ALLOZYMIC AND PARASITIC EXAMINATION OF INTERSPECIFIC INTROGRESSION IN *ONCORHYNCHUS* FROM THE SOUTH FORK OF THE FLATHEAD RIVER DRAINAGE

by

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Allozymic and Parasitic Examination of Interspecific Introgression in Oncorhynchus from the South Fork of the Flathead River Drainage (108 pp.)

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The westslope cutthroat trout (Oncorhynchus clarki lewisi) has declined over much of its range. In Montana, it was historically native to all major drainages west of the Continental Divide and to the upper Missouri and South Saskatchewan drainages east of the divide. Currently they occur in only about 2.5% of their historic range, with the South Fork of the Flathead River drainage considered their "stronghold" in Montana.

A major factor contributing to the decline of most cutthroat has been hybridization with introduced Yellowstone cutthroat trout (O. clarki bouvieri) and rainbow trout (O. mykiss). In some cases, however, these species have failed to become established. It has been hypothesized that an increased sensitivity to endemic parasites may have contributed to their failure.

The primary objective of this study was to determine the distribution and extent of hybridization of westslope cutthroat trout with rainbow trout and Yellowstone cutthroat trout in the South Fork of the Flathead River drainage. A second objective was to determine if hybrid and introduced populations of trout were more susceptible to parasitism than native westslope cutthroat trout populations.

The taxonomic origin of samples collected from forty-nine populations were determined with horizontal starch gel electrophoresis. Of these, only 19, or 39% harbored essentially pure populations of westslope cutthroat trout. Of the remaining 30 populations, 20 (41%) contained hybridized populations, and 10 (20%) contained introduced taxa. In fifteen of these waters, where the percentage of non-native genes and the potential for downstream migration is high, chemical removal of the fish populations is recommended, while in ten waters frequent introductions of hatchery westslope cutthroat trout are recommended. In the five remaining waters no direct action to increase the percentage of westslope cutthroat trout genes is recommended.

Four hundred and thirteen trout from fifteen lakes were also examined for macroparasites. Metazoan parasites belonging to five genera were recovered. Intensity of infection to parasites did not appear to be related to taxonomic status. No significant correlations existed between the percentage of westslope cutthroat trout genes and the abundance of parasites present within populations, although differences in parasite intensities between populations were observed. The differences observed between the populations, therefore, appear to have been generated by environmental factors.

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INTRODUCTION

Three fishes of the genus Oncorhynchus are native to the waters of Montana. The westslope cutthroat trout (Oncorhynchus clarki lewisi), is native to all major drainages west of the Continental Divide, as well as the upper Missouri and South Saskatchewan drainages east of the divide (Trotter 1987; Behnke 1979, 1992). The Yellowstone cutthroat trout, O. clarki bouvieri, and rainbow trout, O. mykiss, had narrower distributions in Montana. The Yellowstone cutthroat trout was native in only the Yellowstone River drainage of south central Montana (Trotter 1987; Behnke 1992) and the rainbow trout was native only to the Kootenai River drainage of northwestern Montana (Allendorf et al. 1980; Holton 1990).

The cutthroat trout is a polytypic species that is distributed throughout most of western North America (Behnke 1979). As many as 16 subspecies have been recognized in the recent literature (Allendorf and Leary 1988). Substantial biochemical genetic differentiation exists between the westslope cutthroat and the Yellowstone cutthroat trout subspecies (Leary et al. 1987). The Nei's standard genetic distance at allozyme loci between these subspecies is 0.295 (Leary et al. 1987). This is comparable to or larger than values observed between many species of fish (Johnson 1975; Avise and Ayala 1976; Buth and Burr 1978; Phelps and Allendorf 1983; Yates et al. 1984). This distance is also greater than that of either subspecies to rainbow trout, a separate species.

Westslope cutthroat trout now inhabit only about 2.5% of their historic range in Montana (Liknes and Graham 1988). It is considered a fish of special concern by the State of Montana (Holton 1990) and the

Montana Chapter of the American Fisheries Society, and a sensitive species by the United States Forest Service. There are areas, however, where native westslope cutthroat are relatively common, but these areas are restricted and many streams have only small relic populations in their extreme headwaters (Hanzel 1960; Brown 1971; Behnke 1979).

