C.1990

ARC-90-12

WESTSLOPE CUTTHROAT TROUT RESTORATION PROGRAM: PAST AND PRESENT DISTRIBUTION, BROOD STOCK PROGRAM, AND CONSERVATION GENETICS COMMITTEE REPORT

Robb F. Leary (Chairperson)
Thurston Dotson
Dave Genter
Bill Hill
George Holton
Joe Huston
Kathy L. Knudsen
Scott Rumsey
G. Kevin Sage

Past and Present Range of Westslope Cutthroat Trout

The waters of Montana were naturally inhabited by two cutthroat trout, *Oncorhynchus clarki*, taxa; westslope, *O. c. lewisi*, and Yellowstone cutthroat trout, *O. c. bouvieri* (Trotter 1987). Yellowstone cutthroat trout were native only to the Yellowstone River drainage of south central Montana. Westslope cutthroat trout had a much broader natural distribution. They inhabited all major drainages west of the Continental Divide and the South Saskatchewan and Missouri river drainages at least as far east as Fort Benton east of the Divide. Furthermore, three distinct life history forms of westslope cutthroat trout have been recognized (Liknes and Graham 1988). The lacustrine-adfluvial form matures in lakes but returns to tributaries to spawn where the resulting young may reside for up to three years. The fluvial-adfluvial form has a similar life history, but moves between mainstem rivers and tributaries. Finally, the fluvial or resident form consists of fish that spend their entire lives in tributary streams. Clearly, the westslope cutthroat trout is an ecologically and behaviorally diverse organism.

Westslope cutthroat trout are now considered a fish of special concern by the State of Montana and the Montana Chapter of the American Fisheries Society and a sensitive species by Region 1 of the United States Forest Service. Its present range has been greatly reduced compared to its historic distribution. Degradation of the environment by human exploitation has made many waters unsuitable for the existence of this fish. Competition with introduced brook, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, is also believed to have caused the displacement of many westslope cutthroat trout populations (Liknes and Graham 1988). This has probably most often occurred in conjunction with habitat degradation which has made waters more suitable for the existence of the introduced than the native fish. The major factor responsible for the loss of westslope cutthroat trout populations, however, has probably been the introduction of Yellowstone cutthroat and rainbow trout, O. mykiss, into its native range. These introductions have resulted in widespread elimination and hybridization between the native and introduced fishes which has destroyed the genetic integrity of most native populations (Allendorf and Leary 1988; Liknes and Graham 1988; Rieman and Apperson 1989).

Historically, genetically pure westslope cutthroat trout populations were distinguished from those in which hybridization has or is occurring (hybrid swarms) by analysis of morphological characters. These comparisons assume that hybrid swarms will be morphologically intermediate to the parental taxa and have increased morphological variance. Some studies, however, have shown that for trout these assumptions are not always valid (Busack and Gall 1981; Leary et al. 1984, 1985a). Morphological comparisons, therefore, can potentially provide misleading information about the genetic status of trout populations. That is, whether they represent a genetically pure population of a taxon or a hybrid swarm.

Protein electrophoresis provides a powerful means of determining the genetic status of trout populations when complete, or nearly complete, allele (form of a gene) frequency differences exist between taxa at several protein coding loci (genes). Because of this attribute, loci at which such differences exist are commonly termed diagnostic loci (Ayala and Powell 1972). Individuals from genetically pure populations will possess alleles at all diagnostic loci characteristic of only that taxon. First generation hybrids will be heterozygous (i.e., possess two different alleles at a locus) at all diagnostic loci for alleles characteristic of both parental taxa (e.g. Leary et al. 1983). When first generation hybrids mate among themselves and with individuals from the parental taxa this initiates the formation of a hybrid swarm. After a few generations, individuals in such populations will have highly variable genetic characteristics. They will be homozygous at some diagnostic loci and heterozygous at others. Furthermore, the particular loci that are homozygous or heterozygous will differ widely among individuals (e.g. Allendorf and Leary 1988). In such situations, no individual in the population is likely to be a genetically pure representative of either parental taxa unless it is a recent immigrant.

Electrophoretic analysis of 45 loci coding for proteins present in muscle, liver, or eye tissue (Table 1) of individuals collected from numerous westslope cutthroat, Yellowstone cutthroat, and rainbow trout populations has revealed that a number of diagnostic loci exist between these taxa (Table 2). Electrophoresis, therefore, provides an extremely powerful means of detecting genetically pure westslope cutthroat trout populations.

