of this taxon is partitioned into within and between population differences. We discuss the results as an example of how this information can be used to help develop management plans concerned with the preservation of this fish.

METHODS

Samples and electrophoresis

Samples of naturally reproducing Salmo populations were collected throughout most of the natural range of the westslope cutthroat trout in Canada and Montana. Horizontal starch gel electrophoresis was used to assay genetic variation at a minimum of 32 protein loci in muscle., liver, and eye homogenates from all of the fish (Table 1). Electrophoresis followed the procedures of Utter et al. (20) using the buffers and stains of Allendorf et al (1). The designation of loci and alleles follows the procedures outlined by Allendorf and Utter (4). Allelic mobilities are relative to the common allele at the homologous locus in rainbow trout. We use this convention to facilitate the electrophoretic comparison of the numerous salmonid species we have analyzed.

The protein products of the duplicated Aat3,4, Mdh1,2, and Mdh3,4 loci in westslope cutthroat trout are electrophoretically indistinguishable (e.g. Aat3 and Aat4). We treated these duplicate pairs as single tetrasomic loci to estimate allele frequencies and in the subsequent analysis of the data. The 'able 1. Enzymes and loci examined (E=eye, L=liver, M=muscle).

nzyme	Loci[1,2]	Tissue
denylate kinase (ADK)	Adk	M
lcohol dehydrogenase (ADH)	Adh	L
spartate aminotransferase (AAT)	Aat-1,2	L
	Aat-(3,4)	M
reatine kinase (CK)	Ck-1,2	M
	Ck-3	E
lucosephosphate isomerase (GPI)	Gpi-1,2,3	M
lyceraldehyde-3-phosphate dehydrogenase (GAP)	Gap-3,4	E
lycerol-3-phosphate dehydrogenase (G3P)	G3p-3,4	L
lycly-leucine peptidase (GL)	Gl-1,2	E
socitrate dehydrogenase (IDH)	Idh-1,2	M
	Idh-3,4	L
actate dehydrogenase (LDH)	Ldh-1,2	M
	Ldh-3,4,5	E
eucyl-glycyl-glycine peptidase (LGG)	Lgg	E
alate dehydrogenase (MDH)	Mdh-(1,2)	L
	Mdh-(3,4)	M
alic enzyme (ME)	Me-1,2,3	M
	Me-4	L
osphoglucomutase (PGM)	Pgm-1,2	M
-phosphogluconate dehydrogenase (6PG)	6Pg	E
rbitol dehydrogenase (SDH)	Sdh	L
peroxide dismutase (SOD)	Sod	L
nthine dehydrogenase (XDH)	Xdh	L

The protein products of the paris of loci in () are electrophoretically identical. Therefore, they are considered to be single tetrasomic loci in all analyses.

Adk, Aat1,2, Gap3,4, Gl1,2, Lgg, 6Pg, and Xdh were not analyzed in the South Saskatchewan drainage samples. Adk, Gl1,2, and Lgg were not analyzed in the upper Missouri drainage sample.

amount of genetic variation in each sample was quantified by calculating the average proportion of heterozygous loci per individual (H) and the proportion of polymorphic loci (P). H was calculated using random mating proportions for all of the loci except the duplicate pairs. We used the observed proportion of heterozygous individuals at these loci to calculate H and scored "genotypes" the same as Leary et al. (9). Loci were considered to be polymorphic when the frequency of the most common allele was less than 0.99.

We determined whether or not a sample came from a genetically "pure" population of westslope cutthroat trout or from an introgressed population with rainbow or Yellowstone cutthroat trout using the electrophoretic data from those loci that differentiate these taxa (Table 2). The efficacy of this

Table 2. Loci that differentiate rainbow trout, westslope cutthroat trout, and Yellowstone cutthroat trout. Alleles are designated as the proportional migration distance in the gel relative to the distance traveled by the common allele in rainbow trout which is given mobility of 100.

