1 March 1988
Conservation Biology (in press)

CONSERVATION BIOLOGY OF FISHES

Fred W. Allendorf

Department of Zoology
University of Montana
Missoula, MT 59812

"I love any discourse of rivers, and fish, and fishing."

Izaak Walton
The Compleat Angler

The following three papers were presented at a symposium on the conservation biology of fishes at the Society for Conservation Biology meeting in June of last year. The first paper presents problems special to species living in rivers; the second paper discusses desert fishes; and the final paper considers one of the most popular sport fishes of North America, the cutthroat trout. A fourth paper on the genetics of exploitation in rockfishes was presented at the symposium by Keith Nelson but is not included in this issue.

Three or four papers obviously are not sufficient to provide a comprehensive overview of the conservation of a taxon with over 20,000 species that last shared a common evolutionary ancestor some 400 million years ago (Mayr 1969). Those interested in broader aspects of fish conservation may consult the following recent publications (FAO/UNEP 1981, Fetterolf 1981, Meffe 1987, Ono et al. 1983, Ryman 1981). The three papers in this issue are concerned primarily with freshwater fishes native to North America. Nevertheless, all three papers stress general principles that are relevant to all fish species.

Some 70% of all of the world's fishes listed as endangered or threatened are native to North America (Ono et al. 1983, page 218). In addition, only one out of 83 species from throughout the world listed as threatened or endangered by the US Fish and Wildlife Service (Federal Register 1987) is a marine species. It is unclear how much the predominance of freshwater fishes from North America on such lists is due to

the fishes *per se* and how much is due to the geographical distribution of ichthyologists. Nevertheless, the topics of these three papers reflect current conservation efforts with fishes.

Fishes present some unusual challenges to conservation biologists because they are different from other vertebrates in a variety of ways. Their tremendous taxonomic diversity is the first challenge. Almost exactly one-half of all vertebrate species are fishes (Mayr 1969). Fish species occur in virtually every aquatic environment on the water-planet: lakes, streams, rivers, vernal pools, desert springs, estuaries, the open ocean, deep oceanic trenches, and underneath the polar icecaps.

Fish also show much more intraspecific phenotypic variation than most other taxa (Allendorf et al. 1987). Individuals within a single species of fish sometimes show enormous differences in size. For example, females from ten populations of Arctic char (*Salvelinus alpinus*) range in mean weight at first sexual maturity from 23 g to nearly 1,000 g (Johnson 1980). However, the larger phenotypic variation within fish species is apparently not associated with greater genetic variability. Heritability is the proportion of the total phenotypic variation that is due to genetic differences between individuals. Heritabilities for such traits as body length and weight are generally much lower within fish populations than within populations of other vertebrates (Allendorf et al. 1987).

These comparisons suggest that the genotypic-phenotypic relationship in fishes may be somewhat different from what it is in other vertebrates. The high phenotypic variation, coupled with lower heritabilities, indicate greater susceptibility to environmental factors. This difference is not surprising in view of the indeterminate growth capacity of most fishes and

the greater metabolic sensitivity to temperature of fishes in comparison to birds and mammals.

The cichlid fishes of the New World and Africa probably best demonstrate the challenges to conservation biologists resulting from the great taxonomic diversity in fish species and their unusual genotypic-phenotypic relationships. Some African rift lakes have "species flocks" consisting of over 300 described endemic species (references in Echelle and Kornfield 1984). However, two morphologically distinct sympatric 'species' of cichlids endemic to Cuatro Cienegas, Mexico have been shown to belong to a single reproductive population (Kornfield et al. 1982). In addition, laboratory experiments with cichlids have shown that changing their diet can result in large differences in morphology (Meyer 1987).

Fishes also show the greatest variety of reproductive systems among the vertebrates. Modes of reproduction in fishes include oviparity, viviparity, ovoviviparity, and ovi-ovoviviparity (Moyle and Cech 1982). Sexuality in fishes also runs the gamut of possibilities: simultaneous hermaphroditism, consecutive hermaphroditism, unisexuality, and bisexuality (Price 1986). Modes of sex determination in fish species includes male heterogamety, female heterogamety, multiple sex chromosomes, polygenic determination, single gene determination, and environmental determination (Price 1986).

The genetic systems of fishes show similar diversity. Most fish species show normal diploid Mendelian inheritance. However, alternative genetic systems in fish species include triploidy, tetraploidy, strict gynogenetic (female) inheritance, and hybridogenesis (Turner 1984). Some of these alternative genetic system also occur in amphibians and reptiles but they are more restricted in those taxa. For example, all of the

described polyploid amphibian and reptilian species have closely related diploid counterparts, and no higher polyploid taxa have been found (Bogart 1980). Tetraploidy among fish taxa is much more widespread (Schultz 1980). Two of the more successful families of fishes apparently are descended from their own tetraploid ancestor: catostomids (suckers: 12 genera, 58 species; Nelson 1976) and salmonids (salmon, trout, char, whitefish, and grayling: 9 genera, 68 species; Nelson 1976).

This diversity in reproduction and genetics is of more than academic interest. The paper in this issue by Allendorf and Leary (1988) discusses several unusual problems associated with the conservation of cutthroat trout. Many of the conservation problems with this salmonid species apparently result from its polyploid ancestry (e.g., fertile hybrids between taxa with large amounts of genetic divergence).

Fishes are unique in that no other major food source of man is captured from wild populations. Nelson and Soule' (1987) have considered this attribute of fishes in a philosophical context. The commercial harvesting of fish also has a variety of important biological implications. Harvested fish populations are subjected to selection on a variety of characteristics that affect an individuals vulnerability to harvesting. Nelson and Soule' (1987) have reviewed the evidence that differential harvesting has caused genetic changes in fish stocks.

The paper presented at the meeting by Nelson examined this problem in detail in rockfish of the genus Sebastes. This genus contains at least 100 species of marine fish (Eschmeyer et al. 1983); many of these species support important fisheries on the west coast of the United States. He concluded that our understanding of the effects of exploitation cannot be

gained by ordinary genetic methods. He recommended the detailed analysis of the empirical effects of exploitation on the age schedule of growth and changes in the size schedule of fecundity.

The commercial and recreational value of fish populations has also led to widespread culture of fishes in hatcheries for release into the wild to supplement natural populations. There is no parallel among other taxa to the massive and continuous release of artificially cultured individuals over large areas such as became possible through the development of hatchery programs in the last century (Allendorf et al. 1987). For example, a single hatchery on Yellowstone Lake collected and shipped over 818 million Yellowstone cutthroat trout (Salmo clarki bouvieri) eggs between 1899 and 1957 (Varley 1979)!

A discussion of the need for protecting fishes on their spawning grounds from an article on "pisciculture" by G. Brown Goode of the U. S. National Museum in the 1898 edition of the Encyclopedia Britannica presents the view of early fish biologists:

> How much must they be protected? Here the fish-culturist comes in with the proposition that "it is cheaper to make fish so plentiful by artificial means that every fisherman may take all he can catch than to enforce a code of protection laws."
>
> The salmon rivers of the Pacific slope of the United States, the shad rivers of the east, and the whitefish fisheries of the lakes are now so thoroughly under control by the fish-culturist that it is doubtful if anyone will venture to contradict his assertion. The

question is whether he can extend his domain to other species.

It is interesting to note that two whitefish species from the Great Lakes are extinct, and three additional species are threatened or endangered (Ono 1983 et al.). The paper by Allendorf and Leary (1988) discusses problems in conservation related to artificial culture and release of salmonids throughout the western United States.

Fish are generally restricted to water. This obvious characteristic has some perhaps not so obvious effects on their conservation. For example, fishes are not as easy to observe and appreciate by humans as birds and mammals. It has therefore been more difficult to attract public support for their conservation. Moreover, it also appears that fishes have been somewhat ignored by conservation biologists. For example, the most recent list of endangered and threatened species by the U.S. Department of the Interior (Federal Register 1987) includes over 300 species of mammals, over 200 species of birds, and only 83 species of fish, even though there are many more species of fish than mammal and bird species combined (Mayr 1969).

The dependence of fish on water has also brought many species into conflict with humans over increasingly valuable water resources. An analysis of the source of threats to the fishes of the United States is revealing. Ono et al. (1983) listed five categories of threats to 151 fish species that they considered to be endangered or threatened: habitat alteration, overutilization for commercial purposes, disease, introduction of exotic or non-native fishes, and restricted natural range. Individual species were threatened by any combination of these five factors. A surprising 98% of all species were threatened by habitat alteration. The

next most common threat was introduced fishes which threatened 37% of the species. The final major threat was restricted natural range (24%). Less than 5% of the species were threatened by either commercial harvesting or disease.

The paper in this issue by Meffe and Vrijenhoek (1988) considers genetic aspects of conservation and recovery programs of fishes in the deserts of western North America, where the conflict for water resources has been most intense. Over 75% of the U. S. federally listed endangered species occur in the southwest (Sheldon 1988). Meffe and Vrijenhoek compare two models of genetic population structure based upon geographic isolation and gene flow. They emphasize "the need to incorporate experimental studies of population genetics and fitness into management of endangered fishes."

Sheldon's paper in this issue describes conservation problems intrinsic to species living in flowing water because of the geometry of river systems. He emphasizes the importance of recognizing the threats of fragmentation of drainage networks by impoundments and the homogenization of faunas by interbasin connections and introductions. His analysis of these problems makes the important conclusion that biogeographic considerations are essential in any plan for the conservation of North American fishes.

These three papers provide different perspectives of the challenges to conservation biology provided by fishes. The most striking common theme of these papers is the issue of the objectives of fish conservation biology. What should we be trying to "conserve"? Each paper struggles with this question, and each concludes with a different answer.

ACKNOWLEDGMENTS

I thank Pete Brussard for inviting me to organize the symposium, the Society for Conservation Biology for providing financial assistance for travel to the speakers, Dave Ehrenfeld for his help and patience, the reviewers of these papers for their time and helpful comments, and Nils Ryman for his suggestions on this paper. I was supported by grant BSR-86000108 from the National Science Foundation while this paper was prepared.

Literature Cited

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2: 00-00.

Allendorf, F. W., N. Ryman, and F. M. Utter. 1987. Genetics and fishery management. Past, present, and future. Pages 1-19 in N. Ryman and F. Utter, editors. Population genetics and fishery management. Seattle: University of Washington Press.

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

Bogart, J. P. 1980. Polyploidy in evolution of amphibians and reptiles. Pages 341-369 in H. L. Lewis, editor. Polyploidy: Biological relevance. New York: Plenum Press.

Echelle, A. A., and I. Kornfield (editors). 1984. Evolution of fish species flocks. Orono: Univ. Maine Press.

Eschmeyer, W. N., E. S. Herald, and H. Hamman. 1983. A field guide to Pacific coast fishes of North America. Boston: Houghton Mifflin Co.

FAO/UNEP. 1981. Conservation of the genetic resources of fish: problems and recommendations. FAO Fish. Tech. Pap. 217. 43 pp. Rome.

Federal Register. 1987. Endangered and threatened wildlife and plants. 50 CFR 1711 & 17.12. U. S. Department of the Interior.

Fetterolf, C. M., Jr. 1981. Foreword to the Stock Concept Symposium. Can. J. Fish. Aquat. Sci. 38:iv-v.

Goode, G. B. 1898. Pisciculture. Pages 126-129 in The Encyclopaedia Britannica. New York: The Werner Company.

Johnson, J.E. 1987. Protected Fishes of the United States and Canada. Bethesda, Maryland: American Fisheries Society.

Johnson, L. 1980. The Arctic charr, Salvelinus alpinus. Pages 15-98 in E. K. Balon, editor. Charrs, salmonid fishes of the genus Salvelinus. The Hague: Dr. W. Junk Publishers.

Meffe, G. K. 1987. Conserving fish genomes: philosophies and practices. Envir. Biol. Fishes 18:3-9.

Meffe, G. K., and R. C. Vrijenhoek. 1988. Conservation genetics in the management of desert fishes. Conservation Biology 2: 00-00.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in Cichlasoma managuense (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution 41:1357-1369.

Moyle, P. B., and J. J. Cech, Jr. 1982. Fishes: An introduction to ichthyology. Englewood Cliffs, New Jersey: Prentice-Hall, Inc.

Nelson, K., and M. Soule'. 1987. Genetical conservation of exploited fishes. Pages 345-368 in N. Ryman and F. Utter, editors. Population

Genetics and Fishery Management. University of Washington Press, Seattle, Washington, USA.

Nelson, J. S. 1976. Fishes of the world. New York: Wiley.

Ono, R. D., J. D. Williams, and A. Wagner. 1983. Vanishing fishes of North America. Washington, D. C.: Stone Wall Press, Inc.

Price, D. J. 1986. Genetics of sex determination in fishes - a review. Pages 77-89 in G. W. Potts and R. J. Wooten, editors. Fish reproduction: strategies and tactics. London: Academic Press.

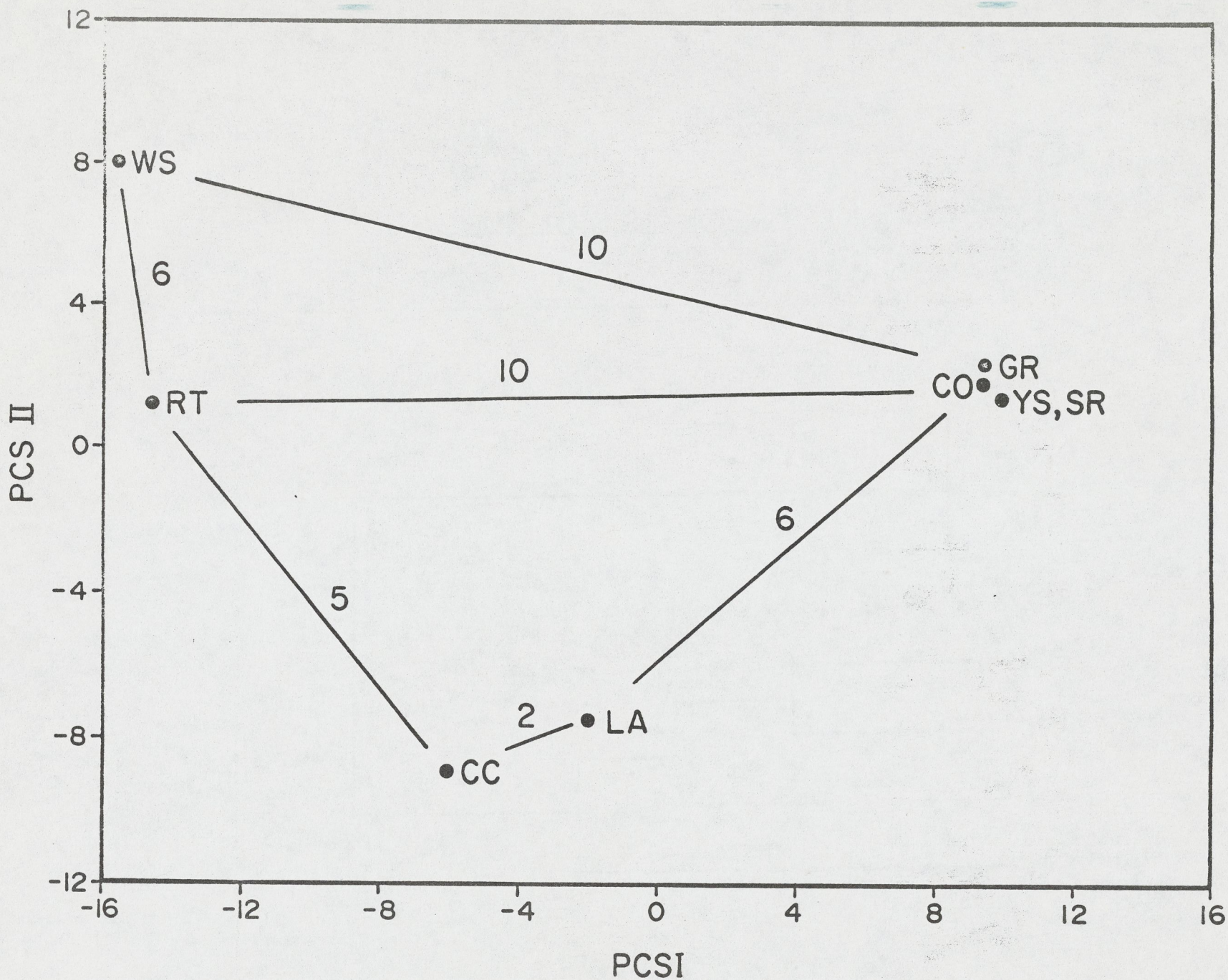
Ryman, N. (editor) 1981. Fish gene pools: Preservation of genetic resources in relation to wild fish stocks. Ecological Bulletin (Stockholm), Vol. 34.