Because reliable identification of westslope cutthroat trout populations requires electrophoretic analysis, the present distribution of this fish in Montana is largely uncertain. Extensive sampling for electrophoretic analysis has been conducted only within the South Fork Flathead River drainage above Hungry Horse Dam, North Fork Flathead River drainage, upper Blackfoot and Little Blackfoot River drainages, and the Clark Fork River drainage in the area of Thompson Falls to the Montana-Idaho border. These are the only regions of Montana, therefore, that we feel we have a reasonably accurate knowledge of the present distribution of westslope cutthroat trout.

Distribution of westslope cutthroat trout in other drainages is poorly understood and based upon past experience is likely to be over estimated. For example, the South Fork Flathead River drainage is considered to be the last remaining stronghold of westslope cutthroat trout in Montana (Liknes and Graham 1988). Of 34 lakes sampled, only six (17.6%) contained westslope cutthroat trout populations. The remaining samples either came from hybrid swarms between westslope cutthroat and Yellowstone cutthroat or rainbow trout (N=19, 55.9%) or populations containing no westslope cutthroat trout genes (N=9, 26.5%). Of the 44 creeks sampled, 30 (68.2%) contained westslope cutthroat trout populations, 13 (29.5%) contained hybrid swarms with westslope cutthroat trout, and one (2.3%) creek contained a rainbow trout population. Furthermore, many of the resident westslope populations are not protected by dispersal barriers from future hybridization. Obtaining a similar understanding of the distribution of westslope cutthroat trout in other areas is considered a primary goal of the restoration program. Without a dramatic increase in the rate at which electrophoretic surveys are being conducted we conservatively estimate that an accurate statewide distribution of westslope cutthroat trout will not be obtained until the year 2020.

Some generalities concerning the distribution of westslope cutthroat trout in Montana appear to be emerging from the few extensive electrophoretic surveys. First, hybrid swarms between westslope and Yellowstone cutthroat trout are usually found only in lakes or tributaries draining lakes with hybrid swarms or Yellowstone cutthroat trout populations. Streams that were stocked with Yellowstone cutthroat trout but do not drain lakes likewise stocked usually fail to show evidence of hybridization with Yellowstone cutthroat trout. This suggests that, in terms of reproduction, Yellowstone cutthroat trout stocking west of the Divide was successful almost exclusively in headwater lakes. Thus, streams in drainages not having headwater lakes stocked with Yellowstone cutthroat trout have a greater probability of still containing pure westslope cutthroat trout populations than those in drainages with a headwater lake stocking history.

In contrast to the above data, both headwater lakes and streams with a rainbow trout stocking history often contain westslope cutthroat-rainbow trout hybrid swarms regardless of whether rainbow trout were introduced into headwater lakes or not. Thus, unlike Yellowstone cutthroat trout, rainbow trout were often successfully stocked in both streams and lakes. Drainages most likely to still contain a high proportion of westslope cutthroat trout populations, therefore, are those with no stocking history.

An absence of stocking records, however, does not guarantee the presence of pure westslope cutthroat trout. Hybridized populations could exist either because of unrecorded stocking or the migration of individuals from hybridized populations.

Most westslope cutthroat trout populations that have been identified exist in low order streams. This is probably due to the general absence of stocking in such small streams and diminished human environmental influence in more remote areas. In terms of life history forms, therefore, most remaining westslope cutthroat trout populations would be classified as resident.

Identification is only the initial step of a conservation program. Once identified, steps must be taken to ensure the continued existence of the population. This is especially true of many westslope cutthroat trout populations that exist either upstream or downstream from hybridized populations or introduced Yellowstone cutthroat or rainbow trout populations. These westslope cutthroat trout populations will continually be threatened with future hybridization and need to be protected. We feel that this can be accomplished by chemical removal, construction of barriers, or genetic restoration. Chemical removal is not likely to be commonly used because of adverse public and departmental opinions and practical reasons. Many lakes and streams containing hybridized or non-native populations exist in remote areas. Barriers can be constructed to prevent upstream migration in certain situations. Hatchery westslope cutthroat trout can be used in genetic restoration programs; that is, stocked in upstream populations or downstream populations when barriers are not practical. The premise is that these introductions will reduce the percentage of non-native genes in populations. This will be accomplished by displacement of hybrids by the westslope cutthroat trout and by successful reproduction of the stocked fish. Through repeated introductions it may be possible to restore a population to virtually pure westslope cutthroat trout (i.e., genetically 99% or greater). Preliminary results from some experimental introductions into headwater lakes in the South Fork Flathead River drainage suggest that this practice may be an effective means of restoration.