	Alleles		
Loci	Rainbow	Westslope	Yellowstone
Aat-1	100	200,250	165
Ck-2	100	84	84
Gl-1	100	100	101
Gpi-3	100	92,100	100
Idh-1	100	100	-75
Idh-3,4	100,114,71,40	100,86,40,71,null	100,71
Lgg	100	100	135
Me-1	100,57	88	100
Me-3	100	100	84
Me-4	100,75	100	110
Pgm-1	100,null	100,null	null
Sdh	100,200,40	40	100

technique has been fully discussed (10). In the analysis of the data, we used only those samples that came from pure populations of westslope cutthroat trout and in which more than 20 individuals were analyzed. The following samples, with sample sizes in parentheses, met these criteria:

South Saskatchewan River drainage, Banff National Park, Alberta, Canada: Block Lake (25), Elk Lake (35), Fish Lake 2 (28), Fish Lake 3 (25), Marvel Lake (25), and Mystic Lake (25).

Upper Missouri River drainage, Montana: North Fork of the Dry Fork of the Smith River (29).

Columbia River drainage, Montana: Crazy Fish Lake (41), Emery Creek (27), Felix Creek (25), Groom Creek (25), Hungry Horse Creek (48), Quintonkon Creek (22), Six Mile Creek (25), Sullivan Creek (25), and Tin Creek (30) in the Flathead River drainage; Granite Creek (29), Martin Creek (27), O'Keefe Creek (51), and the Vermilion River (27) in the Clark Fork river drainage; Dodge Creek (26) in the Kootenai River drainage.

RESULTS

Genetic variation within among populations

Genetic variation was detected at 21 loci among all of the samples (Tables 3a-c). Few of these loci, however, are variable

Table 3a. Electrophoretic variation in samples of westslope cutthroat trout collected from populations in the South Saskatchewan River drainage. (H=average heterozygosity; P=proportion of loci polymorphic).

		Samples and Allele Frequencies					
Locus	Alleles	Block	Elk	Fish 2	Fish 3	Marvel	Mystic
Ck1	100	1.000	0.186	1.000	1.000	1.000	1.000
	115	--	0.814	--	--	--	--
Ldh3	100	1.000	1.000	1.000	0.735	1.000	1.000
	33	--	--	--	0.265	--	--
Ldh4	100	0.980	1.000	1.000	1.000	1.000	1.000
	35	0.020	--	--	--	--	--
Pgm2	100	0.600	1.000	1.000	1.000	1.000	1.000
	85	0.400	--	--	--	--	--
H		0.017	0.010	0.000	0.013	0.000	0.000
P		0.067	0.033	0.000	0.033	0.000	0.000

Note: all samples are monomorphic for the Idh4(100) allele.

in any one sample. We detected most of the 24 variable alleles in only one (54%) or two samples (25%). The only locus that we found to be commonly variable is Idh4. This locus is variable in om populations in the Flathead River drainage. (H=average heterozygosity; P=proportion loci polymorphic).

cus	Alleles	Crazy Fish	Emery	Felix	Groom	Hungry Horse	Quintonkon	Six Mile	Sullivan	Tin
		Samples and Allele Frequencies								
t1	200	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.950
	250	--	--	--	--	--	--	--	--	0.050
p4	100	1.000	0.963	0.980	1.000	1.000	1.000	1.000	1.000	1.000
	null	--	0.037	0.020	--	--	--	--	--	--
i1	100	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000
	156	--	--	--	--	0.010	--	--	--	--
i3	92	0.927	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	100	0.073	--	--	--	--	--	--	--	--
h3	86	1.000	0.926	1.000	1.000	0.928	1.000	1.000	1.000	0.966
	71	--	--	--	--	--	--	--	--	0.016
	null	--	0.074	--	--	0.072	--	--	--	0.018
h4	100	0.976	0.446	0.740	0.780	0.396	0.614	0.820	0.360	0.500
	40	0.024	0.554	0.260	0.220	0.604	0.386	0.180	0.640	0.500
h1,2	100	1.000	0.972	1.000	1.000	0.995	1.000	1.000	0.980	1.000
	40	--	0.028	--	--	0.005	--	--	0.020.	--
h3,4	100	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000
	83	--	--	--	--	0.010	--	--	--	--
m1	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.967
	null	--	--	--	--	--	--	--	--	0.033
h	40	1.000	0.981	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	100	--	0.019	--	--	--	--	--	--	--
d	100	1.000	1.000	0.980	1.000	1.000	1.000	1.000	1.000	1.000
	152	--	0.020	--	--	--	--	--	--	--
		0.005	0.020	0.012	0.009	0.017	0.012	0.008	0.013	0.019
		0.051	0.128	0.077	0.026	0.103	0.026	0.026	0.051	0.013