Schultz, J. 1980. Pages 313-340 in H. L. Lewis, editor. Polyploidy: Biological relevance. New York: Plenum Press.

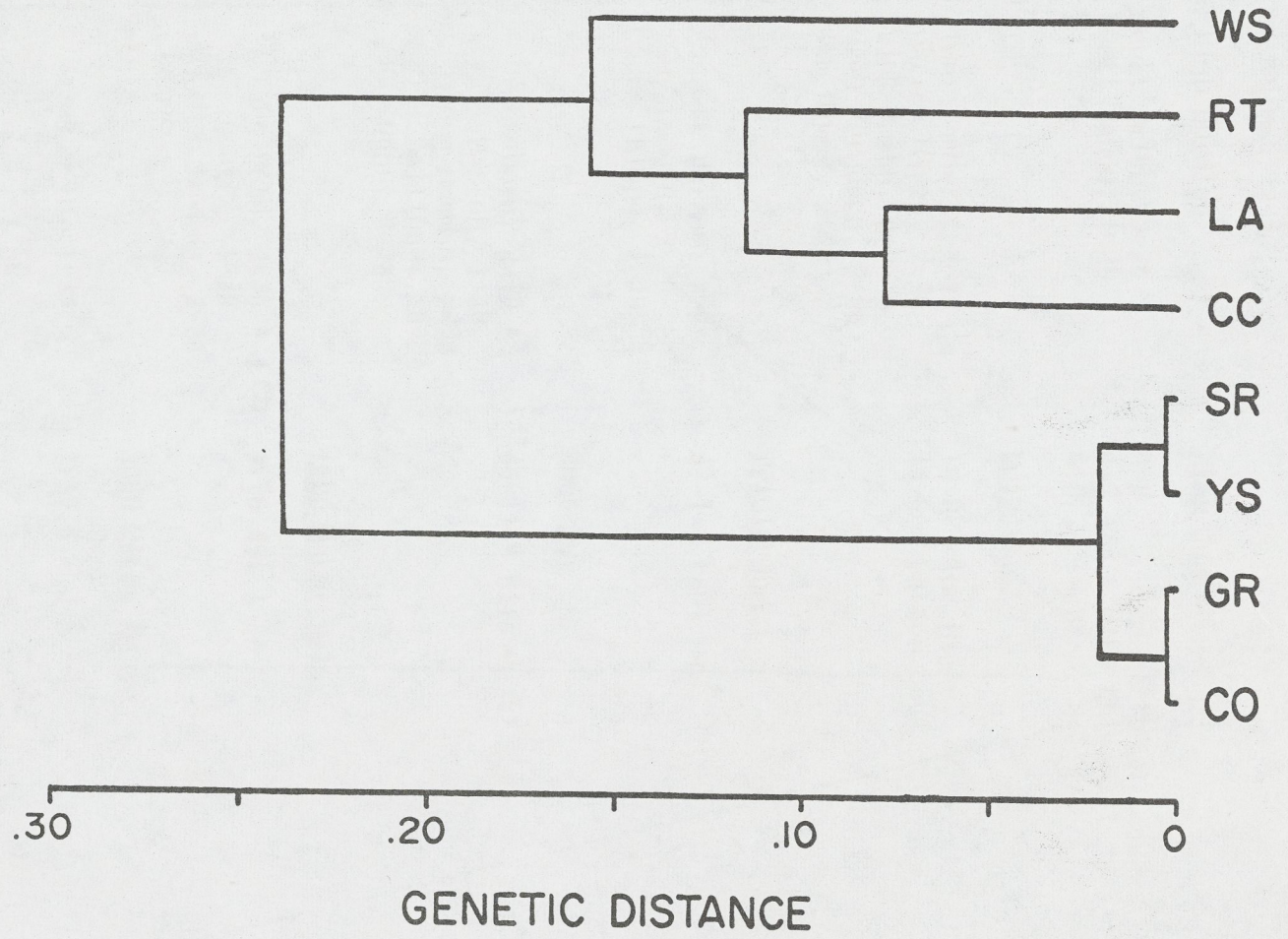
Sheldon, A. L. 1988. Conservation of stream fishes: patterns of diversity, rarity, and risk. Conservation Biology 2: 00-00.

Turner, B. J. (editor) 1984. Evolutionary genetics of fish. New York: Plenum Press.

Varley, J. D. 1979. Record of egg shipments from Yellowstone fishes, 1914-1955. Information paper no. 36. Yellowstone National Park. U. S. Dept. Interior.


12
8
4
0
-4
-8
-12
-16
-12
-8
-4
0
4
8
12
16
PCS II
PCSI
WS
RT
CC
LA
CO
GR
YS, SR
10
6
10
5
2
6

A.5.3



A.S. 2

Fig. 1

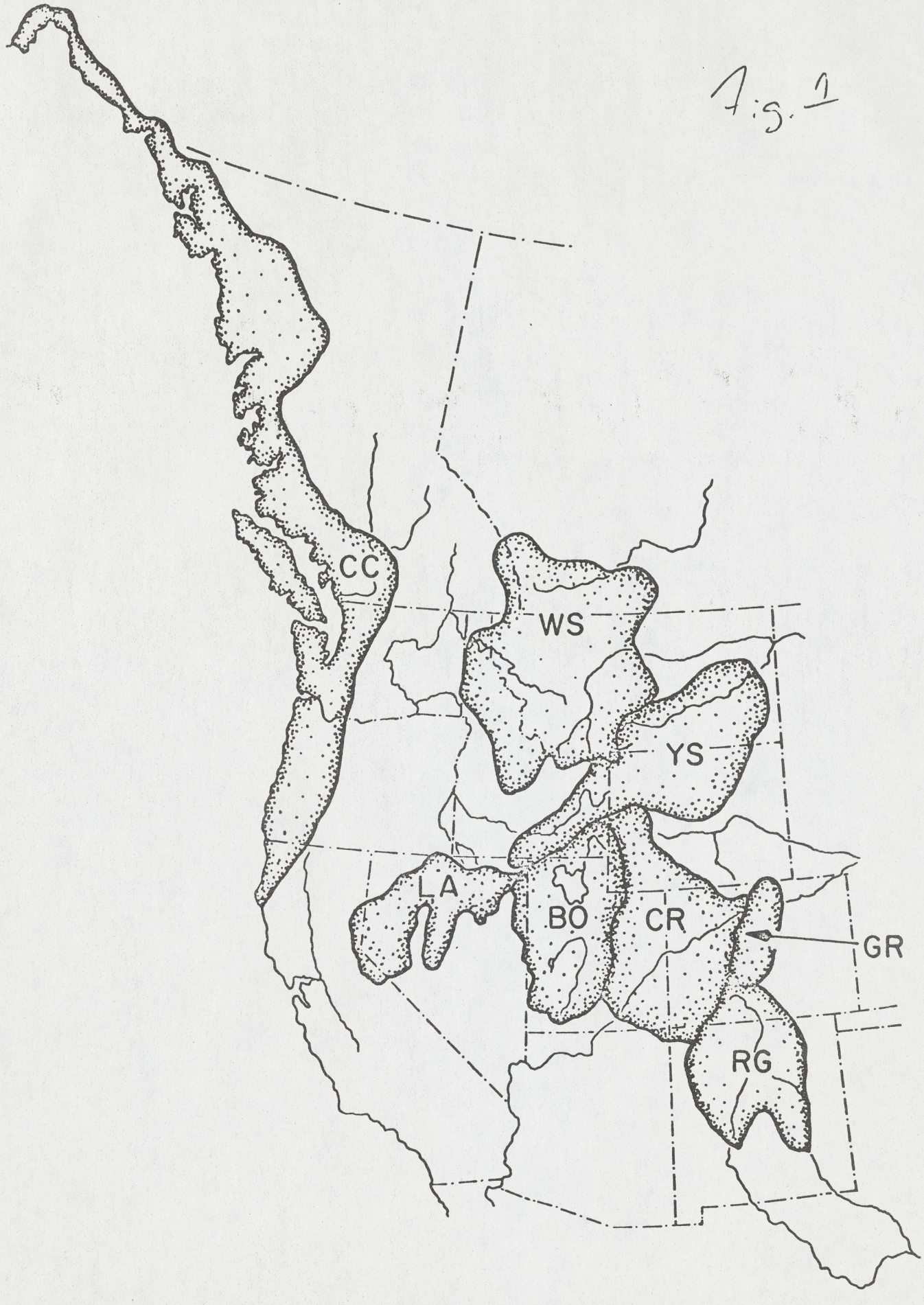


FIGURE LEGENDS

Figure 1. Range of eight major subspecies of cutthroat trout in western North America (based on Behnke 1979).

Figure 2. Dendrogram (unweighted average linkage method) based on Nei's genetic distance for seven subspecies of cutthroat trout and the rainbow trout.

Figure 3. Plot of first two principal component scores of allele frequencies at 16 diagnostic loci among seven subspecies of cutthroat trout and the rainbow trout.

Table 6. Allele frequencies in eight populations of Yellowstone cutthroat trout from the Yellowstone River drainage, Montana.

		Samples and Allele Frequencies							
Locus	Alleles	Anderson	Billman	Mill Fork Mission	Miner	Rock	Six Mile	Tom Miner	Turkey
Aat-3,4	100	0.590	0.697	0.488	0.634	0.530	0.850	0.580	0.712
	110	0.260	0.105	0.179	0.250	0.280	0.090	0.250	0.173
	90	0.150	0.197	0.333	0.116	0.190	0.060	0.170	0.115
Adh	-100	1.000	1.000	0.952	1.000	1.000	1.000	1.000	1.000
	0	-	-	0.048	-	-	-	-	-
Gl-1	101	1.000	1.000	0.982	1.000	1.000	1.000	1.000	1.000
	88	-	-	0.018	-	-	-	-	-
Igg	135	1.000	1.000	1.000	0.982	1.000	1.000	1.000	1.000
	100	-	-	-	0.018	-	-	-	-
Sdh-1,2	100	1.000	1.000	1.000	0.982	1.000	1.000	1.000	1.000
	200	-	-	-	0.018	-	-	-	-

Table 7. Allele frequencies in the 1985 year class of hatchery Yellowstone cutthroat trout and the progeny of fish from the wild population from which the hatchery population was founded.

Locus	Alleles	Hatchery	Wild	Probability
Aat-3,4	100	0.655	0.685	*
	110	0.125	0.195	
	90	0.220	0.120	
Acp-1	-100	0.920	1.000	**
	-33	0.080	-	
Fum-1	95	0.900	0.880	NS
	81	0.100	0.120	
A-glu	70	0.867	0.917	NS
	100	0.133	0.083	
Hex	100	0.760	0.900	**
	72	0.240	0.100	
Mdh-1,2	100	0.995	0.995	NS
	44	0.005	0.005	
Tpi-3,4	100	0.995	1.000	NS
	93	0.005	-	
Average observed heterozygosity		0.027	0.022	

NS = not significant; * = $P < 0.05$; ** = $P < 0.01$.

Table 4. Mean length of parental types and hybrids between westslope cutthroat trout and rainbow trout.

Age (days)	Length (mm) WS	WS x RT	Prob.	Age (days)	Length (mm) RT	RT x WS	Prob.
73	22.7	22.3	NS	72	25.3	24.5	**
89	29.0	27.2	***	100	33.4	31.2	**
112	40.1	33.6	***	130	46.3	46.3	NS
				181	69.6	62.7	***

The maternal species is listed first. NS = not significant; ** = $P < 0.01$; *** = $P < 0.001$.

Table 5. Analysis of genic diversity and degree of differentiation in eight taxa of salmonid fishes.

Taxa	No. Pop.	No. Loci	H_T	H_S	Relative gene diversity: Between drainages	Between samples within drainages	Within samples
Cutthroat trout							
CC	21	31	0.101	0.095	2.2	3.6	94.2
LA	15	35	0.065	0.036	---	44.5*	55.5
WS	103	29	0.029	0.019	16.7	15.7*	67.6
YS	8	46	0.014	0.013	---	3.7*	96.3
Atlantic salmon	53	38	0.040	0.023	37.4	3.6	59.0
Brown trout	38	35	0.040	0.025	7.5	29.2*	63.3
Rainbow trout	38	16	0.069	0.058	7.3	7.7	85.0
Sockeye salmon	18	26	0.046	0.044	2.5	3.1	94.4

H_T = total gene diversity; H_S = average gene diversity within local populations. The data are from the following sources: Atlantic salmon (Salmo salar), brown trout (Salmo trutta), rainbow trout, and sockeye salmon (Oncorhynchus nerka) from Ryman (1983); Lahontan cutthroat trout from Loudenslager and Gall (1980); coastal cutthroat trout from Campton and Utter (1987). * = samples obtained from non-anadromous populations.

Table 2. Nei's genetic distance between seven subspecies of cutthroat trout and the rainbow trout (RT) below the diagonal and number of diagnostic loci between the taxa above the diagonal.