Rating of populations for conservation and management purposes

We feel a rating system based upon the genetic status of populations and the likelihood of future hybridization is essential for implementing an effective conservation program. With this system, management policies can be formulated for groups of populations and as the data base expands populations will have a pre-existing policy dictated largely by their rating. We propose the following rating system be used.

A1: Results from electrophoretically testing at least 25 individuals indicate the population is genetically pure (100%) westslope cutthroat trout. The population is also isolated because of natural or man made barriers protecting it from future hybridization. These populations have extremely high conservation status and all efforts should be taken to minimize human effects on the environment that may reduce the chances of the populations continued viability. These populations also represent a potential source of fish and gametes for a hatchery brood stock or introduction into other waters. Immediately before collection of fish or gametes for such purposes, however, 50 fish should be electrophoretically analyzed to reconfirm the population's genetic status.

A: Results from electrophoretically testing at least 25 individuals indicate the population is genetically pure (100%) westslope cutthroat trout. Unlike A1 populations, however, these fish are not protected from potential future hybridization because of a lack of barriers. Before fish or gametes are collected from these populations for a hatchery brood stock or introduction into other waters, it is imperative that their genetic status be reconfirmed by electrophoretic analysis of at least 50 fish including those potentially supplying gametes.

B: 1) Results from electrophoretically testing less than 25 fish indicate no evidence of hybridization, 2) results from at least 25 fish indicate the population is a hybrid swarm but contains at least a 98% westslope cutthroat trout genetic contribution, 3) those populations not electrophoretically tested but suspected of being pure westslope cutthroat trout because of an absence of stocking history, remote location, or morphological analysis. Populations in this category should be managed as pure westslope cutthroat trout but are not suitable sources of fish or gametes for a hatchery brood stock or introduction into other waters unless upgraded by future analysis.

C: Hybrid swarms containing less than a 98% westslope cutthroat trout genetic contribution. If such populations threaten the status of class A populations chemical removal, construction of barriers, or genetic restoration through introduction of hatchery westslope cutthroat trout should be considered.

D: This category constitutes genetically pure rainbow and Yellowstone cutthroat trout populations outside that species' natural range. If they exist in headwater lakes or tributaries and their presence threatens the status of class A populations, then rehabilitation efforts should seriously be considered. If they represent little potential for hybridization, then the possibility of leaving them in their present state as a conservation measure for these fishes should be considered. For example, a population of Colorado River cutthroat trout, O. c. pleuriticus, exists in Williamson Lakes, California. Although it is far outside the taxon's native range, it is only one of two populations that are now known to be pure Colorado River cutthroat trout.

Westslope cutthroat trout hatchery brood stock histories

The first attempt by the Department of Fish, Wildlife, and Parks to establish a westslope cutthroat trout brood stock occurred in 1952. In January, Bob Mitchell, Ed Furnish, and a Great Falls game warden flew into the Big Prairie Ranger Station in the Bob Marshall Wilderness. They captured 32 fish by hook and line from Big Salmon Lake in about 4 to 5 days. The fish were temporarily held in a live box, subsequently, anaesthetized, packed in moss-lined boxes, and flown to the Jocko River State Trout Hatchery. Only a small number of eggs were obtained from these fish in the spring of 1953 and 1954. In May of 1955, the fish from these two egg takes were transferred to the Hamilton hatchery where a brood stock was maintained until the hatchery closed in 1961. The brood stock was then transferred to the Libby hatchery.

It is believed that the fish obtained from Big Salmon Lake to establish the brood stock were slightly hybridized with rainbow trout when obtained in 1952. In 1964, an attempt to collect additional fish for the brood stock from Big Salmon Lake was stopped when "good looking" rainbow trout were captured. Furthermore, North Bigelow Lake was barren until it was stocked with fish from the brood stock in 1961. This was the only time the lake was stocked and electrophoretic analysis of 25 fish collected 5 September, 1984 indicated the population was a westslope cutthroat-rainbow trout hybrid swarm with a 3% rainbow trout genetic contribution.