Table 3c. Electrophoretic variation in samples of westslope cutthroat trout collected from populations in the Upper Missouri (Smith), Kootenai (Dodge), and Clark Fork (others) River drainages. (H=average heterozygosity; P=proportion of loci polymorphic)

		Samples and Allele Frequencies					
Locus	Alleles	Smith	Dodge	Granite	Martin	O'Keefe	Vermilion
Aat3,4	100	1.000	1.000	0.957	1.000	0.863	1.000
	77	--	--	0.043	--	0.137	--
Gap4	100	1.000	1.000	0.862	1.000	0.941	1.000
	null	--	--	0.138	--	0.059	--
Gpi1	100	1.000	0.808	0.948	1.000	0.931	0.981
	156	--	0.192	0.052	--	0.069	0.019
Gpi3	92	1.000	1.000	1.000	1.000	0.990	1.000
	100	--	--	--	--	0.010	--
G3p1	100	1.000	1.000	1.000	0.935	1.000	1.000
	81	--	--	--	0.065	--	--
Idh4	100	0.550	1.000	0.448	0.788	0.834	0.852
	71	--	--	--	0.154	--	--
	40	0.450	--	0.552	0.058	0.157	0.148
	null	--	--	--	--	0.010	--
Ldh1	100	1.000	1.000	0.897	1.000	1.000	1.000
	50	--	--	0.103	--	--	--
Ldh3	100	1.000	1.000	0.897	1.000	1.000	0.963
	null	--	--	--	--	--	0.037
Ldh4	100	1.000	0.865	1.000	1.000	1.000	0.759
	112	--	--	--	--	--	0.241
	35	--	0.135	--	--	--	--
Pgm1	100	1.000	1.000	1.000	1.000	0.882	0.852
	110	--	--	--	--	0.118	--
	null	--	--	--	--	--	0.148
Pgm2	100	1.000	1.000	1.000	1.000	0.902	1.000
	85	--	--	--	--	0.098	--
Sdh	40	1.000	1.000	0.983	1.000	1.000	1.000
	100	--	--	0.017	--	--	--
Sod	100	1.000	1.000	0.845	1.000	1.000	1.000
	152	--	--	0.155	--	--	--
H		0.014	0.014	0.036	0.012	0.030	0.025
P		0.029	0.051	0.180	0.051	0.180	0.128

ractically every sample, except those from the South Saskatchewan drainage (Tables 3a-c). The average percentage of heterozygous loci per individual in the samples ranges from 0.0 to only 3.6%, and the proportion of polymorphic loci from 0.0 to .18 (Tables 3a-c). Thus, populations of westslope cutthroat rout generally have low amounts of electrophoretically detectable variation compared to salmonid fishes in particular 4,7,11,17) and fishes in general (14).

The total amount of genetic variation, H(T), among the sampled populations was divided into the average amount of genetic variation within populations, H(S), and the amount due to genetic divergence between populations, D(ST), using the procedure of Nei (12). H(T) is the sum of H(S) and D(ST). Thus, he amount of genetic divergence between populations relative to he total amount of genetic variation can be expressed as (ST)=D(ST)/H(T). When G(ST) equals one, all the variation is lue to genetic divergence between populations. That is, there is o genetic variation within populations but different populations re invariant for different alleles. When G(ST) equals zero, here are no genetic differences between the populations. All he populations have the same alleles at the same frequencies.