		Cutthroat Trout Subspecies							
	RT	WS	CC	LA	YS	SR	GR	CO	RG
Rainbow	—	6	5	6	10	10	10	10	10
Westslope	0.130	—	7	7	10	10	10	10	10
Coastal	0.099	0.164	—	2	7	7	7	7	7
Lahontan	0.138	0.175	0.077	—	6	6	6	6	6
Yellowstone	0.246	0.295	0.191	0.164	—	0	0	0	1
Snake River	0.247	0.297	0.192	0.165	0.006	—	0	0	1
Greenback	0.229	0.268	0.194	0.151	0.022	0.025	—	0	1
Colorado	0.223	0.280	0.193	0.150	0.012	0.023	0.005	—	1

Table 3. Allozyme genotypes at 8 nuclear loci and mtDNA genotypes in a hybrid swarm of westslope and Yellowstone cutthroat trout in Forest Lake, Montana.

		Nuclear encoded loci							
No.	mtDNA	Aat1	Gpi3	Idh1	Lgg	Me1	Me3	Me4	Sdh
1	YS	W	W	WY	W	W	W	W	Y
2	YS	W	WY	WY	WY	Y	W	WY	Y
3	WS	WY	Y	Y	W	Y	WY	Y	WY
4	WS	Y	W	WY	WY	W	Y	W	WY
5	YS	Y	Y	Y	WY	WY	WY	Y	Y
6	YS	WY	Y	W	WY	W	W	W	Y
7	WS	WY	WY	Y	W	WY	W	W	W
8	WS	WY	Y	WY	WY	Y	W	Y	Y
9	WS	Y	Y	WY	WY	W	WY	WY	W
10	WS	WY	Y	WY	WY	WY	Y	W	Y
11	YS	Y	W	W	WY	W	Y	W	Y
12	WS	W	WY	Y	WY	W	WY	WY	Y
13	YS	W	Y	W	Y	W	WY	W	W
14	YS	Y	Y	WY	WY	WY	WY	WY	W
15	WS	WY	Y	WY	Y	W	Y	WY	W

W = homozygous for westslope allele; Y = homozygous for Yellowstone allele; WY = heterozygous for westslope and Yellowstone alleles.

Thorgaard, G. H. 1983. Chromosomal differences among rainbow trout populations. Copeia 1983:650-662.

Thorgaard, G. H., and F. W. Allendorf. 1987. Developmental genetics of fishes. In G. M. Malacinski, editor. Developmental Genetics of Animals and Plants. New York: Macmillan Publishing Company. In press.

Whitmore, D. H. 1983. Introgressive hybridization of smallmouth bass (Micropterus dolomieui) and Guadalupe Bass (M. treculi). Copeia 1983:672-679.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 in M. E. Soule', editor. Conservation Biology: The Science of Scarcity and Diversity. Sunderland, Massachusetts: Sinauer Associates.

Wilson, A. C., R. L. Cann, S. M. Carr, M. George, Jr., U. B. Gyllensten, K. M. Helm-Bychowski, R. G. Higuchi, S. R. Palumbi, E. M. Prager, R. D. Sage, and M. Stoneking. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linnaean Soc. 26:375-400.

Yates, T. L., M. A. Lewis, and M. D. Hatch. 1984. Biochemical systematics of three species of catfish (Genus Ictalurus) in New Mexico. Copeia 1984:97-101.

Zouros, E., and D. W. Foltz. 1987. The use of allelic isozyme variation for the study of heterosis. Isozymes: Current Topics in Biological and Medical Research 13:1-59.

Table 1. Subspecies of cutthroat trout and their protection status (Behnke 1979, Williams 1987).

Common Name	Subspecies	Abbrev.	Legal Protection
Bonneville	S. c. utah	BO	US ID NV UT WY
Coastal	S. c. clarki	CC	--
Colorado	S. c. pleuriticus	CO	US CO UT WY
Greenback	S. c. stomias	GR	US CO
Lahontan	S. c. henshawi	LA	US CA UT
Rio Grande	S. c. virginalis	RG	CO NM
Westslope	S. c. lewisi	WS	ID MT
Yellowstone	S. c. bouvieri	YS	ID MT
Alvord	S. c. subsp.	AL	extinct
Bear Lake	S. c. subsp.	BL	ID
Humboldt	S. c. subsp.	HU	--
Mountain	S. c. alpestris	MO	--
Paiute	S. c. seleniris	PA	US CA
Snake River	S. c. subsp.	SR	ID
Willow/Whitehorse	S. c. subsp.	WW	US
Yellowfin	S. c. macdonaldi	YF	extinct

The eight subspecies in the top group are the major subspecies which are endemic to large geographical areas (see Figure 1). Italicized abbreviations represent legal protection and unitalicized abbreviations represent fishes of Special Concern according to Johnson (1987). US=United States; CA=California; CO=Colorado; ID=Idaho; MT=Montana; NM=New Mexico; NV=Neveda; UT=Utah; WY=Wyoming.

Population genetic structure of westslope cutthroat trout: Genetic variation within and among populations. Proc. Montana Acad. Sci. 45:37-45.

Leary, R. F., F. W. Allendorf, S. R. Phelps, and K. L. Knudsen. 1987. Genetic divergence among seven subspecies of cutthroat trout and rainbow trout. Trans. Amer. Fish. Soc. 116:580-587.

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

Loudenslager, E. J., and G. H. Thorgaard. 1979. Karyotypic and evolutionary relationships of the Yellowstone (Salmo clarki bouvieri) and west-slope (S. c. lewisi) cutthroat trout. J. Fish. Res. Bd. Canada 36:630-635.

Marnell, L. F., R. J. Behnke, and F. W. Allendorf. 1987. Genetic identification of the cutthroat trout (Salmo clarki) in Glacier National Park, Montana. Can. J. Fish. Aquat. Sci. 43:in press.

Martin, M. A., D. K. Shiozawa, E. J. Loudenslager, and J. N. Jensen. 1985. Electrophoretic study of cutthroat trout populations in Utah. Great Basin Naturalist 45:677-687.

Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. Ann. Rev. Ecol. Syst. 15:479-499.

Nei, M. 1975. Molecular Population Genetics and Evolution. New York: Elsevier North-Holland.

Neff, N. A., and G. R. Smith. 1979. Multivariate analysis of hybrid fishes. Syst. Zool. 28:176-196.

O'Brien, S. J., M E. Roelke, L. Marker, A. Newman, C. A. Winkler, D.

Meltzer, L. Colly, J. F. Evermann, M. Bush, and D. E. Wildt. 1985. Genetic basis for species vulnerability in the cheetah. Science 227:1428-1434.

Palmer, A. R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. Ann. Rev. Ecol. Syst. 17:391-421.

Phelps, S. R., and F. W. Allendorf. 1983. Genetic identity of pallid and shovelnose sturgeon (Scaphirhynchus albus and S. platorynchus). Copeia 1983:696-700.

Quinn, J. F., and A. Hastings. 1987. Extinction in subdivided habitats. Conservation Biology 1:198-208.

Rinne, J. N., and J. N. Hanson. 1981. Chemical treatment of Ord Creek, Apache County, Arizona, to re-establish Arizona trout. J. Arizona-Nevada Acad. Sci. 16:74-78.

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

Sage, R. D., D. Heyneman, K-C. Lim, and A. C. Wilson. 1986. Wormy mice in a hybrid zone. Nature 324:60-62.

Sigler, W. F., W. T. Helm, P. A. Kucera, S. Vigg, and G. W. Workman. 1983. Life history of the Lahontan cutthroat trout Salmo clarki henshawi, in Pyramid Lake, Nevada. Great Basin Naturalist 43:1-29.

Templeton, A. R. 1986. Coadaptation and outbreeding depression. Pages 105-116 in M. E. Soule', editor. Conservation Biology: The Science of Scarcity and Diversity. Sunderland, Massachusetts: Sinauer Associates.

Templeton, A. R., C. F. Sing, and B. Brokaw. 1976. The unit of selection in Drosophila mercatorum. I. The interaction of selection and meiosis in parthenogenetic strains. Genetics 82:349-376.

Gyllensten, U. 1985. The genetic structure of fish: Differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. J. Fish Biol. 26:691-699.

Gyllensten, U., R. F. Leary, F. W. Allendorf, and A. C. Wilson. 1985. Introgression between two cutthroat trout subspecies with substantial karyotypic, nuclear, and mitochondrial genomic divergence. Genetics 111:905-915.

Gyllensten, U., and A. C. Wilson. 1987. Mitochondrial DNA of salmonids: inter- and intraspecific variability detected with restriction enzymes. Pages 301-317 in N. Ryman and F. Utter, editors. Population genetics and fishery management. Seattle: University of Washington Press.

Hanzel, D. A. 1959. The distribution of cutthroat trout (Salmo clarki) in Montana. Proc. Montana Acad. Sci. 19:32-71.

Hedrick, P. W., P. F. Brussard, F. W. Allendorf, J. A. Beardmore, and S. Orzack. 1986. Protein variation, fitness, and captive propagation. Zoo Biology 5:91-99.

Hubbs, C. L. 1955. Hybridization between fish species in nature. Syst. Zool. 4:1-20.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. Bethesda, Maryland: American Fisheries Society.

Johnson, M. S. 1975. Biochemical systematics of the Atherinid genus Menidia. Copeia 1975:662-691.

Jordan, D. S., and B. W. Evermann. 1896. The Fishes of North and Middle America. Washington: U. S. Government Printing Office.

Joswiak, G. R., R. H. Stasiak, and W. S. Moore. 1982. Allozyme analysis of the hybrid Phoxinus eos x Phoxinus neogaeus (Pisces: Cyprinidae) in

Nebraska. Can. J. Zool. 60:968-973.

Lacey, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, selection and population subdivision. Conservation Biology 1:143-157.

Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1983. Consistently high meristic counts in natural hybrids between brook trout and bull trout. Syst. Zool. 32: 369-376.

Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1984a. Superior developmental stability of enzyme heterozygotes in salmonid fishes. Amer. Nat. 124:540-551.

Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1985a. Developmental instability as an indicator of reduced genetic variation in hatchery trout. Trans. Amer. Fish. Soc. 114:230-235.

Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1985b. Developmental instability and high meristic counts in interspecific hybrids of salmonid fishes. Evolution 39:1318-1326.

Leary, R. F., F. W. Allendorf, and K.L. Knudsen. 1985c. Inheritance of meristic variation and the evolution of developmental stability in rainbow trout. Evolution 39:308-314.

Leary, R. F., F. W. Allendorf, K. L. Knudsen, and G. H. Thorgaard. 1985d. Heterozygosity and developmental stability in gynogenetic diploid and triploid rainbow trout. Heredity 54:219-225.

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

Leary, R. F., F. W. Allendorf, S. R. Phelps, and K. L. Knudsen. 1985e.

Fish. Aquat. Sci. 38:939-951.

Buth, D. G., and B. M. Burr. 1978. Isozyme variability in the cyprinid genes Campostoma. Copeia 1978:298-311.

Buth, D. G., C. B. Crabtree, R. D. Orton, and W. J. Rainboth. 1984. Genetic differentiation between the freshwater subspecies of Gasterosteus aculeatus in southern California. Biochem. Syst. Ecol. 12:423-432.

Buth, D. G., R. W. Murphy, and L. Ulmer. 1987. Population differentiation and introgressive hybridization of the flannelmouth sucker and of hatchery and native stocks of the razorback sucker. Trans. Amer. Fish. Soc. 116:103-110.

Campton, D. E. 1987. Natural hybridization and introgression in fishes: methods of detection and genetic interpretations. Pages 161-192 in N. Ryman and F. Utter, editors. Population Genetics and Fishery Management. Seattle: University of Washington Press.

Campton, D. E., and F. M. Utter. 1985. Natural hybridization between steelhead trout (Salmo gairdneri) and coastal cutthroat trout (Salmo clarki) in two Puget Sound streams. Can. J. Fish. Aquat. Sci. 42:110-119.

Campton, D. E., and F. M. Utter. 1987. Genetic structure of anadromous cutthroat trout (Salmo clarki clarki) populations in the Puget Sound area: Evidence for restricted gene flow. Can. J. Fish. Aquat. Sci. 44:573-582.

Chakraborty, R. 1980. Gene-diversity analysis in nested subdivided populations. Genetics 96:721-726.

Dobzhansky, Th. 1948. Genetics of natural populations. XVIII. Experiments on chromosomes of Drosophila pseudoobscura from different geographical

regions. Genetics 33:588-602.

Dobzhansky, Th. 1970. Genetics of the Evolutionary Process. New York: Columbia Univ. Press.

Ferguson, M. M., and R. G. Danzmann. 1987. Deviation from morphological intermediacy in interstrain hybrids of rainbow trout, Salmo gairdneri. Environmental Biol. Fishes 18:249-256.

Ferguson, M. M., R. G. Danzmann, and F. W. Allendorf. 1985a. Developmental divergence among hatchery strains of rainbow trout (Salmo gairdneri). II. Hybrids. Can. J. Genet. and Cytol. 27:298-307.

Ferguson, M. M., R. G. Danzmann, and F. W. Allendorf. 1985b. Absence of developmental incompatibility in hybrids between rainbow trout and two subspecies of cutthroat trout. Biochem. Genet. 23:557-570.

Ferguson, M. M., R. G. Danzmann, and F. W. Allendorf. In press. Developmental success of hybrids between two taxa of salmonid fishes with moderate structural gene divergence. Biochem. Genet.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford: University Press.

Frankham, R. 1980. The founder effect and response to artificial selection in Drosophila. Pages 87-90 in A. Robertson, editor. Selection Experiments in Laboratory and Domestic Animals. Farnham Royal, Commonwealth Agricultural Bureaux, Slough, U. K.

Gold, J. R. 1977. Systematics of western North American trout (Salmo), with notes on the redband trout of Sheepheaven Creek, California. Can. J. Zool. 55:1858-1873.

Gold, J. R., J. C. Avise, and G. A. E. Gall. 1977. Chromosome cytology in the cutthroat series Salmo clarki (Salmonidae). Cytologia 42:377-382.

Literature Cited

Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology 5:181-190.

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in M. E. Soule', editor. Conservation Biology: The Science of Scarcity and Diversity. Sunderland, Massachusetts: Sinauer Associates.

Allendorf, F. W., and S. R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Trans. Amer. Fish. Soc. 109:537-543.

Allendorf, F. W., and N. Ryman. 1987. Genetic management of hatchery stocks. Pages 141-160 in N. Ryman and F. Utter, editors. Genetics and Fishery Management. Seattle: University of Washington Press.

Allendorf, F. W., and G. H. Thorgaard. 1984. Polyploidy and the evolution of salmonid fishes. Pages 1-53 in B. J. Turner, editor. The Evolutionary Genetics of Fishes. New York: Plenum Press.

Avise, J. C. 1974. Systematic value of electrophoretic data. Syst. Zool. 23:465-481.