The second attempt to establish a westslope cutthroat trout brood stock occurred in 1954. In June, personnel from the United States Fish and Wildlife Service, Montana Department of Fish, Wildlife, and Parks, and Kalispell sportsmen caught about 135 adult fish from several Hungry Horse Reservoir tributaries including Felix, Hungry Horse, Murray, Quintonkon, and Sullivan creeks. The fish were taken to the Creston National Fish Hatchery where they were successfully spawned in late June. In 1955 and 1956, however, males and females ripened at different times so milt from Yellowstone cutthroat trout maintained at the hatchery was often used to fertilize the eggs. This brood stock and production fish were transferred to the Anaconda hatchery in the spring of 1957 and all fish were subsequently stocked.

Prior to hybridization in the hatchery, the fish used to establish the above brood stock are believed to have been genetically pure westslope cutthroat trout. Electrophoretic analysis of samples obtained from the tributaries in 1983 indicated they all contained pure westslope cutthroat trout.

In 1956, the Somers hatchery obtained fertilized eggs from 2 or 3 pair of westslope cutthroat trout spawned at the Creston National Fish Hatchery. The progeny from these eggs were then stocked into Laurie Lake in 1958 after it had been chemically rehabilitated. The lake was used as a brood lake from 1960 until 1965 when the population had essentially disappeared.

The Creston National Fish Hatchery apparently did not raise westslope cutthroat trout between 1957 and 1964. In 1964, however, fish from Laurie Lake were transferred to the hatchery and a brood stock was maintained until 1971 when it had to be destroyed for furunculosis disinfection.

When fish from the Hamilton hatchery were transferred to Libby they were mixed with individuals derived from Laurie Lake. These fish were used to establish a brood stock which was maintained at the hatchery until 1969 when all fish were stocked and the hatchery was closed.

Laurie Lake fish were also used to establish another brood stock. In 1965, fish were transferred to Spoon Lake and eggs obtained from the lake were used in the hatchery program through 1970.

In 1965 and 1967, the Department of Fish Wildlife and Parks again attempted to establish a hatchery westslope cutthroat trout brood stock. Each year fertilized eggs from about 15 pair of fish collected from Emery Creek and Hungry Horse Creek were transferred to the Jocko River State Trout Hatchery. Progeny from these fish were first successfully spawned in 1968. By the early 1970's, the brood stock was large enough to be capable of producing over one million eggs for production fish.

In 1977, evidence that the brood stock had undesirable genetic attributes began to accumulate. Compared to fish in Hungry Horse Creek, the brood stock was significantly less variable (Allendorf and Phelps 1980). Furthermore, genetic differences were observed among the 1971 through 1976 year classes indicating a continual loss of genetic variation. This loss of genetic variation was believed to result from founding the brood stock from a limited number of parents and spawning practices in the hatchery. Selection was usually for larger fish and spawning time as future brood fish were retained from only a small portion of the spawning season. This selection would directly alter the genetic characteristics of the population at the genes influencing the targeted traits. It would also induce genetic changes at other genes because the small number of individuals used to perpetuate the brood stock would increase the rate of genetic drift.

By 1983, there was good evidence that the loss of genetic variation was adversely affecting the fish. Hatching success was low and developmental problems revealed by morphological deformities and right-left differences of meristic counts on individuals were prevalent (Leary et al. 1985b). Because of these problems it was decided that efforts to maintain the brood stock would be terminated and in 1986 all fish were stocked.

Present brood stock and stocking policies

The present brood stock was founded in 1983 and 1984 from fish collected from South Fork Flathead River tributaries above Hungry Horse Dam and Clark Fork River tributaries in the Noxon area (Table 3). Prior to collection, electrophoretic analysis indicated that all these streams contained pure westslope cutthroat trout populations. Disease analysis also indicated a lack of detectable pathogens. The objective of founding this brood stock was to establish a genetically diverse hatchery population of westslope cutthroat trout that would be capable of surviving and reproducing in a variety of natural situations.

In order to incorporate genetic diversity into the brood stock, fish were collected from a number of streams. Electrophoretic data indicate that westslope cutthroat trout populations are characterized by having little genetic variation within them but substantial differentiation among them even over short geographic distances (Allendorf and Leary 1988; Leary et al 1988). This genetic divergence is largely due to the presence of many alleles that exist at appreciable frequency in only a small proportion of the populations. It was felt that by collecting fish from many populations a number of variant alleles would be introduced into the brood stock thereby increasing genetic diversity. Analysis of the 1986 through 1989 year classes indicated that this goal was achieved (Leary, unpublished data).