We calculated G(ST) using a geographical, hierarchial esign. This allows us to determine what geographic divisions ave major contributions to the observed overall value of G(ST). ur design to estimate G(ST) was as follows: use all the samples based on 32 loci), use only the Columbia and upper Missouri amples (38 loci), use only the South Saskatchewan samples (32 oci), use only the Columbia samples (42 loci), use only the lathead drainage samples (42 loci), use only the Clark Fork rainage samples (42 loci). G(ST) within the upper Missouri and he Kootenai drainages could not be estimated because only one ample was available from each.

The occurrence of most of the variant alleles in only one or wo samples results in a very large proportion of the total mount of genetic variation being attributable to genetic ivergence among populations. Considering all of the samples, (ST) equals 32.8% (Table 4). That is, about one third of the otal amount of genetic variation detected is due to genetic ifferences among populations. Nei (13) has estimated that G(ST) quals only 7% among the races of the human species. Thus, opulations of westslope cutthroat trout are four to five times enetically more divergent among themselves than are the human aces.

Approximately half of the total amount of genetic divergence mong all of the populations is apparently due to genetic ifferences between populations in the South Saskatchewan rainage and those in the upper Missouri and Columbia drainages.

Table 4. Genetic variation in westslope cutthroat trout partitioned into within and between population components.

Drainages	Total (H_t)	Within (H_s)	Between (D_{st})	Proportion Between
South Saskatchewan, Upper Missouri, and Columbia	.0238	.0160	.0078	32.8%
Upper Missouri and Columbia	.0221	.0181	.0040	18.1%
Columbia	.0198	.0165	.0033	16.7%
South Saskatchewan	.0155	.0069	.0086	55.5%
Flathead	.0152	.0127	.0025	16.5%
Clark Fork	.0294	.0259	.0035	11.9%

G(ST) among the samples from the latter two drainages is 18.1%, and within the Columbia drainage it is 16.7% compared to the total of 32.8% (Table 4). There appears, therefore, to be about as much genetic divergence among populations within the Columbia drainage as these is between populations from the Columbia and upper Missouri drainages. These two estimates of G(ST) still represent substantial genetic divergence among populations. They are higher than some estimates of G(ST) for salmonid species with an extensive geographic distribution; G(ST) equals only 8% in the rainbow trout (2; Table 5).

There does not appear to be much more genetic divergence among populations throughout the Columbia drainage than there is among populations within major river systems of the drainage. G(ST) among the Clark Fork samples is 11.9% and among the Flathead samples 16.5% (Table 4). Both are comparable to the estimate of 16.7% for the entire Columbia drainage.

The highest amount of genetic divergence occurs among the South Saskatchewan samples where G(ST) equals 55.5% (Table 4). This represents a tremendous amount of genetic divergence between populations, especially considering the small geographic area in which the sampled lakes occur. This suggests that populations in lakes receive fewer migrants per generation than those in streams and rivers.

able 5. Genetic variation in salmonid fishes partitioned into ithin and between population components.

axa	H_t	H_s	D_{st}	Proportion Between	Reference
tlantic salmon (*Salmo salar*)	.034	.026	.008	21.4%	17
rown trout (*Salmo trutta*)	.040	.025	.015	36.7%	17
ainbow trout (*Salmo gairdneri*)	.064	.059	.005	7.8%	2
estslope cutthroat trout (*Salmo clarki lewisi*)	.024	.016	.008	32.8%	This Report
ellowstone cutthroat trout (*Salmo clarki bouvieri*)	.022	.020	.002	8.2%	11
ahontan cutthroat trout (*Salmo clarki henshawi*)	.065	.036	.029	44.5%	11
rtic char (*Salvelinus alpinus*)	.011	.008	.003	24.0%	5
ockeye salmon (*Oncorhynchus nerka*)	.035	.031	.004	11.4%	19

enetic exchange among populations

The amount of genetic divergence among populations is highly ependent upon the effective population size (*N*) and the igration rate (*m*). That is, genetic divergence is affected by he number of migrants (*Nm*) per generation and not the proportion f migrants between populations. Allendorf and Phelps (3) discuss he biological basis for this relationship. Higher values of *Nm* re expected to result in lower amounts of genetic divergence etween populations.