----------. 1986. Mitochondrial DNA and the evolutionary genetics of higher animals. Phil. Trans. R. Soc. Lond. B 312:325-342.

Avise, J. C., and F. J. Ayala. 1976. Genetic differentiation in speciose and depauperate phylads: evidence from the California minnows. Evolution 30:46-58.

Avise, J. C., E. Bermingham, L. G. Kessler, and N. C. Saunders. 1984. Characterization of mitochondrial DNA variability in a hybrid swarm between subspecies of bluegill sunfish (Lepomis macrochirus). Evolution

38:931-941.

Avise, J. C., and M. H. Smith. 1977. Gene frequency comparison between sunfish (Centrarchidae) populations at various stages of evolutionary divergence. Syst. Zool. 36:319-335.

Avise, J. C., and R. C. Vrijenhoek. 1987. Mode of inheritance and variation of mitochondrial DNA in hybridogenetic fishes of the genus Poeciliopsis. Molec. Biol. Evol. 4:514-525.

Ayala, F. J. 1965. Evolution of fitness in experimental populations of Drosophila serrata. Science 150:903-905.

Ayala, F. J. 1969. Evolution of fitness. V. Rate of evolution in irradiated populations of Drosophila. Proc. Nat. Acad. Sci. USA 63:790-793.

Ayala, F. J., and J. R. Powell. 1972. Allozymes as diagnostic characters of sibling species of Drosophila. Proc. Nat. Acad. Sci. USA 69:1094-1096.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Bd. Canada 29:539-571.

Behnke, R. J. 1979. Monograph of the native trouts of the genus Salmo of western North America. Unpublished report.

Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered trouts. U.S. Forest Service General Technical Report RM 28.

Bermingham, E., and J. C. Avise. 1986. Molecular zoogeography of freshwater fishes in the Southeastern United States. Genetics 113:939-965.

Busack, C. A. 1977. Genetic variation among populations of Paiute trout (Salmo clarki seleniris). M. S. Thesis, Univ. of California, Davis.

Busack, C. A., and G. A. E. Gall. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (Salmo clarki seleniris). Can. J.

Outbreeding depression can also result because coadapted gene complexes may depend on the interaction between specific gene loci. That is, the genes in an evolutionary lineage (population or species) have been selected to interact with each other within the internal genetic and biochemical environment. For example, Sage et al. (1986) have shown that mouse interspecific hybrids are more susceptible to parasites than either parental species. The concept of coadapted gene complexes was first used in 1948 to explain reduced fitness in hybrids between populations of the fruit fly Drosophila pseudoobscura (Dobzhansky 1948, 1970). However, experiments with Drosophila mercatorum indicate that this type of outbreeding depression may be only a temporary problem (Templeton et al. 1976). New coadapted gene complexes with fitnesses equal or superior to the parental strains quickly evolved through natural selection.

The phenotypic characteristics of hybrids described earlier in this paper suggest that outbreeding depression and coadapted gene interactions do occur in Salmo. Overall, hybrids do not perform as well as either parental type for a wide variety of phenotypic measures. Nevertheless, the widespread success of hybrid trout populations suggests that outbreeding depression is not a serious problem. The major danger of introgression is the homogenization of the many divergent evolutionary lineages and the loss of important and potentially valuable locally adapted populations.

ACKNOWLEDGMENTS

We dedicate this paper to George Holton on his retirement from a career of conservation with the MDFWP. We are indebted both to George Holton and Joe Huston of the MDFWP who have enthusiastically supported us in this work, even though bad news and some embarrassment were often their immediate reward. F. W. Allendorf was supported by grant BSR-8600108 from the National Science Foundation while this paper was prepared; R. F. Leary was supported by the MDFWP and the United States Fish and Wildlife Service. We are grateful to the following agencies for the collection of samples and financial support: Montana Department of Fish, Wildlife, and Parks; Idaho Department of Fish and Game; United States Fish and Wildlife Service; United States Forest Service; Bureau of Land Management; Greenback Cutthroat Trout Recovery Team, consisting of members from the United States Fish and Wildlife Service, Colorado Division of Wildlife, United States Forest Service, and the National Park Service; Confederated Salish and Kootenai Tribes of the Flathead Reservation; Pyramid Paiute Tribe; Parks Canada; British Columbia Ministry of Environment Fish and Wildlife Branch; British Columbia Conservation Foundation; the Nature Conservancy. We thank Mike Japhet of the Colorado Division of Wildlife for providing the timely samples of Rio Grande cutthroat trout, and Steve Forbes, Kathy Knudsen, Nils Ryman, Tony Echelle, Rick Williams, and Bob Behnke for their helpful comments and suggestions on this paper.

biology. Populations of 'trout' are not lost by introgression; trout remain in the rivers, streams, and lakes of the western United States. Furthermore, alleles are not lost directly through introgression. Rather, the native alleles are simply diluted by the stocking of trout from other sources. It has been suggested that natural selection will act to preserve those genetic types that are important for local adaptation so that the native type will reevolve in a reasonably short length of time. Perhaps, therefore, we should consider the position that the introduction of new genetic variation through widespread introgression with non-native fishes may actually be beneficial, especially from the perspective of those responsible for managing these populations as a recreational fisheries resource.

There are several compelling reasons why we should be concerned about the potential harmful effects of widespread introgression. The eventual outcome of widespread introgression and continued introduction of hatchery rainbow trout is the homogenization of western North American trout into a single taxon (Salmo ubiquiti?). Thus, we would exchange all of the diversity within and between many separate lineages, produced by millions of years of evolution, consisting of taxa capable of existing from the Arctic to the desert, for a single new mongrel species. This would be a great loss of biological diversity - and of recreational fisheries resources. Sport-fishing groups are active in many conservation programs to preserve local native fishes. The loss of these local native trout would reduce the quality of these resources for many persons.

One danger of homogenization is the loss of valuable locally adapted populations. This danger seems especially important because of the

tendency for salmonid species to evolve genetically discrete, ecologically specialized populations (reviewed by Behnke 1972). The loss of the Lahontan cutthroat trout native to Pyramid Lake is a spectacular example of the value of locally adapted populations. Evolution of these trout in a continuous lake environment for 50,000-100,000 years with an abundant prey species (tui chub, Gila bicolor) resulted in the world's largest cutthroat trout, up to 20 kg (Sigler et al. 1983). The cutthroat trout native to Pyramid Lake disappeared in the late 1930's primarily due to loss of spawning habitat.

Another danger of widespread hybridization is outbreeding depression. That is, hybrids between genetically differentiated populations often have reduced fitness (Templeton 1986). This reduction in fitness may occur either in the first generation hybrids or may be delayed until the backcross or later generations. Outbreeding depression is caused by the existence of coadapted genic or chromosomal complexes. For example, the production of gametes through meiosis usually requires two matched sets of chromosomes. If the two sets of chromosomes differ in number or structure, however, abnormal meiosis can produce gametes that will not produce viable progeny. Hybrids between populations of animal species that have chromosomal differences often have reduced fertility because of meiotic problems (Templeton 1986).

The available evidence indicates that hybrids between the chromosomally differentiated rainbow and cutthroat trout subspecies (Allendorf & Thorgaard 1984) do not have meiotic problems. The common existence in nature of hybrid swarms demonstrates that these hybrids do not have severely reduced fertility.

1986). Thus, allelic diversity of the enzymes detected with electrophoresis in Yellowstone cutthroat trout might essentially be conserved by ensuring the continued existence of a few populations.

Nevertheless, low genetic divergence among populations at isozyme loci does not indicate the absence of important genetic differences between populations. Some populations may be adapted to unusual local conditions, e.g., warmer or more saline water. These populations may possess genetic adaptations for existence under these circumstances that will not be indicated by allelic divergence at isozyme loci. Ensuring the continued existence of these potentially valuable populations should be a concern of conservation programs.

Introgression

Introgression is the most important factor responsible for the loss of native cutthroat trout populations. The presence of numerous introgressed populations throughout the range of cutthroat trout threatens the remaining native populations. If this condition persists, the only remaining native populations will be those isolated by dispersal barriers. This fragmentation into a number of small, isolated refuges will increase the chances of extinction (Wilcove et al. 1986, Quinn & Hastings 1987). Furthermore, the lack of gene flow among refuges will accelerate the loss of genetic variation by genetic drift.

Conservation of cutthroat trout, therefore, may sometimes require the destruction of introgressed populations. Poisons have often been used in such attempts (e.g. Rinne & Hanson 1981). This practice, however, is not without problems. Concentrations of poisons that are likely to extirpate a

trout population will also affect many other forms of aquatic life. In addition, many introgressed or non-native populations occur in remote areas or waters that are too large for poisoning to be effective.

The State of Montana has initiated a restoration policy for westslope cutthroat trout that includes extirpation of non-native populations (Joe Huston, MDFWP, personal communication). Populations in the South Fork of the Flathead River drainage that contain a substantial proportion of non-native genes may be poisoned when this is likely to be effective. After the poison has detoxified, westslope cutthroat trout from a hatchery population will be introduced periodically. These fish are expected to spawn among themselves and with any non-native trout that survived the poison. The continued introduction of hatchery fish should reduce the frequency of non-native genes. When poisoning is not practical, stocking is the sole means of restoration. The efficacy of this program depends on having hatchery fish capable of surviving and reproducing in the wild.

Although the above program may not eliminate all non-native genes from a population, it can reduce their frequency so that the result can be viewed as effective restoration. There is likely to be no universal criterion of when restoration has been achieved effectively. We suggest that a level of 1% or less foreign genes may suffice for two reasons. Levels of introgression this low are often difficult to detect conclusively. Furthermore, this amount of introgression is unlikely to alter the biological characteristics of the fishes from those of genetically pure westslope cutthroat trout.

The problem of introgression among western trout raises questions about what genetic resources we should be trying to preserve in conservation

CONSERVATION ISSUES

Subspecies Problem

The classification of such genetically diverged taxa into a single species, cutthroat trout, creates a problem in the conservation of these fishes. This classification implies that the subspecies are distinguishable only by minor and recently evolved genetic differences. Protein data, however, indicate that some groups of cutthroat trout have been separate evolutionary units for long intervals of time. The relatively ancient separation of cutthroat lineages is supported by other considerations. R. J. Behnke (personal communication) has estimated, on the basis of historical biogeographic considerations, that the westslope and Yellowstone cutthroat trout have been isolated for 1-2 million years. Also, the amount of differences in mtDNA molecules (Gyllensten and Wilson 1987) correspond to a divergence time of about one million years (Wilson et al. 1985). These subspecies also have diverged in many other characteristics (e.g., behavior, habitat preference, etc.). Thus, morphological evolution in cutthroat trout apparently has been very slow so that these subspecies remain morphologically similar, even after a long time of evolutionary independence.

We feel that taxonomic revision of cutthroat trout is warranted in order to portray accurately their evolutionary history. Furthermore, such reclassification would be especially helpful to those involved with the management and conservation of cutthroat trout. For example, we believe that the westslope cutthroat trout should be recognized as a distinct species. A taxonomic revision of cutthroat trout is beyond the purview of

this paper but we believe it is necessary in order to develop a sound conservation program for these fishes.

Local Populations

Conservation programs should be concerned with the conservation of alleles, rather than just allele frequencies. Allele frequencies are an ephemeral characteristic of populations that can be changed by genetic drift or natural selection. No specific allele frequency now or in the future should be the goal of a conservation program. However, loss of an allele represents a permanent decrease in genetic diversity. Once an allele is lost it can be recovered only by mutation, the probability of which is minuscule. The loss of alleles, therefore, permanently reduces the ability of populations to make adaptive responses to altered environmental conditions and can also reduce their resistance to disease (Allendorf 1986).

Allelic variation in the westslope cutthroat trout is composed largely of alleles that have a narrow geographic distribution, but occur at relatively high frequencies in local populations. Maintenance of the allelic diversity of this subspecies, therefore, requires the continued existence of many populations throughout its range. Limited data suggest that this conclusion is also true for Lahontan cutthroat trout.

The available data from Yellowstone cutthroat trout demonstrates relatively little allelic diversity between local populations. The alleles that occur at appreciable frequencies exist in practically all populations; the other alleles are rare everywhere. We do not feel that conservation biologists need to be concerned about preserving rare alleles. The loss of rare alleles is not likely to be harmful to a population (Hedrick et al.

By 1983, there was compelling evidence that loss of genetic variation in this hatchery population was having deleterious effects on a variety of phenotypic characters. An unusually high proportion of individuals in this year class had obvious morphological deformities, such as abnormal vertebral columns and missing fins. Individuals in this hatchery population also had an unusually high amount of asymmetry in the counts of five bilateral meristic characters compared to individuals from natural populations of westslope cutthroat trout, including Hungry Horse Creek (Leary et al. 1985a). The high proportion of deformed fish and levels of asymmetry are indicative of a reduction in the ability of individuals to develop precisely along genetically determined pathways.

This reduction in developmental stability was considered a consequence of the loss of genetic variation. Previous studies of salmonids revealed a negative association between heterozygosity at protein loci and asymmetry among individuals in populations (Leary et al. 1984a, 1985c). Highly inbred individuals also have unusually high levels of asymmetry that are comparable to that observed in the hatchery population (Leary et al. 1985d). Reduced developmental stability, poor fertility, and poor survival led the MDFWP to abandon this broodstock in 1986. They are now establishing a new broodstock with a procedure similar to the one described below.

A hatchery population of Yellowstone cutthroat trout was founded by the MDFWP from an unknown number of males and females collected from McBride Lake, Yellowstone National Park in 1969. Since then, gametes have been obtained periodically from individuals collected from McBride Lake. The progeny from these gametes have been raised at the hatchery and are mated with hatchery fish. This broodstock, therefore, has periodically received

infusions of genes from a wild population. Recent data indicate that this policy has effectively incorporated and maintained the genetic variability in the natural fish in this hatchery population.

We obtained samples (N=50) from the 1985 hatchery year-class and progeny from 11 female and 22 male fish collected from McBride Lake in 1985. The genotype of each fish was determined at 71 loci coding for 31 enzymes (details are available on request). The two samples have significant allele frequency differences at three of seven polymorphic loci (Table 7). The hatchery fish also appear to have a higher level of heterozygosity than the progeny from the wild fish. Although this difference is not statistically significant (Wilcoxon two-sample test; P=0.10), the allele frequency differences suggest it is biologically meaningful. In addition, fish from this hatchery stock have a low amount of developmental instability (Leary et al. 1984a, 1985a) and they have high fertility and survival in the hatchery (Thurston Dotson, MDFWP, personal communication).

These results demonstrate the value of maintaining genetic variation by founding a hatchery population from a large number of individuals and by periodically introducing genes from individuals collected from natural populations into the hatchery population. These actions will also reduce undesirable genetic changes (Allendorf & Ryman 1987) that may occur due to adaptation to domestic conditions. Lacey (1987) has considered in detail the genetics of managed populations and the importance of infusions of genes from natural populations.

substantially lower than that detected among populations of westslope cutthroat trout (Table 5).