Efforts will be made to maintain genetic variation in the brood stock. Individuals will be spawned at random with each fish having an equal chance of mating with any other fish. The only fish that purposefully will not be spawned are those with obvious morphological deformities. To avoid selecting for early maturity, future brood stock will be retained from crosses between four year old males and five year old females. At these ages, 90% of the individuals of each sex have attained maturity. This practice will also result in genetic exchange among year classes preventing the establishment of a number of reproductively isolated brood stocks in the hatchery. Selection for time of spawning during the season will be avoided by randomly choosing one percent of the eyed eggs from each spawning period for future brood stock. The efficacy at which this procedure maintains genetic variation will be monitored by obtaining electrophoretic data from 70 loci and the counts of five bilateral meristic characters from 50 randomly sampled individuals from each year class of future brood stock when they are about one year old.

Every ten years wild fish from aboriginal populations will have a five to 10% genetic contribution to the brood stock for three successive years. This will be accomplished by the introduction of gametes or fish from immediately confirmed A1 or A populations that are certified disease free. It is hoped that this will prevent developing a highly domestic brood stock which could adversely affect survival of the fish in the wild. Hatchery personnel will monitor the brood stock for obvious signs of domestication. If this appears to be happening, wild fish will be collected more frequently or given a greater genetic contribution.

To avoid altering the genetic characteristics of native westslope cutthroat trout populations by the introduction of hatchery fish, it would be necessary to maintain numerous brood stocks. Space and financial constraints, however, dictate that only one brood stock can be maintained. Thus, it is important to adopt stocking guidelines to minimize the potential effects of hatchery fish on wild fish.

No fish from the brood stock will be introduced into waters containing class A1 populations. The continued viability of these populations should be ensured by maintaining adequate environmental conditions and possibly restrictive regulations. If augmentation of natural reproduction is considered essential, the gametes or fish for the introductions will be collected from the population itself. These fish or the resulting progeny will temporarily be raised in isolation at one of the hatcheries.

Fish from the brood stock will be used in genetic restoration programs west of the Divide designed to protect class A populations with the following exceptions; those that exist in unusual environments (e.g., warm or saline water) or have unusual behavioral characteristics (e.g., spawning time) unless they are in imminent danger of becoming hybridized in which case genetic restoration of the hybridized population may require the introduction of hatchery fish. This eventually may alter the genetic characteristics of the class A populations, but it is considered more desirable that westslope mate with westslope cutthroat trout than with hybrid or non-native fishes resulting in the further loss of class A populations.

Although electrophoretic data have failed to indicate that populations east and west of the Divide constitute genetically distinct groups (Phelps and Allendorf 1982; Leary and Sage 1990), we feel it is initially best to adopt a conservative policy and avoid genetic exchange across the Divide. Electrophoresis allows one to examine genetic variation at only a small fraction of all the genes. Eastern and western populations, therefore, could be distinct at unexamined genes.

Because the present brood stock was founded from fish west of the Divide, fish derived from it will not be introduced into waters east of the Divide. Furthermore, eastern populations will not serve as a source of wild fish or gametes for the brood stock. For eastern genetic restoration programs, fish can be introduced directly into the target populations from nearby class A1 or A populations. Alternatively, fish from the latter populations can be transferred to a hatchery, temporarily raised in isolation, and spawned. The resulting progeny can then be used in genetic restoration programs or released back into the water from which the parents were obtained to prevent adversely affecting natural reproduction by the removal of adult fish. If the cost of implementing this policy is found to hinder effective management of the present brood stock or restoration efforts, then use of this brood stock in eastern waters or foundation of another brood stock will seriously be considered.

Private hatcheries or trout ponds that raise non-native salmonids within the natural range of the westslope cutthroat trout can constitute a threat to the continued existence of this fish in particular areas. These hatcheries will be encouraged to convert to westslope cutthroat trout with the State of Montana possibly supplying the original eggs or fish. Regardless of whether they convert or not, permit renewal and new hatchery permits will require the rearing of only westslope cutthroat trout. Finally, the State of Montana will exercise its legal power to require the introduction of only westslope cutthroat trout into private ponds connected to natural waters within the native range of this fish.