We were interested in estimating *Nm* because of the elatively large estimates of G(ST). We used a graphical rocedure developed by Slatkin (18) to estimate *Nm* to be about .25 among all the populations. That is, the observed pattern of enetic divergence among the populations suggests that on the verage each receives only about 1.25 migrants from other opulations per generation. In the Columbia drainage *Nm* is about .5, and in the South Saskatchewan drainage it is about 0.25.

DISCUSSION

Distribution of genetic variation

The population genetic structure of westslope cutthroat trout can be characterized as follows: low amounts of genetic variation within populations and substantial genetic divergence between populations. Few loci are variable in any one sample, and most (79%) of the variant alleles occur in only one or two samples. The population within the South Saskatchewan drainage appear to be genetically the most divergent both among themselves and in comparison to those in the upper Missouri and Columbia drainages. There appears to be little or no more genetic divergence between populations from the latter two drainages than there is among populations in the Columbia drainage. This conclusion is tentative, however, since only one sample from the upper Missouri drainage is included in the data. Finally, within the Columbia drainage there appears to be as much genetic divergence among populations within major river systems as there is between the river systems.

We feel that our estimates of the number of migrants per generation, especially among populations in the Columbia drainage, are higher than current values. Most of our samples from this drainage come from populations that are either isolated from other populations because of barriers to migration or are in close proximity to introgressed populations. The fact that the populations are still genetically pure westslope cutthroat trout indicates that they have recently been receiving virtually no migrants. This view agrees with that of Larson et al. (8) who suggest that protein variation may contain information more relevant to historical patterns of gene exchange than to current patterns of gene exchange.

Estimates of the relative amount of genetic divergence mong populations are available for eight taxa of salmonid fishes Table 5). Populations within these taxa are either genetically s divergent as the human races, G(ST)=7%, or three to six times ore divergent. In general, taxa that inhabit interior waters how greater divergence among populations than taxa with a large umber of anadromous populations. The high amount of genetic ivergence among Atlantic salmon populations is due to the xistence to two genetically different groups; those that spawn n rivers flowing into the Baltic Sea and those that spawn in ivers flowing into the Atlantic Ocean (17). Within each of hese groups G(ST) is about 9%, which is comparable to that eported for the other two largely anadromous species. Whether he low amount of genetic divergence among Yellowstone cutthroat rout populations represents the natural situation or is due to he human introduction of fish from one population into others annot be determined from the data. The long historical use of ellowstone Lake as a source of cutthroat trout for stocking purposes lends credibility to the latter explanation, but without accurate stocking records this will always remain speculative.

Management implications

Each population of westslope cutthroat trout contains only a small fraction of the allelic variation of the taxon. Considering the entire genome, the electrophoretic data suggest that practically every population contains some unique alleles. Preservation of the genetic variability and the biological resource represented by the remaining populations of westslope cutthroat trout will require the continued existence of many populations throughout its range. Genetic material from a number of populations will have to be incorporated into a domestic broodstock in order for it to serve as a representative source of the genetic variation of the remaining westslope cutthroat trout population. Management plans designed to preserve this fish will have to address these points in order for the goal of preservation to be obtained.

We do not consider it wise to treat a population that is known to contain a unique electrophoretic variant as more valuable than one that does not. Only a small proportion of the genome is amenable to electrophoretic analysis. Electrophoretic data provide an estimate of the amount of genetic variation in the entire genome that is contained within and between populations. Considering a population less valuable because it does not contain a unique electrophoretic variant ignores that each population very likely contains unique alleles at unexamined loci.

ACKNOWLEDGMENTS

Appreciation is extended to David McAllister of Techman Engineering Ltd.; to Joe Huston, Don Peters and Steve Leathe of The Montana Department of Fish, Wildlife and Parks (MDFWP); and to Mark Aronson for their help in collecting the samples. We also thank H. McPherson for stimulating conversation. George Holton of the MDFWP is owed special thanks for enthusiastically supporting this work.