Analysis of the population genetic structure of other salmonid species suggests that the differences in the amount of divergence among populations largely reflects different amounts of gene flow (Gyllensten 1985). Anadromous salmonids usually have relatively little genetic divergence among populations (Table 5). In contrast, more sedentary freshwater fishes generally exhibit substantial divergence among populations (Table 5). The simplest explanation for this dichotomy is that the high mobility of the former fishes increases gene flow among populations and hinders accumulation of genetic differences through natural selection and genetic drift (Gyllensten 1985).

Ryman (1983) has discussed the significance of the large divergence among local populations of brown trout (Salmo trutta) in Europe for fishery management and conservation biology. The westslope and Lahontan cutthroat trout have a genetic population structure that is similar to that of brown trout (Table 5). The Yellowstone cutthroat trout is exceptional as the only non-anadromous species in Table 5 that shows relatively little genetic divergence among local populations. These results are supported by Loudenslager and Gall (1980); they estimated that only 8% of the genetic variation in 10 Yellowstone cutthroat trout populations sampled from a broader geographic area than the populations in Table 5 was due to divergence among them.

HATCHERY POPULATIONS

Captive populations can play an integral role in conservation programs. These populations serve two major purposes. First, they can represent a captive source of some of the genetic variability in a taxon; i.e., they serve as a 'gene bank'. Captive populations also represent a readily accessible source of individuals for reestablishing extinct populations or for establishing new populations in suitable habitat within the taxon's natural range but unoccupied because of barriers to dispersal. Loss of genetic variation in hatchery populations can be a serious problem. Allendorf and Ryman (1987) have considered the genetic management of hatchery populations of salmonids and have reviewed the published results demonstrating examples of loss of genetic variation in hatchery populations.

A hatchery broodstock of westslope cutthroat trout was founded by the MDFWP from about 15 males and 15 females collected from a population in Hungry Horse Creek, Flathead County, Montana during June of 1965 and 1967. Electrophoretic analysis of the proteins encoded by 35 loci indicated that by 1976 the hatchery population contained substantially less genetic variation than fish from Hungry Horse Creek (Allendorf & Phelps 1980). Furthermore, significant heterogeneity in allele frequencies was observed among the 1971 to 1976 hatchery year-classes. Loss of variation and temporal instability of allele frequencies in this population were considered to result from two major factors: (1) founding the population from a small number of individuals, all of which probably were not reproductively successful, and (2) perpetuating the population from individuals that were mature during only a small proportion of the reproductive season.

(1985) found evidence of introgression from rainbow trout in 7 of 39 populations of cutthroat trout sampled in Utah. Introgressed populations of Paiute and coastal cutthroat trout with rainbow trout have also been described (Busack & Gall 1981, Campton & Utter 1985).

POPULATION GENETIC STRUCTURE OF SUBSPECIES

Until this point, we have taken a typological viewpoint of subspecies of cutthroat trout. That is, we have treated each subspecies as being genetically homogeneous. We now abandon this view and address the amount and pattern of genetic diversity within the westslope and Yellowstone cutthroat trout. The westslope cutthroat trout represents a situation of extreme genetic divergence among populations, while there appears to be little genetic divergence among Yellowstone cutthroat trout populations.

The population genetic structure of westslope cutthroat trout is based upon analysis of proteins encoded by 29 loci (see Leary et al. 1985e for procedures and loci) in samples obtained from 103 populations throughout most of its natural range. Sample locations are available on request. We analyzed the data using the hierarchical gene diversity analysis of Chakraborty (1980). The total amount of genetic diversity among samples ($H=0.0287$) is partitioned into the proportion due to allele frequency differences among 10 drainages (Table 5, $H=0.0048$, 16.7%), allele frequency differences among populations within drainages ($H=0.0045$, 15.7%), and genetic variation within local populations ($H=0.0194$, 67.6%). Thus, each local population contains only about two thirds of the genetic variation that exists in the taxon. This is a relatively high amount of genetic divergence among conspecific populations but is not unusual among

conspecific populations of salmonids inhabiting interior drainages (reviewed by Gyllensten 1985).

The pattern in which alleles are distributed among populations of westslope cutthroat trout reveals two interesting features. First, a large number of alleles (29, 43.9%) exist in all populations at high average frequency (i.e., greater than 0.95). These ubiquitously distributed alleles represent the common allele at all the loci examined. Secondly, a high proportion (37.8%) of the remaining alleles were detected in only one or two populations. Furthermore, a number of these geographically 'rare' alleles occur at a relatively high frequency within their respective local populations. Thus, high genetic divergence among westslope cutthroat trout is largely due to numerous alleles, often at high frequencies, with a narrow geographic distribution. Conservation of the genetic diversity in westslope cutthroat trout, therefore, requires ensuring the continued existence of many populations throughout its range.

Limited electrophoretic data indicate that the Yellowstone cutthroat trout in the Yellowstone River drainage has a markedly different population genetic structure than the westslope cutthroat trout. We detected evidence of genetic variation at only 5 of 46 protein loci (see Leary et al. 1987 for details) examined (Table 6). Genetic variation at 4 of the 5 polymorphic loci was restricted to a rare allele (<0.05) found in only one of the eight samples. Genetic variation at Aat-3,4 is present in all of the populations, and the allele frequencies are highly heterogeneous ($P<0.001$). Allele frequency differences among samples, however, account for only 3.7% of the total amount of genetic variation detected, the remainder is attributable to genetic variation within local populations. The former value is

Occurrence of Hybridization

We began a project approximately five years ago, in cooperation with Montana Department of Fish, Wildlife, and Parks (MDFWP), to assess the extent of hybridization in native populations of westslope cutthroat trout. Approximately one-half of the populations of westslope cutthroat trout in the state at that time were classified, on the basis of morphology, as being hybridized with either rainbow trout or Yellowstone cutthroat trout. We now have analyzed 46 enzyme loci from samples of over 125 populations of cutthroat trout in Montana.

Our results indicate that hybridized populations of westslope cutthroat trout are much more common than previously thought. Thirty-two out of 80 samples (40%) from populations classified as 'genetically pure' westslope cutthroat trout showed evidence of hybridization with either rainbow trout or Yellowstone cutthroat trout, or both of these fishes. All samples from streams classified as containing hybrid populations did show evidence of hybridization. Similar results from samples taken from Glacier National Park have been reported by Marnell et al. (1987).

An interesting and dangerous pattern has emerged from the analysis of samples from the South Fork of the Flathead River drainage. This region is considered to be one of the last remaining 'strongholds' of native westslope cutthroat trout in Montana (Hanzel 1959). Only 2 of 19 headwater lakes sampled contained pure populations of westslope cutthroat trout. Analysis of streams in this drainage indicates that hybridized populations in headwater lakes are 'leaking' into downstream populations. This movement and gene flow is often unidirectional because of barrier waterfalls. Thus,

the stream populations are expected to become genetically more and more similar to the lake populations through time.

The constant spread of non-native fishes from headwater lakes into downstream populations is not unique to this area. Many headwater lakes throughout the west did not contain native trout populations because of recent glaciation and barriers to upstream migration. Six headwater lakes in Glacier National Park that were previously barren of fish now have populations of apparently pure non-native Yellowstone cutthroat trout (Marnell et al. 1987). The Camas Creek drainage provides a clear example of the effects of these headwater populations. The two highest lakes (Evangeline and Camas) have populations of pure Yellowstone cutthroat trout. The next highest lake in the drainage (Arrow) had a hybridized population consisting of approximately 90% westslope genes and 10% Yellowstone cutthroat trout genes. The bottom lake in the drainage (Trout) contained a population of apparently pure westslope cutthroat trout.

Introgression also appears to be common in the native Yellowstone cutthroat trout of the Yellowstone River drainage. Sixteen samples were collected without prior information as to purity from Yellowstone River tributaries in Montana. Thus, these samples should be a reliable indicator of the proportion of hybridized populations in this drainage. Evidence of hybridization and introgression between the Yellowstone cutthroat and rainbow trout was detected in half of the samples.

These results suggest that the introduction of non-native fishes is likely to be responsible for the loss of many native populations of cutthroat trout throughout its range. This conclusion is supported by results with other cutthroat trout subspecies. For example, Martin et al.

cutthroat trout (Table 2; Figure 3). Thus, electrophoresis is not a reliable means of detecting interbreeding between these taxa. In contrast, we found two or more diagnostic loci between coastal cutthroat, Lahontan cutthroat, westslope cutthroat, and rainbow trout populations, as well as between all these fishes and the other five subspecies of cutthroat analyzed (Table 2). Thus, electrophoresis can be used to detect interbreeding between all of the subspecies of cutthroat trout we analyzed and rainbow trout, as well as between many pairs of cutthroat trout subspecies.

All individuals in samples obtained from genetically pure populations will possess genotypes of only that taxon at all diagnostic loci. In contrast, first generation hybrids will be heterozygous for alleles characteristic of both parental taxa at all diagnostic loci between them. Matings between parental types and hybrids will produce individuals that are homozygous at some diagnostic loci and heterozygous at others. The multiple locus genotype will be highly variable in mixed populations when the alleles characteristic of the parental taxa are randomly distributed among individuals. Table 3 shows the multiple locus genotypes of 15 individuals from such a hybrid swarm of westslope and Yellowstone cutthroat from Forest Lake, Montana (Gyllensten et al. 1985).

Analysis of mitochondrial DNA (mtDNA) has revealed a great deal of intra- and inter-specific variability in fishes (Avise 1986, Avise et al. 1984, Bermingham & Avise 1986, Gyllensten & Wilson 1987). MtDNA is inherited maternally, and thus provides information about the sexes of the parental types involved in hybrid matings. For example, if only males of a taxon participate in hybrid matings, then the mtDNA of this taxon will not be present in the hybridized population. However, if both sexes of both

taxa make equal genetic contributions, then the proportion of mtDNA from each parental taxon is expected to be similar to the proportional genetic contribution estimated from diagnostic nuclear loci. The limited data available from salmonids is consistent with the latter situation in introgressed populations (Gyllensten et al. 1985).

Certain properties of mtDNA diminish its value as a sole criterion to determine the genetic status of individuals or populations. An individual generally contains only one type of mtDNA. Thus, it is not possible to distinguish hybrids from the parental types (Avise et al. 1984, Gyllensten et al. 1985, Avise & Vrijenhoek 1987). Furthermore, if only males of a taxon participate in hybrid matings then the mtDNA of this taxon will be absent from hybrid populations. The effective population size of mtDNA is smaller than nuclear DNA; thus mtDNA frequencies will be more strongly affected by genetic drift than nuclear gene frequencies. When the proportional contribution of a taxon to a hybrid swarm is small, the less frequent mtDNA may be lost by genetic drift. Furthermore, since there is no recombination between mtDNA molecules, the whole mtDNA genome is in terms of identification only a single gene; in contrast, there are many unlinked nuclear genes that can be used for identification purposes.

The analysis of proteins encoded by multiple diagnostic nuclear loci, therefore, is the most sensitive and reliable method available to identify genetically pure populations of cutthroat trout taxa that have diagnostic differences. Busack and Gall (1981) came to a similar conclusion in their study of Paiute cutthroat trout. Studies with other groups of fish also support this conclusion (Whitmore 1983, Buth et al. 1987, Joswiak et al. 1982).

do not differ between them (Leary et al. 1983, 1985b; Ferguson & Danzmann 1987). Interspecific hybrids of other fishes have also been found not to be morphologically intermediate to the parental taxa (Neff & Smith 1979, Joswiak et al. 1982, Campton 1987). Lack of meristic intermediacy results from developmental genetic incompatibility between the parental genomes (see discussion in Ferguson & Danzmann 1987).

Other developmental and morphological characteristics demonstrate similar results. For example, hybrids between hatchery strains of rainbow trout tend to have a slower developmental rate than the parental strains (Ferguson et al. 1985a). Hybrids between rainbow trout and three different subspecies of cutthroat trout all have decreased developmental stability (Leary et al. 1985b). Hybrids between westslope and Yellowstone cutthroat trout also have reduced developmental stability (Ferguson et al. in press).

We produced experimental hybrids between rainbow trout and westslope cutthroat trout to test for differences in growth rate. The hybrids were produced by crossing hatchery strains of both parental taxa at the Creston National Fish Hatchery of the United States Fish and Wildlife Service in 1982 and 1983. The experiment was done in two parts because there was no overlap in time of spawning between females from the two strains. On 22 March 1983, 20 westslope cutthroat trout males and rainbow trout (24 females and 31 males) were mated together by first pooling together approximately equal numbers of gametes. The reciprocal matings were done on 14 May 1982, with 24 rainbow trout males and 24 westslope cutthroat trout of both sexes. Both hybrids had slower growth rates than the parental taxa under these hatchery conditions (Table 4). In contrast, Ferguson et al. (in press)

report some evidence for increased growth in westslope-Yellowstone cutthroat trout hybrids.

Methods of Detection

Historically, detection of hybridization and introgression in salmonid fishes has relied upon morphological characters. There are two fundamental problems with this approach. First, these comparisons often assume that hybrid individuals will be morphologically intermediate to the parental types. We have already discussed experimental results that show that this is not a good assumption.

Secondly, a small genetic contribution of one taxon to a mixed population or hybrid swarm may not be morphologically detectable. For instance, the presence of less than 10% genes from rainbow trout in introgressed populations with westslope cutthroat does not detectably alter the counts of meristic characters from distributions characteristic of pure westslope cutthroat trout (Leary et al. 1984b). Thus, the reliance on morphological characters can seriously underestimate the extent of hybridization and introgression between native and introduced salmonid fishes. This can provide misleading information about the genetic status of individuals and populations.

The presence of fixed allelic differences at several loci between taxa provides a means of identifying samples and of detecting interbreeding. Because of this attribute, such loci are commonly referred to as diagnostic loci (Ayala & Powell 1972). We did not detect any diagnostic loci among the Colorado River, Snake River, greenback, and Yellowstone cutthroat trout; we found only one diagnostic locus between these subspecies and Rio Grande

These data present a discordant view of genetic divergence among cutthroat trout subspecies. Some subspecies show little or no evidence of genetic divergence at isozyme loci and are well within the range of genetic divergence seen between geographically continuous conspecific populations. Similarly, Busack (1977) found that the Paiute is allozymically identical to the Lahontan cutthroat trout, and Loudenslager and Gall (1980) found that the Bonneville is very similar to the Yellowstone cutthroat trout. On the other hand, the amount of genetic divergence between westslope cutthroat trout and the other subspecies far surpasses that reported for other conspecific groups of fish. Coastal and Lahontan cutthroat trout also show extreme genetic divergence from the other subspecies.