Conserving natural genetic diversity of westslope cutthroat trout

The primary goal of a conservation program from a genetics perspective is to ensure that existing genetic variation is maintained. This genetic variation is the result of some three billion years of evolution and represents the evolutionary legacy of a taxon. 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 taxon: growth, survival, fertility, developmental rate, and the ability of individuals to develop properly (reviewed by Mitton and Grant 1984; Allendorf and Leary 1986; Palmer and Strobeck 1986; Zouros and Foltz 1987). Furthermore, the loss of variation is expected to reduce the ability of a population to adapt to changing environmental conditions and to increase its susceptibility to epizootics (Ayala 1969; Frankham 1980; O'Brien et al 1985). Thus, the loss of genetic variation is generally expected to increase the chances of extinction.

The total amount of genetic variation in a taxon usually has a hierarchial geographic structure that is commonly referred to as its population genetic structure. For example, a certain proportion of the total genetic variation in a taxon 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 interactions among four evolutionary forces: mutation, natural selection, genetic drift, and migration (i.e., exchange of genes among populations).

The relative importance of these evolutionary factors is likely to differ among taxa and, therefore, population genetic structures may be quite different, even among closely related taxa. An understanding of the population genetic structure of a taxon aids in formulating a genetically rational conservation program. When substantial genetic differences exist among geographic groups of populations, maintaining 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 relatively little genetic divergence exists among regions and most variant alleles are ubiquitously distributed throughout the taxon's range, then a conservation program can place less emphasis on geographical considerations alone.

As previously mentioned, the population genetic structure of westslope cutthroat trout can be characterized as low amounts of genetic variation within populations and substantial genetic divergence between populations (Allendorf and Leary 1988; Leary et al. 1989). Few of the loci examined electrophoretically were found to be variable in any one population and a high proportion (37.8%) of the variant alleles were detected in only one or two of the 103 populations sampled. Furthermore, many of these geographically "rare" alleles occur at a relatively high frequency within their respective local populations. Thus, high genetic divergence among westslope cutthroat trout populations is largely due to numerous alleles, often at high frequencies, with an exceptionally narrow geographic distribution. Conservation of the genetic diversity of westslope cutthroat trout, therefore, requires ensuring the continued existence of many class A1 and A populations throughout its native range. In some areas attaining this goal is likely to require extensive habitat protection and rehabilitation efforts.

Mission statement

Protect, maintain, and improve existing wild westslope cutthroat trout and their hatchery progeny from now until eternity. This time frame may appear ridiculously long, but this fish has shown in the past to be highly susceptible to mismanagement and misuse of the environment. Thus, it is felt its continued existence can be assured only through the continued implementation of an effective conservation program.

Literature Cited

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. Sinauer Associates.

Allendorf, F.W., and R.F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2: 170-184.

Allendorf, F.W., and S.R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Transactions of the American Fisheries Society 109:537-543.

Ayala, F.J. 1969. Evolution of fitness. V. Rate of evolution in irradiated populations of Drosophila. Proceedings of the National Academy of Sciences USA 63:790-793.

Ayala, F.J., and J.R. Powell. 1972. Allozymes as diagnostic characters of sibling species of Drosophila. Proceedings of the National Academy of Sciences USA 63:790-793.

Busack, C.A., and G.A.E. Gall. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (Salmo clarki seleniris). Canadian Journal of Fisheries and Aquatic Sciences 38:939-951.

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.

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

Leary, R.F., F.W. Allendorf, and K.L. Knudsen. 1985a. 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. 1985b. Developmental instability as an indicator of reduced genetic variation in hatchery trout. Transactions of the American Fisheries Society 114:230-235.

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

Leary, R.F., F.W. Allendorf, S.R. Phelps, and K.L. Knudsen. 1988. Population genetic structure of westslope cutthroat trout: genetic variation within and among populations. Proceedings Montana Academy of Sciences 48:57-70.

Leary, R.F., and G.K. Sage. 1990. Genetic divergence among westslope cutthroat trout populations in the Blackfoot, Little Blackfoot, and upper Missouri River drainages: update. University of Montana Population Genetics Laboratory Report 90/3.

Liknes, G.A., and P.J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. American Fisheries Society Symposium 4:53-60.

Mitton, J.B., and M.C. Grant. 1984. Association among protein heterozygosity, growth rate, and developmental homeostasis. Annual Review of Ecology and Systematics 15:479-499.

O'Brien, S.J., M.E. Roelke, L. Marker, et al. 1985. Genetic basis of species vulnerability in the cheetah. Science 227:1428-1434.