LITERATURE CITED

1. Allendorf, F.W., N. Mitchell, N. Ryman and G. Stahl. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86:179-190.
2. Allendorf, F.W. and S.R. Phelps. 1981. Isozymes and the preservation of genetic variation in salmonid fishes. Ecological Bulletins 34:37-52.

Allendorf, F.W. and S.R. Phelps. 1981. Use of allelic frequencies to describe population structure. Canadian Journal of Fisheries and Aquatic Sciences 38:1507-1514.

Allendorf, F.W. and F.M. Utter. 1979. Population genetics. In Hoar, W.S., D.J. Randall, and J.R. Brett (Eds.). Fish Physiology, Vol. 8. p. 407-454. Academic Press, New York, New York.

Andersson, L., N. Ryman and G. Stahl. 1983. Protein loci in the arctic char, Salvelinus alpinus L.: electrophoretic expression and variability patterns. Journal Fish Biology 23:75-94.

Behnke, R.J. 1972. The systematics of salmonid fishes of recently glaciated lakes. Journal of the Fisheries Research Board of Canada 29:539-571.

Kornfield, I., K.F. Beland, J.R. Moring and F.W. Kircheis. 1981. Genetic similarity among endemic Arctic char (Salvelinus alpinus) and implications for their management. Canadian Journal of Fisheries and Aquatic Sciences 38:32-39.

Larson, A., D.B. Wake and K.P. Yanev. 1984. Measuring gene flow among populations having high levels of genetic fragmentation. Genetics 106:293-308.

Leary, R.F., F.W. Allendorf and K.L. Knudsen. 1983. Developmental stability and enzyme heterozygosity in rainbow trout. Nature 301:71-72.

Leary, R.F., F.W. Allendorf, S.R. Phelps and K.L. Knudsen. 1984. Introgression between westslope cutthroat and rainbow trout in the Clark Fork River drainage, Montana. Proceedings Montana Academy of Sciences 43:1-18.

Loudenslager, E.J. and G.A.E. Gall. 1980. Geographic patterns of protein variation and subspeciation in cutthroat trout, Salmo clarki. Systematic Zool. 29:27-42.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences, U.S.A. 70:3321-3323.

Nei, M. 1975. Molecular population genetics and evolution. American Elsevier, New York, New York.

Nevo, E. 1978. Genetic variation in natural populations: pattern and theory. Theoretical Population Biology 13:121-177.

Phelps, S.R. and F.W. Allendorf. 1982. Genetic comparison of upper Missouri cutthroat trout to other Salmo clarki lewisi populations. Proceedings Montana Academy of Sciences 41:14-22.

Reinitz, G.L. 1977. Electrophoretic distinction of rainbow trout (Salmo gairdneri), westslope cutthroat trout (Salmo clarki) and their hybrids. Journal of the Fisheries Research Board of Canada 34:1236-1239.

Ryman, N. 1983. Patterns of distribution of biochemical genetic variation in salmonids: differences between species. Aquaculture 33:1-21.

18. Slatkin, M. 1981. The distribution of mutant alleles in a subdivided population. Genetics 94:503-524.
19. Utter, F., P. Abersold, J. Helle and G. Winans. 1984. Genetic characterization of populations in the southeastern range of sockeye salmon. In Walton, J.M. and D.B. Houston (Eds.). Proc. Olympic Wild Fish Conference, pp. 17-31. Peninsula College and Olympic National Park, Port Angeles, Washington.
20. Utter, F.M., H.O. Hodgins, and F.W. Allendorf. 1974. Biochemical genetic studies of fishes: potentialities and limitations. In Malins, D.C. and J.R. Sargent (Eds.). Biochemical and biophysical perspectives in marine biology, Vol. 1 pp. 213-238. Academic Press, New York, New York.
21. Wright, S. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago, Illinois.

Editor's note: The above article, by Leary et al., was originally printed in Volume 45 of the Proceedings, but through editorial oversight, the Tables were omitted. This reprinting of the article, including Tables, is intended to compensate for that regrettable oversight, and yet preserve the original date of publication.