The data from 46 allozyme loci suggest that cutthroat trout may be polyphyletic (Figure 2). However, morphological, karyotypic, and mtDNA data all suggest that the cutthroat trout subspecies are more similar to each other than they are to rainbow trout (Gold 1977, Leary et al. 1984b, Gold et al. 1977, Loudenslager & Thorgaard 1979, Thorgaard 1983, Gyllensten & Wilson 1987). The conventional view of the evolutionary relationship of these taxa is that cutthroat trout subspecies are members of a single phylogenetic divergence from rainbow trout.

The discordance in patterns of similarity indicates that evolutionary divergence of the protein loci and these other attributes have proceeded at different rates among these fishes. There are several hypotheses that can account for this difference. For example, we have suggested that secondary contact between the rainbow trout and some cutthroat trout subspecies could have resulted in temporary periods of limited introgression in the past

(Leary et al. 1987). This and other possibilities are considered in detail by Leary et al. (1987).

INTERBREEDING BETWEEN TAXA

Natural hybridization is much more common among freshwater fishes than in other vertebrates (Hubbs 1955, Campton 1987). Hybridization is more likely to occur between fish taxa for a variety of reasons, e.g., external fertilization, weak ethological isolating mechanisms, and competition for limited spawning habitat (Campton 1987). In addition, hybrids between distantly related fish species are sometimes viable, suggesting that fishes have less severe developmental incompatibilities than other vertebrate species with comparable levels of genetic divergence (Thorgaard & Allendorf 1987). This appears to be especially true for salmonids in which hybrids appear to be developmentally more compatible than other fishes and hybrids between distantly related taxa are often fertile (Ferguson et al. 1985b). These authors have suggested that this may result from the polyploid ancestry of salmonid fishes (Allendorf & Thorgaard 1984).

Phenotypic Characteristics of Hybrids

We are not aware of any comprehensive investigations of natural populations that compare hybridized and native populations of cutthroat trout. Most available information comes from experiments performed in hatcheries, and generally suggests that hybrids have lower fitness than the parental taxa.

Salmonid hybrids often have meristic counts identical to the parental type with the higher count or higher than the parentals for characters that

We used two approaches to assess electrophoretic divergence among taxa: Nei's measure of standard genetic distance (Nei 1975) and principal components analysis of the arcsine transformation of the square root of allele frequencies. Genetic distance estimates have heuristic value because they are available between populations of various taxonomic rank for a diversity of fishes. Comparison of our estimates with others allows us to make qualitative judgments about the amount of divergence observed among subspecies of cutthroat trout. Combining all allele frequency information into a single distance metric (i.e., Nei's genetic distance) is valuable in depicting similarities among taxa. Nevertheless, collapsing this information into a single dimension causes the loss of information and may oversimplify patterns of similarity. Principal components analysis provides a powerful means of pictorially representing patterns of allele frequency variation among taxa in multivariate space.

A highly variable pattern of genetic divergence exists among the seven subspecies (Table 2). Very little genetic divergence exists among Colorado, Snake River, greenback, and Yellowstone cutthroat trout. Nei's genetic distance between these subspecies are typical of those reported for conspecific populations in a diversity of freshwater and anadromous fishes (Avise 1974, Avise & Smith 1977, Buth & Burr 1978, Loudenslager & Gall 1980, Buth et al. 1984). In contrast, substantial biochemical genetic divergence exists between coastal, Lahontan, and westslope cutthroat trout and between these fishes and the other four subspecies. These genetic distances are truly exceptional for conspecific populations; they are similar to or larger than values observed between many species of fish (Johnson 1975, Avise & Ayala 1976, Buth & Burr 1978, Phelps & Allendorf 1983, Yates et al. 1984).

Surprisingly, the coastal, Lahontan, and westslope cutthroat trout are as similar or more similar to the rainbow trout than they are to the other subspecies. This pattern of genetic divergence is summarized in Figure 2.

Principal components analysis provides a concordant view of genetic divergence among these taxa. The first principal component, which accounts for 50% of the variance in allele frequencies, separates the cutthroat trout subspecies and rainbow trout into three groups: Colorado, Snake River, greenback, and Yellowstone cutthroat trout; coastal and Lahontan cutthroat trout; westslope cutthroat and rainbow trout (Figure 3). The second principal component, which accounts for an additional 25% of the variation, separates the westslope cutthroat from the rainbow trout and increases the separation of the coastal, Lahontan, and westslope cutthroat trout from each other and the other four subspecies (Figure 3). The coastal, Lahontan, and westslope cutthroat trout are all genetically as similar or more similar to rainbow trout than they are to the other four subspecies analyzed, which are all genetically very similar to each other.

We obtained 26 Rio Grande cutthroat trout from two samples from the Rio Grande River drainage after the first version of this manuscript was submitted. These fish were examined for the 46 allozyme loci analyzed in rainbow trout and other cutthroat trout subspecies. We have not reanalyzed the data with these samples included. However, a comparison of diagnostic loci indicates that the Rio Grande cutthroat trout is similar to the Yellowstone group of subspecies, but it is distinct from the Yellowstone, Snake River, greenback, and Colorado cutthroat trout at one allozyme locus (Me3) and nearly so at another (Gpi3) (Table 2).

virginalis
Me 3
Gpi 3

CUTTHROAT TROUT

> "There is no other group of fishes which offers so many difficulties to the ichthyologist, with regard to the distinction of the species, as well as to certain points in their life history, as this genus" (page 484, Jordan & Evermann 1896).

We believe that current workers would not disagree with this judgement about western trout of the genus Salmo in North America. The cutthroat trout is a polytypic species with a wide geographic range that includes the coastal and interior waters of most of the western United States and Canada, from Alaska to the Pecos River of New Mexico (Fig. 1). Despite over a century of intensive systematic investigation, the amount and distribution of genetic diversity among the subspecies remains poorly understood. This confusion largely arises from extreme genetic, morphological, and ecological variation within and among subspecies.

At least 16 subspecies of cutthroat trout have been recognized in the recent literature (Behnke 1979, Johnson 1987). Eight of these are 'major' subspecies that are native to large geographic regions (Figure 1 and Table 1). Another eight 'minor' subspecies are either undescribed, are native to a very small geographic area (e.g., a single lake), or both (Table 1). It is becoming increasingly important to obtain a reliable understanding of the amount of genetic divergence that exists within and among the subspecies of cutthroat trout. Many of the subspecies are threatened by human alteration of their habitat and by the human introduction of brook trout (Salvelinus

fontinalis), rainbow trout (Salmo gairdneri), and subspecies of cutthroat trout into waters outside their native range (Behnke 1972, Behnke & Zarn 1976). Eleven subspecies currently have protected legal status in one or more states, and two minor subspecies apparently are extinct (Table 1).

The greatest danger to the trout of the American west is the introduction of non-native species. Introduced taxa often have serious harmful effects on native taxa through competition or the introduction of pathogenic agents. In cutthroat trout, however, the main impact of introductions has been interbreeding between native and introduced fishes (Busack & Gall 1981, Leary et al. 1984b, Campton & Utter 1985, Gyllensten et al. 1985, Martin et al. 1985). Hybrid progeny from these matings are often fertile and capable of interbreeding with each other and the parental taxa. This situation destroys the genetic integrity of native populations and results in introgressed populations or hybrid swarms. That is, populations in which genes from the parental types are randomly distributed among individuals so that no individual is likely to be a 'genetically pure' representative of either parental taxon.

GENETIC DIVERGENCE AMONG SUBSPECIES

We have used allozymes to obtain estimates of genetic divergence among seven cutthroat trout subspecies and rainbow trout. We used horizontal starch gel electrophoresis to assay genetic variation at 46 loci encoding for proteins present in muscle, liver, or eye tissue. Sample locations, sample sizes, loci assayed, and allele frequencies are given by Leary et al. (1987).

INTRODUCTION

The primary genetic goal of a conservation program is to ensure the maintenance of existing genetic variation. This genetic variation is the result of some three billion years of evolution and represents the evolutionary legacy of a species. More importantly, loss of genetic variation has a variety of harmful effects on characteristics of individuals that are important to the continued existence of a species: growth, survival, fertility, developmental rate, and the ability of individuals to develop properly (reviewed by Mitton & Grant 1984, Allendorf & Leary 1986, Palmer & Strobeck 1986, Zouros & Foltz 1987). Furthermore, the loss of variation is expected to reduce the ability of populations to adapt to changing environmental conditions and to increase their susceptibility to epizootics (Fisher 1930; Ayala 1965, 1969; Frankham 1980; O'Brien et al. 1985). Thus, the loss of genetic variation is generally expected to increase the probability of extinction.

The total amount of genetic variation within a species usually has a hierarchical geographic structure that commonly is referred to as its population genetic structure. For example, a certain proportion of the total genetic variation in a species may be attributable to genetic differences among populations inhabiting particular regions, among populations within regions, and finally within local populations. The distribution of genetic variation among these levels is the result of long and complex interaction among four evolutionary forces; mutation, natural selection, genetic drift, and migration (i. e., exchange of genes between geographical areas).

The relative importance of these evolutionary factors is likely to differ among species and, therefore, the population genetic structure may be quite different, even among closely related species. An understanding of the population genetic structure of a species will aid in formulating a genetically rational conservation program. For example, when substantial divergence exists among geographic groups of populations, maintenance of genetic diversity requires continued existence of populations in each region. This is especially true when alleles are restricted to particular regions but are common where they occur. In contrast, when little genetic divergence exists between regions and most alleles are ubiquitously distributed throughout the range of the species, then a conservation program should place less emphasis on geographical considerations alone.

In this paper, we provide an overview of current conservation genetic efforts with a polytypic species, the cutthroat trout Salmo clarki. This species presents some unusual problems to conservation biologists. The first problem is the enigmatic pattern of genetic divergence among some 15 or so recognized subspecies. Hybridization and introgression resulting from introductions by humans of cutthroat trout subspecies and other trout species outside of their native range presents a second unusual problem. Finally, the role of hatcheries in providing fish for recreation and to reestablish native cutthroat trout populations also creates some unusual problems and challenges. Reintroduction of animals raised in captivity is becoming increasingly important in many conservation projects. The long history of fish hatcheries and introductions provide useful experience for the development of such programs with other animals.

ABSTRACT: The cutthroat trout (Salmo clarki) presents a series of unusual and difficult problems in conservation biology. As many as 16 subspecies have been recognized in the recent literature. The genetic distance between subspecies based upon 46 enzyme loci ranges from that usually seen between congeneric species to virtual genetic identity. Subspecies from the western portion of the range of the cutthroat trout are genetically more similar to rainbow trout (Salmo gairdneri) than they are to the other subspecies of cutthroat trout. In addition, much of the genetic variation within the westslope cutthroat trout (S. c. lewisi) results from alleles that are found in only one or two local populations, but are often at high frequencies in those populations. Thus, preserving the genetic variation in westslope cutthroat trout entails the preservation of as many local populations as possible.

Captive populations of cutthroat trout present a series of opportunities and genetic problems. A number of management agencies are using captive populations to supplement and reestablish natural populations. Basic genetic principles must be understood and followed in the establishment and maintenance of captive populations. We describe examples of unsuccessful and successful efforts by management agencies to develop captive populations.

The greatest danger to the conservation of the cutthroat trout is introgressive hybridization among subspecies and with rainbow trout. Several factors make salmonid fishes especially susceptible to problems associated with introgressive hybridization. We conclude that biochemical analysis provides a more reliable and informative means of detecting interbreeding than morphological characters. Interbreeding between westslope and Yellowstone cutthroat trout and non-native Salmo appears to be common and widespread throughout the natural range of these subspecies.

9 February 1988
Revised

Conservation Biology (in press)

CONSERVATION AND DISTRIBUTION OF GENETIC VARIATION IN A POLYTYPIC SPECIES, THE CUTTHROAT TROUT

Fred W. Allendorf

and

Robb F. Leary

Department of Zoology
University of Montana
Missoula, MT 59812

CONTENTS

Thanks,

Fred

R.B.

Transactions of the American Fisheries Society 109:537–543, 1980

Loss of Genetic Variation in a Hatchery Stock of Cutthroat Trout

FRED W. ALLENDORF AND STEVAN R. PHELPS

Department of Zoology, University of Montana
Missoula, Montana 59812

Abstract

We have detected significant reduction in genetic variation at isozyme loci in a hatchery stock of west-slope cutthroat trout (*Salmo clarki*) in comparison to the wild stock from which it was derived 14 years earlier. This conclusion is supported by (1) a 57% reduction in the proportion of polymorphic loci, (2) a 29% reduction in the average number of alleles per locus, (3) a 21% reduction in the average heterozygosity per individual, and (4) significant changes in allelic frequencies between age-classes. This loss of variation is attributed to both a limited number of founders of the hatchery stock and the effects of genetic drift in the maintenance of the hatchery stock.

Genetic variability is the primary biological resource in the successful artificial propagation of any species. Fishery biologists have long been aware of the importance of genetic variability in the maintenance of hatchery populations. Only recently, however, has this problem been approached experimentally in the culture of salmonid fishes. Two fundamentally different but complementary approaches have been used. First, is the classical approach of quantitative genetics, which is to partition the phenotypic variability present for traits of interest into genetic and environmental components. In this way, the amount and type of genetic variability present for individual traits can be estimated in order to predict the expected phenotypic improvement to be realized from certain selection schemes. These estimates are specific to a particular trait in a particular set of experimental conditions.

The second approach is to examine genetic variation at a large number of individual genetic loci that are identified by their enzymatic gene products. Variation at these loci is not reflected in any obvious phenotypic effect, except for banding patterns on electrophoretic gels. This information can be used to estimate the relative amount of total genetic variability in a particular stock. The strength of this second approach is that an estimate of genetic variability can be quickly obtained for comparison with other stocks, or even species (Allendorf and Utter 1979).

In the present paper, we use electrophoretic examination of 17 enzymes coded by 35 loci to quantify the loss of genetic variability in a hatchery population of west-slope cutthroat trout (*Salmo clarki*).

History of the Brood Stock

This brood stock was derived from two separate samples from wild west-slope cutthroat trout from Hungry Horse Creek, Flathead County, Montana. These fish are thought to represent one of the few remaining "pure" populations of west-slope cutthroat trout in Montana (George Holton, Montana Department of Fish, Wildlife, and Parks [MDFWP], personal communication). The parental fish were trapnetted during the spring spawning run in June 1965 and 1967. Gametes from approximately 15 males and 15 females were mated in the field each year and brought to the Jocko River State Trout Hatchery to hatch and be raised. Thus, a total of 60 fish are the basis of the present brood stock.

Initial maturation of males and females is 2 and 3 years of age respectively. At the present time, each individual contributes to the brood stock only at the time of initial maturation. In earlier years, however, some individuals may have contributed offspring in more than 1 year. Spawn is taken twice, 1 week apart, in the middle of the spawning season to maintain the brood stock.