Palmer, A.R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. Annual Review of Ecology and Systematics 17:391-421.

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

Rieman, B.E., and K.A. Apperson. 1989. Status and analysis of salmonid fisheries: westslope cutthroat trout synopsis and analysis of fishery information. Idaho Fish and Game Project F-73-R-11, Subproject No. 11, Job No. 1.

Trotter, P.C. 1987. Cutthroat: native trout of the west. Colorado Associated University Press.

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

Enzymes and loci examined. E = eye, L = liver, M = muscle

Enzyme	Loci	Tissue
Adenylate kinase	AK-1,2	M
Alcohol dehydrogenase	ADH	L
Aspartate aminotransferase	sAAT-1,2	L
	sAAT-(3,4)	M
Creatine kinase	CK-A1,2	M
	CK-B, CK-C1,2	E
Dipeptidase	PEPA-1,2	E
Glucose-6-phosphate isomerase	GPI-A, GPI-B1,2	M
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH-3,4	E
Glycerol-3-phosphate dehydrogenase	G3PDH-1,2	L
Isocitrate dehydrogenase	mIDHP-1,2	M
	sIDHP-1,2	L
L-Iditol dehydrogenase	sIDDH	L
L-Lactate dehydrogenase	LDH-A1,2	M
	LDH-B1,2, LDH-C	E
Malate dehydrogenase	sMDH-A(1,2)	L
	sMDH-B(1,2)	M
Malic enzyme	mMEP-1,2, sMEP-1	M
	sMEP-2	L
Phosphoglucomutase	PGM-1,2	M
Phosphogluconate dehydrogenase	PGDH	M
Superoxide dismutase	sSOD-1	L
Tripeptide aminopeptidase	PEPB	E
Xanthine dehydrogenase-like	XDHℓ	L

NOTE: The common alleles at the pairs of loci in parentheses produce a protein with identical function and electrophoretic mobility in westslope and Yellowstone cutthroat trout. Such pairs of loci are commonly termed isoloci, and their existence can be conclusively determined only when genetic variation exists at one or both loci. In these situations, however, it is not possible to determine at which locus of the pair a variant allele exists. In order to estimate allele frequencies at the isoloci, therefore, each pair was considered a single gene with four instead of two copies per individual.

TABLE 2

Diagnostic loci between westslope and Yellowstone cutthroat trout and between westslope cutthroat and rainbow trout. When more than one allele (form of a gene) exists at a locus within a taxon, the most common allele is listed first.

	Characteristic alleles			Characteristic alleles	
Locus	Westslope	Yellowstone	Locus	Westslope	Rainbow
CK-C1	100, 38	38	CK-A2	84, 100	100, 76
GPI-A	92, 100	100	GPI-A	92, 100	100
mIDHP-1	100	-75	mMEP-1	88	null
mMEP-1	88	null	sAAT-1	200, 250	100
PEPA-1	100	101	sIDDH	40, 100	100,200,40
PEPB	100	135	sIDHP-(1,2)	86,114,100 71,40	100,114,71,40
PGM-1	100, null	null			
sAAT-1	200, 250	165			
sIDDH	40, 100	100, -63			
SIDHP-1	86,114,71	71			
sMEP-1	100	90			
sMEP-2	100	110			

NOTE: In rainbow trout, sIDHP-(1,2) constitute a pair of isoloci. In hybridized populations between westslope cutthroat and rainbow trout, therefore, these loci are treated as isoloci. The 86 allele at these loci is characteristic of westslope cutthroat trout and it usually exists at a frequency of 0.500 in a non-hybridized population. Thus, in hybridized populations the proportion of westslope cutthroat trout genes at these loci is estimated to be twice the frequency of the 86 allele.

TABLE 3. Source and numbers of fish collected for the present westslope cutthroat trout brood stock.

Source		Year and collection size	
Drainage	Stream	1983	1984
South Fork Flathead	Sullivan Drainage		
	Ball	105	--
	Branch	175	130
	Connor	350	470
	Battery	35	25
	Quintonkon Creek	150	365
	Felix Creek	200	100
	Hungry Horse Drainage		
	Hungry Horse	230	150
	Lost Mare	230	100
	Tiger	345	200
	Margaret	395	200
	Emery Creek	800	400
	Tin Creek	--	240
Clark Fork	Marten Creek	--	600
	Vermillion River	--	450
	TOTAL	3,015	3,430