Methods

Six year classes (1971–1976) of the west-slope cutthroat trout brood stock were collected from the Jocko River State Trout Hatchery of the

TABLE 1.—*Enzymes and loci examined from cutthroat trout.*

Enzyme	Enzyme Council number	Abbreviation	Loci
Aspartate aminotransferase	2.6.1.1	AAT	Aat-1,2,3
Alcohol dehydrogenase	1.1.1.1	ADH	Adh
α-glycerophosphate dehydrogenase	1.1.1.8	AGP	Agp-1,2
Creatine kinase	2.7.3.2	CK	Ck-1,2
Diaphorase	1.6.4.3	DIA	Dia
Glutamate dehydrogenase	1.4.1.2	GDH	Gdh
β-glucoronidase	3.2.1.31	GUS	Gus
Isocitrate dehydrogenase	1.1.1.42	IDH	Idh-1,2,3,4
Lactate dehydrogenase	1.1.1.27	LDH	Ldh-1,2,3,4,5
Malate dehydrogenase	1.1.1.37	MDH	Mdh-1,2,3,4
Malic enzyme	1.1.1.40	ME	Me-1,2
Phosphoglucose isomerase	5.3.1.9	PGI	Pgi-1,2,3
Phosphoglucomutase	2.7.5.1	PGM	Pgm-1,2
Phosphomannose isomerase	5.3.1.8	PMI	Pmi
6-phosphogluconate dehydrogenase	1.1.1.44	6PGDH	6Pgdh
Sorbitol dehydrogenase	1.1.1.14	SDH	Sdh
Superoxide dismutase	1.15.1.1	SOD	Sod

MDFWP in May 1977. The 1971–1973 year classes were pooled together for analysis because of the small number of older fish available. Juvenile west-slope cutthroat trout from Hungry Horse Creek were collected by electroshocking in August 1977.

Electrophoretic analysis of skeletal muscle, liver, and eye extracts followed the methods described in Allendorf et al. (1977). The nomenclature used to describe the gene loci and the allele variants encoding the enzymes surveyed follows the system proposed by Allendorf and Utter (1979). A capitalized abbreviation is chosen to represent each enzyme (Table 1). That abbreviation with only the first letter capitalized represents the locus coding for that enzyme. When multiple loci code for an enzyme, a hyphenated numeral is included to represent the individual loci, with the least anodal mobility designated as 1. The allelic variants at a specific locus are designated according to their relative mobility. The migration distance of the most common isozyme is assigned a mobility of 100. Thus, an allele of the most cathodic locus of the LDH enzyme migrating one-half as far as the common allele would be designated as Ldh-1(*50*).

Results

Electrophoresis

Seventeen enzymes coded by 35 loci were resolved clearly in all samples (see Table 1 for enzymes, abbreviations, and locus designations). Eight loci were polymorphic. All of these variants have previously been shown to segregate as simple Mendelian characters in either the west-slope cutthroat trout or the closely related rainbow trout (*Salmo gairdneri*) (Morrison 1970; Allendorf and Utter 1973, 1976; Allendorf 1975). Six of the eight variable loci produce simple codominant phenotypes from which the genotypes can be individually identified directly from a gel.

The genotypes resulting in variation seen at the duplicated Idh-3 and Idh-4 loci in liver extracts cannot be individually identified from phenotypes. The same three electrophoretically distinguishable alleles appear to be present at both loci. Previous studies with rainbow trout, having the same polymorphic system of liver IDH, have shown this variability to have a simple genetic basis (Allendorf and Utter 1973; Ropers et al. 1973; Reinitz 1977). Each individual carries four gene doses resulting from the two loci. The number of doses of a particular allele possessed by an individual cannot be reliably scored from gels. The Idh-3,4(*86*) allele was present in all individuals examined (Table 2). Thus, we could only distinguish the four phenotypes resulting from the presence or absence of the other two alleles: (*86*); (*86, 43*); (*86, 100*); and (*86, 43, 100*). It is impossible to accurately estimate allelic frequencies at the two individual loci with this system of genotypes and phenotypes. An estimate of allelic frequencies for Idh-3,4 together can be made with the generalized gene counting method of Ceppel-

IDENTIFICATION OF INTRASPECIFIC DIVERSITY IN CUTTHROAT TROUT: FOR WHAT PURPOSE?

Robert J. Behnke
Professor, Fishery Biology
Department of Fishery and Wildlife Biology
Colorado State University

I recognize 14 subspecies of cutthroat trout; they represent a classic polytypic species. A basic goal of any fisheries program should be the preservation of indigenous biodiversity. To achieve this goal by concentrating on the preservation of a recognized taxon, for example, a subspecies of cutthroat trout native to a state, without understanding the diversity contained within the taxon, can be a serious mistake because it may allow some of the most valuable part of this diversity to be lost. This is due to the fact that life history attributes most significant to fisheries management are not associated with taxonomic recognition. Evolution of local populations during the past several thousand years, exposed to different selective factors concerning predator-prey relationships, competitive interactions, parasites and disease, flow and temperature regimes, lacustrine specializations, etc. have resulted in a genetic basis for different life history strategies. Some of these life history strategies such as age at maturity, maximum life span, feeding specializations, temperature tolerances, etc. can be of great value for fisheries management. Because they have evolved relatively rapidly, it is not likely that distinct populations or races within a subspecies can be identified by morphological, karyological or electrophoretic characters. Thus, by preserving only token representatives of pure populations of a subspecies, much may be overlooked and lost. Many examples can be cited to illustrate this point. The cutthroat trout native to Pyramid Lake, Nevada is part of the subspecies, Salmo clarki henshawi. The Pyramid Lake population, however, was the only population of henshawi that continued to evolve in a large lake environment, after the final desiccation of Lake Lahontan about 8000 years ago, where it could continue to perfect its predatory feeding on Lahontan tui chub. The genetic basis of the special life history adaptations of the Pyramid Lake trout became apparent after the original population was lost. After stocking millions of trout from other races of henshawi into Pyramid Lake for more than 30 years, no fish has attained more than half the maximum size of the original race (Behnke 1986).

In 1938, U.S. Fish and Wildlife Service biologists observed and recorded the demise of the original Pyramid Lake trout (Sumner 1940). Not a word was expressed concerning the possibility that the genotype of this, the world's largest and about to become extinct, population of cutthroat trout, might possess some unique, valuable attribute that could prove useful in the future. The prevailing opinion at that time was likely to be that the subspecies of Lahontan cutthroat trout (or the cutthroat trout species as a whole) was not extinct so why worry? Like interchangeable parts, other populations of the subspecies could be obtained for stocking Pyramid Lake and they would duplicate the performance of the native population.

I could also quote from a 1953 unpublished USFWS report concerning the trout of Crescent Lake, Washington. Crescent Lake has a native population of coastal rainbow trout which specialized to feed on kokanee and attain the largest size of any lacustrine population of coastal rainbow. The 1953 report discussed the difficulties of attempting to propagate the native trout in a hatchery and concluded that it would be best to forget about trying to maintain the native trout and to stock the lake heavily with "a good strain of hatchery rainbow."

Fortunately, the native rainbow trout of Crescent Lake maintained itself by limited natural reproduction. During a fishery study on Crescent Lake, 668,000 fin-clipped hatchery rainbows were stocked from 1967 to 1971. Creel surveys showed virtually no survival after the first year and no marked trout were caught exceeding three pounds in weight. During this same period, the small population of native trout was annually contributing 10-15 pound fish to the fishery (Behnke 1984). The Crescent Lake rainbow was originally described as a subspecies, Salmo gairdneri beardslei. Later, when no "identifying" characters could be found to differentiate beardslei from S. gairdneri irideus, the "Beardslee" rainbow was considered a synonym of the coastal rainbow trout. This is certainly a correct procedure from a strictly taxonomic point of view, but taxonomic synonymy does not mean genetic synonymy--and this significant difference must be recognized in fisheries management. The 1953 USFWS report on Crescent Lake reflected a contemporary (and, unfortunately, still current) view that confused taxonomic identity with genetic identity.

The basis for this confusion began in the 1930's when several papers were published, demonstrating that some "identifying" characters used in taxonomy such as number of scales and vertebrae could be modified by the environment. From this, an unwarranted inductive leap was made to assume that not only taxonomic differences, but also life history differences were predominantly under environmental, not hereditary, control. Thus, if nurture, not nature, was the major determinant for growth and survival of trout or salmon in interaction with different biotic and abiotic components in any environment then fisheries management could be simplified by developing a program using interchangeable parts--any member of a taxon can duplicate all the attributes of any other member. How wrong and how costly this belief system can be has been amply demonstrated by many years of empirical evidence derived from attempts to maintain anadromous runs of salmon and steelhead trout by the propagation and stocking of non-native races (see the stock concept volume of the Canadian Journal of Fisheries and Aquatic Sciences 1981, volume 38 number 12; Ricker 1972; Ryman 1981; and Ryman and Utter 1987).

A test of a hypothesis concerning nature vs. nurture as determinants of performance and its significance to fisheries management can be performed in Utah using native cutthroat trout. The cutthroat trout native to the Bonneville basin is recognized as S. c. utah. It's evolutionary separation from Yellowstone cutthroat, S. c. bouvieri, is relatively recent in terms of geologic time (about 30,000 years) and the quantified genetic similarity between utah and bouvieri is virtually identical. This similarity has led to

a proposal that utah and bouvieri should be regarded as a single subspecies (Loudenslager and Gall 1980).

During the pluvial period when Lake Bonneville filled the basin and after its desiccation, different populations of bouvieri and utah were subjected to very different selective pressures which determined the acquisition of different life history strategies.

Although S. c. utah is indeed extremely closely related to S. c. bouvieri, three distinct groups of utah can be distinguished by morphological differences--the Snake Valley form of the western border of the basin, the Bear River drainage form and the main Bonneville basin form. The morphological differentiation between the three forms of S. c. utah denotes some genetic differentiation, but life history differences determining success in different environments differ greatly. There is no known example where the Snake Valley or main Bonneville forms have continued to coexist with non-native trouts. These forms are completely vulnerable to replacement by brook, brown or rainbow trout. The Bear River form of utah, however, not only coexists with, but dominates over non-native trouts in many parts of the Bear River drainage (Behnke 1981). Slight genetic differences between the three forms of Bonneville cutthroat trout determine very different responses to interactions with non-native trouts.

The Bear River drainage form of utah native to Bear Lake has evolved for a long time in a unique lacustrine environment and with a unique fish fauna. If what has been discussed concerning the adaptive advantages expected of a native population or race in its native environment is true, then it can be predicted that S. c. utah native to Bear Lake will have higher survival in Bear Lake than will any other population of utah or bouvieri. This hypothesis can be tested by stocking Bear Lake with progeny derived from the cutthroat native to the lake and with progeny from other forms of Bonneville and Yellowstone cutthroat trout. I would confidently predict a greater success of the native genotype, unless major changes (new selective pressures) have occurred in the environment. Be aware, however, that the Bear Lake cutthroat possesses no unique "identifying" characters. It's genetic differentiation is manifested in subtle life history distinctions such as feeding, growth, survival, age at maturity, etc.

Final Comments

The point of emphasis is that often the most significant traits from fisheries management viewpoint have been evolved by local populations in relatively recent geological times, and therefore may lack "identifying" characters. A program to preserve native trouts which concentrates on "identifying" characters may not be adequate to protect biodiversity.

In general, the amount of diagnostic characters available to identify different taxa is related to the length of evolutionary separation of the taxa. For example, the evolutionary lines leading to the "major" subspecies of cutthroat trout--coastal cutthroat, S. c. clarki, westslope cutthroat, S.

c. lewisi, and "Yellowstone" cutthroat, S. c. bouvieri, have probably been separated from a common ancestor for a million years or more. Clear-cut diagnostic or identifying characters occur between these three subspecies in their chromosomes, proteins and morphology. In fact, the electrophoretic protein difference between westslope and Yellowstone cutthroat trout is greater than it is between westslope cutthroat and rainbow trout.

Subspecies derived in recent geological times from the Yellowstone cutthroat, such as the Bonneville cutthroat, the fine-spotted Snake River cutthroat, Colorado River cutthroat, greenback cutthroat, and Rio Grande cutthroat, may lack clear-cut identifying characters, except for differences in spotting and coloration. It is obvious that all subspecies of cutthroat trout are not equal in regards to time of evolutionary origins. This does not mean that more recently evolved subspecies are less "valid" if no "genetic" differences can be quantified. The fine-spotted Snake River cutthroat cannot be genetically distinguished from Yellowstone cutthroat and the Pauite cutthroat (S. c. seleniris) cannot be genetically separated from Lahontan cutthroat expect by observation of spotting patterns (which can be accomplished with accuracy by a young child). In such situations, dealing with subspecies of recent evolutionary origin, phenotypic-morphological characters are the only method for correct identification. Electrophoretic evidence can better quantify the degree of hybridization between any subspecies of cutthroat trout and rainbow trout and it can also estimate times of evolutionary origins and closest affinities of subspecies. For example, many years ago I realized that the fine-spotted Snake River cutthroat trout is quite distinct from any other subspecies, but I did not know its origin--from the coastal, westslope or Yellowstone evolutionary lines? Chromosomal evidence (diploid number of 64) demonstrated it is derived from a Yellowstone ancestor, and electrophoretic evidence (no consistent detectable difference) indicates its origin can be placed in recent geological times.

Thus, as with methods of sampling in fisheries work, where some methods work better in some situations and other methods are more effective in other situations, the "best" method for identification of cutthroat trout subspecies depends on the purpose of identification and the length of time of evolutionary separation of a particular subspecies.

A final word of caution must be expressed concerning the artificial propagation of cutthroat trout in hatcheries. With a captive brood stock fed a hatchery diet, exposed to crowding and disease, some selection for domestication is unavoidable. A great danger is the loss of heterozygosity in hatchery stocks (Allendorf and Phelps 1980). No matter what method is used for propagation, care should be taken to maintain the desired attributes possessed by a particular stock of wild trout in the genotype of the eggs taken for propagation. For example, in large lacustrine predators such as the Bear Lake and Pyramid Lake cutthroat trout and the Gerrard strain of Kamloops trout of Kootenay Lake, the modal age at first spawning may be five or six. If 10% or less of a population spawn at age three or four, but most or all of the eggs taken for propagation are taken from the youngest spawners, an undesirable hereditary shift can be expected in the hatchery fish for a

younger age of maturity (and a shorter maximum life span and a lesser maximum size). Any cutthroat trout management program that includes hatchery propagation should require more than routine involvement of fish culturists if undesirable genetic changes are to be avoided.

LITERATURE CITED

Allendorf, F. W. and S. R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Trans. Am. Fish. Soc. 109:537-543.

Behnke, R. J. 1981. Systematic and zoogeographical interpretation of Great Basin Trouts. Pages 95-124 **in** R. J. Naiman and D. L. Soltz (eds.). Fishes in North American deserts. John Wiley and Sons.

Behnke, R. J. 1984. Beardslee rainbow trout. Trout Mag. 25(4):42-46.

Behnke, R. J. 1986. Pyramid Lake and its cutthroat trout. The Am. Fly Fisher 13(1):18-22.

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

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 19-160 **in** R. A. Simon and P. A. Larkin (eds.). The stock concept of Pacific salmon, H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Ryman, N. (ed.). 1981. Fish gene pools. Ecol. Bull. 34 (Stockholm).

Ryman, N. and F. Utter (eds.). 1987. Population genetics and fishery management. Univ. Wash. Press.

Sumner, F. 1940. The decline of the Pyramid Lake fishery. Trans. Am. Fish. Soc. 69:216-224.

CUTTHROAT TROUT

A Biochemical-Genetic Assessment of Their Status and Systematics

Eric J. Loudenslager

and

Graham A. E. Gall

Department of Animal Science

University of California

Davis, CA 95616

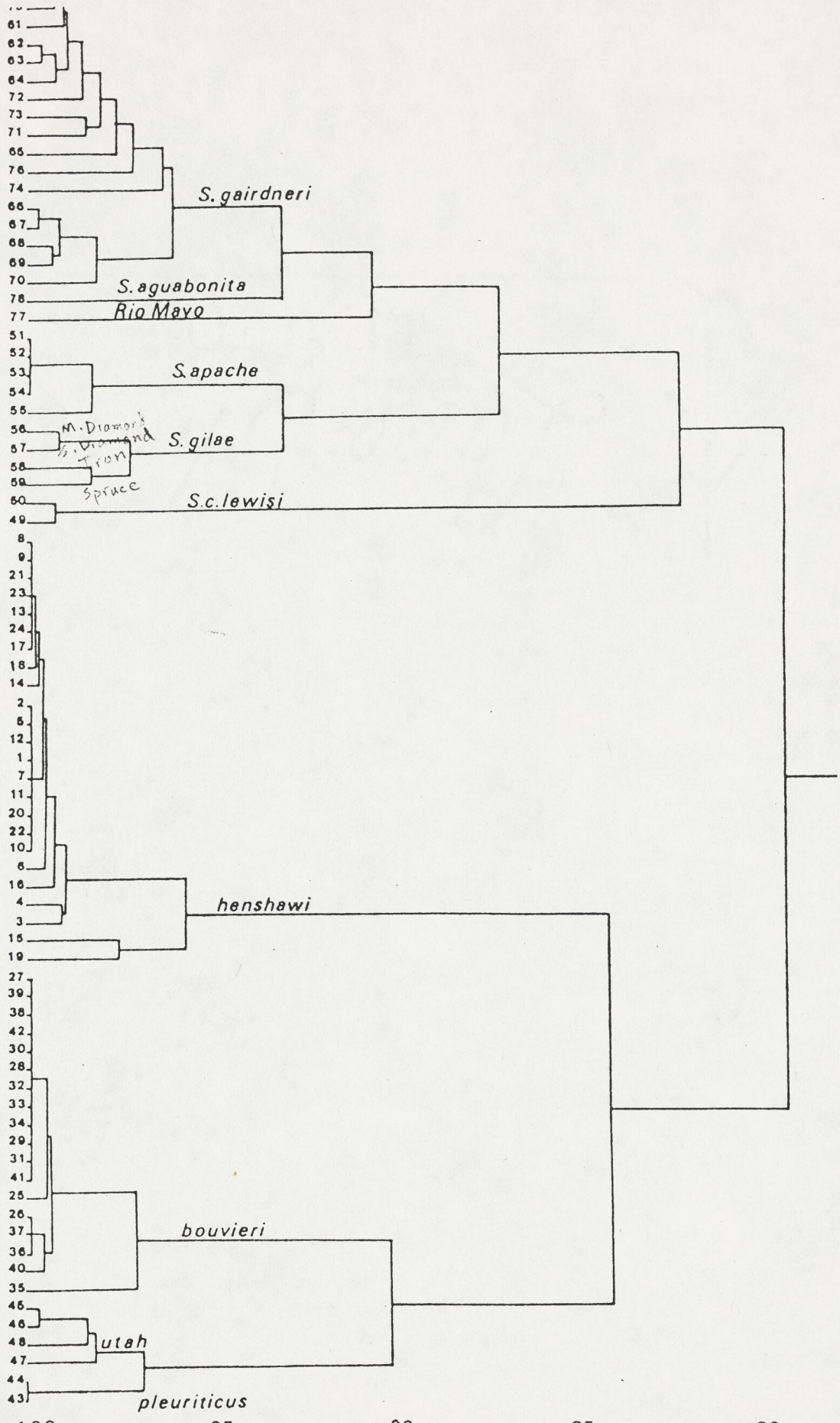


Fig. 13. UPGMA dendrogram of 78 populations of western Salmo representing nine recognized taxa.

COLLEGE OF AGRICULTURE AND HOME ECONOMICS

DEPARTMENT OF FISHERY AND WILDLIFE SCIENCES
Box 4901/Las Cruces, New Mexico 88003
Telephone (505) 646-1544

March 17, 1985

Dr. Bob Behnke
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado 80523

Dear Bob:

I didn't get a thorough reading of your article on the Gila trout until spring break. I have written several comments in the margin and enclosed some items for your consideration. The Gila National Forest has been extremely helpful in packing in our gear and assisting in restoration activities in the last two years. They have done everything I have requested of them. The controlled grazing program they have instituted in ~~the~~ McKnight Creek ~~population~~ is working extremely well with good reproduction of willows and narrowleaf cottonwood and improved watershed conditions. If you get a chance give the Gila National Forest some positive encouragement in your article, please do so - I think the [redacted] current supervisor has more interest in Gila trout than the supervisor that was on the Gila in the 70's.

As the enclosed progress report documents, we have been making better progress in our recovery efforts in the last two years because of excellent cooperation and the research funding by New Mexico Game and Fish (from Share with Wildlife tax checkoff) and the Agricultural Experiment Station at New Mexico State University. I expect good year classes by the transplanted populations of Gila trout in Iron and Little creeks this year. We also should be able to transplant 100-200 S. gilae from Spruce Creek to the headwaters of Big Dry Creek this fall--if everything goes according to schedule. Our next replication would come from South Diamond Creek.

I have enclosed a copy of the dendrogram from Gall and Loudenslager's manuscript. I have no idea whether it has been published anywhere, but it is quite a manuscript -- all 70-80 pages of it.

If you have any questions about any of my comments, feel free to contact me.

Sincerely,

Paul

Paul R. Turner

PRT/ejk

LABORATOIRE
MARITIME
HUNTSMAN
MARINE
LABORATORY

**NORTH AMERICAN
SALMON RESEARCH CENTER**
ST. ANDREWS, N.B.
CANADA EOG 2XO
Tel. 506-529-8891

Paul
Here is letter
from Eric. I
sent John H.
a copy also so
he would
be aware of
See you next
week. John R.

November 2, 1982

Dr. John Rinne
Forest Sciences Lab
ASU Campus
Tempe, Arizona
U. S. A. 85287

Dear John;

I am writing a letter, which will be followed in a month or so by a full report, concerning the genetic analysis of the S. gilae collected in 1979.

We initially sampled South Diamond, Main Diamond, Iron and Spruce Creeks, and you subsequently sent me samples from Lipsey Creek and the West fork of Mogollon Creek. The original four samples were screened for twenty proteins encoded by thirty six gene loci. The later samples were only screened for the loci that could be useful in determining the status of the populations.

The questions we wanted to ask were:

1. How are populations classified as S. gilae related to S. gairdneri, S. clarki, and S. apache;

2. Are there biochemical genetic loci potentially useful in determining hybridization between S. gilae and stocked exotics, particularly S. gairdneri and S. clarki;

3. Are all four populations of S. gilae the same?

All of these questions were answered by our analysis.

I have prepared a brief table of allele frequencies for selected ~~isozyme~~ 2 loci to support my statements, but will not go into elaborate detail in this letter.

1. S. gilae and S. apache are closely related genetically. Based on Nei's index of genetic identity S. gilae is closely related to S. gairdneri not to S. clarki.

2. S. gilae, although closely related to S. gairdneri, is distinct at several gene loci. As a consequence hybridization should be identifiable using electrophoresis. The same situation exists between S. gilae and S. clarki. S. gilae and S. apache are not easily distinguishable electrophoretically, and electrophoresis can not reliably identify hybrids. I pointed out in the hybridization section of my report with G. A. E. Gall that the mixing of exotic salmo and natives has had variable outcomes. In many populations there is no evidence that hybridization ever occurred. While in some populations we now find natives, exotics, F_1 hybrids and backcross hybrids, there are also populations that

I called introgressed. That is, a few genes from the exotic have been incorporated into a population that is essentially composed of a native gene pool

We could make these strong statements because S. clarki and S. gairdneri are fixed for alternate alleles at a sufficient number of loci. Between S. gilae and S. gairdneri there are only two loci (ADH & GCP) that are fixed, or nearly so, for alternate alleles, while MDH exhibits allele frequency differences. The common allele in S. gilae is also the common allele in S. apache. At least one population of either S. gilae or S. apache is polymorphic with the common S. gairdneri allele in low frequency. I can't say whether the low frequency S. gairdneri allele is the result of introgression or recent common ancestory. However, if a population included S. gairdneri, S. gilae, and various hybrids there would be a high frequency of both species alleles, and hybridization would be obvious.

With this as my rationale I feel South Diamond, Main Diamond, Iron and Spruce Creeks all represent S. gilae and none of the samples included S. gairdneri or any suspected hybrids. The sample from the west fork Mogollon contained S. gairdneri. However the frequencies of the S. gilae alleles at ADH, ~~GCP~~, and MDH (3,4) are higher than typically seen in S. gairdneri. I suspect that hybridization between S. gairdneri and S. gilae has occurred and that S. gilae is being replaced by S. gairdneri. The Lipsey Creek sample contained S. gairdneri, but the S. gilae alleles were present. I conclude that S. gilae has been replaced by S. gairdneri, the presence of the S. gilae alleles suggest that hybridization probably occurred in the past.

3. There are allele frequency differences among S. gilae populations. For example, ME and MDH. These differences are not greater than drainage system differences in Lahontan Basin S. c. henshawi or Central Valley California S. gairdneri. I would conclude that the variation is expected intraspecific variation and not of taxonomic significance. I would recommend however that the differences deserve to be preserved and considered in designing management plans. That is, don't mix the four existing populations in their current stream or origin. Also, try to plant all to new locations where they can be preserved.

Unelss new questions arise, I can't see a need for Dr. Yates to repeat our sampling. However, there would be justification to continue sampling suspected hybrid populations. I would also like to make a cautionary remark. Our sampling of S. gilae was in conjunction with sampling S. clarki, S. gairdneri, S. apache, and S. aguabonita: several thousand individuals representing several hundred populations. A lot of shortcuts can be made because of our pioneering efforts. However, anyone attempting a complete analysis that management agencies can rely on, should obtain standards of all the broodstocks. Only this way can comparisons be made with other investigations.

Sincerely yours,

Eric J. Loudenslager, Ph.D.
Geneticist
Salmon Genetics Research Program
Biological Station
St. Andrews, N. B. EOG 2XO

Locus / Allele / pop	ADH ★ -80	ADH ★ -100	ADH ★ -120	GCD ★ 100	GCD ★ 150	GCD ★ 160	MDH-3 100	MDH-3 95	MDH-3 75	MDH-4 100	MDH-4 95	MDH-4 75	ME 125	ME 100	ME 85
South Diamond Ck	1.00				1.00		.900		.100			1.00		.900	.100
Main Diamond Ck	1.00				1.00		.969		.031	.469		.531		1.00	
Eron Ck	.90	.10			1.00		.867		.133	.067		.933		.933	.067
SPRUCE Ck	1.00				1.00		1.00			1.00				.750	.250
Salmo gairdneri		1.00		1.00			1.00			.911	.089			.714	.286
S. clarki henshawi		1.00			1.00		1.00			1.00			1.00		
S. clarki pleuriticus		1.00				1.00	1.00			1.00			1.00		
Lipsey Ck		1.00		.970	.030		1.00			.900		.100		1.00	
L.F. Mogollon Ck	.330	.670		.930	.070		.930		.070	.900		.100		1.00	
apache X-MASS TRT C.	1.00			.018	.982		.071		.929	.018		.982		1.00	

Shasta Strain

Allele frequencies in western Salmo

	CK-2		SDH-2		
	100	70	250	40	00
South Diamond Ck	1.00			1.00	
Main Diamond Ck	1.00			1.00	
Iron Ck	1.00			1.00	
Spruce Ck	1.00			1.00	
Salmo gairdneri	1.00			1.00	
S clarki henshawi		1.00	1.00		
S. clarki pleuriticus		1.00			1.00
Lipsey Ck	—	—	—	—	—
N.F. Mogollon Ck	—	—	—	—	—
Apache X-MASS Tree L.	1.00			1.00	

Shasta Strain

Proc. Mont. Acad. Sci. 39: 28-36 (1980)

COEXISTENCE OF NATIVE AND INTRODUCED RAINBOW TROUT IN THE KOOTENAI RIVER DRAINAGE

Fred W. Allendorf, Department of Zoology, University of Montana, Missoula, MT 59812, and Darryl M. Espeland and Dean T. Scow, Department of Biology, Carroll College, Helena, MT 59601, and Stevan Phelps, Department of Zoology, University of Montana, Missoula, MT 59812

Abstract --Rainbow trout (*Salmo gairdneri*) have been suspected to be native to some Montana drainages, although previous reports have indicated the contrary. We collected and electrophoretically examined 218 rainbow trout from six sampling locations in the Kootenai River drainage of northwestern Montana and Idaho with the goal of detecting any extant native populations. Large allelic differences exist among these samples collected within a small geographical area. Two of the population samples share close affinity to other inland rainbow trout populations and are very different from hatchery stocks of rainbow trout that have been planted in this area. One population sample was found to have intermediate frequencies, indicating an apparently random mating population containing both native and introduced trout. We conclude that populations of native and introduced rainbow trout, as well as their hybrids, presently exist in this drainage.

There is presently much interest in the preservation of native stocks of salmonid fishes. The great majority of the original populations of native trout in the interior of the western U.S.A. have been lost in the last 100 years [8]. The remaining genetic diversity among native populations of salmonid species in western North America must be comprehended and preserved. Fisheries biologists in the past have been hindered by a typological concept of species management; this generalized notion of a species type is erroneous and has sometimes led to unsound management practices [6].

The rationale of perpetuating native races centers on the value of perpetuating genetic diversity. This is important both for the continued existence of native stocks, which are adapted to local environmental conditions, and for preserving the storehouse of genetic variability desirable for the continued successful domestication of any plant or animal species. Plant breeders have long recognized the importance of maintaining genetic variability through the preservation of natural types. "The extinction of the natural sources of adaptation and productivity represented by primitive varieties may turn out to be an irreparable loss to future generations" [9]. The artificial propagation of salmonids is serving an important