The drastic declines in the distribution and abundance of the westslope cutthroat trout can be attributed to many factors: habitat degradation, exploitation, competition or replacement, and hybridization. Habitat degradation caused by hydroelectric development, grazing, logging, road construction, and stream diversion, have all led to declines in the abundance of westslope cutthroat trout populations (Nelson 1965; Behnke 1972; Behnke and Zarn 1976; Roscoe 1974). Overexploitation from increased fishing pressure may have also led to declines in westslope cutthroat trout numbers. Behnke (1979) stated that fishing pressures of 50 hours/acre per year would result in overexploitation of stream populations of cutthroat trout. MacPhee (1966) found that cutthroat trout were caught twice as easily as brook trout.

The introduction of non-native salmonids has also led to declines in the abundance of westslope cutthroat trout populations (Hanzel 1960; Reinitz 1974; Behnke 1988; Liknes and Graham 1988). Exotic trout have been introduced into all of the major drainages originally occupied by cutthroat trout (O. clarki) in Montana (Hanzel 1960; Brown 1971). Brown trout (Salmo trutta) were introduced in 1891, and have become the predominant species in the valley streams of the cutthroat trout's range (Hanzel 1960). Eastern brook trout (Salvelinus fontinalis) were introduced in 1894, and now occupy many of the small valley brooks and

mountain headwater creeks, as well as a considerable number of mountain lakes (Hanzel 1960).

The most important factor for the loss of the native trout populations, however, has been the introduction of rainbow trout and subspecies of cutthroat trout into waters outside their natural range (Leary et al. 1984). These introductions have resulted in widespread hybridization and introgression, and the subsequent loss of many native trout gene pools (Behnke 1972; Leary et al. 1984; Allendorf and Leary 1988). Rainbow trout were first introduced outside of their natural range in Montana in 1891, and since that time have been stocked extensively (Hanzel 1960). Yellowstone cutthroat trout were also stocked extensively in the westslope cutthroat trout's range from the early 1900's until the late 1960's. With the establishment of a westslope cutthroat trout broodstock by the Montana Department of Fish, Wildlife and Parks, however, the introduction of non-native trout within the range of the westslope cutthroat trout has essentially ended.

Unfortunately, the damage caused by these introductions had already occurred. Marnell et al. (1987) sampled 47 waters in Glacier National Park known or suspected to contain resident cutthroat trout. Of those, adequate samples could not be obtained from four waters, 14 no longer contained westslope cutthroat trout, three had westslope cutthroat x Yellowstone cutthroat trout populations, four had Yellowstone cutthroat x rainbow trout populations, six had pure populations of Yellowstone cutthroat trout, and 16 had pure westslope cutthroat trout populations. Of the 16 westslope cutthroat trout populations, however, only 12 were believed to be indigenous. The pure populations in Glacier Park also

occurred only on the west side of the Continental Divide; the westslope cutthroat trout was evidently unable to gain access to the headwater lakes of the South Saskatchewan and Missouri River drainages on the east side of the Divide (Marnell et al. 1987).

Leary et al. (1984) analyzed six creeks in the Clark Fork River drainage that were classified as pure westslope cutthroat trout by the Montana Department of Fish, Wildlife and Parks, and found only two that contained pure westslope cutthroat trout while four contained introgressed westslope cutthroat x rainbow trout populations. These surveys suggest that relatively few pure populations of westslope cutthroat trout still remain in the Clark Fork River drainage or in Glacier National Park, and indicate that hybridization is probably common throughout the range of the westslope cutthroat trout in Montana.

Historically, the determination of hybridized or genetically pure populations of westslope cutthroat trout was based on the analysis of morphological characters. These comparisons assumed that naturally occurring hybrid fishes could be identified by their intermediacy in characters that distinguish between the two parental types (Hubbs 1940, 1955; Neff and Smith 1979). Many studies, however, have shown that for trout these assumptions are not always valid (Zimmerman 1965; Busack and Gall 1981; Leary et al. 1983, 1984, 1985b; Rinne et al. 1985). Morphological analysis, therefore, can potentially provide erroneous information on the genetic status of trout populations.

Protein electrophoresis provides a powerful method of stock identification between some species and subspecies of trout (Leary et al. 1987; Phelps and Allendorf 1982). The presence of fixed allelic

differences at several loci between taxa provides a means of identifying samples and detecting interbreeding (Allendorf and Leary 1988). These loci are commonly termed diagnostic loci (Ayala and Powell 1972). There are 10 diagnostic loci that can be used to distinguish between westslope cutthroat and Yellowstone cutthroat trout, six between westslope cutthroat and rainbow trout, and 10 between Yellowstone cutthroat and rainbow trout (Allendorf and Leary 1988). 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 of parental types with hybrids and hybrids with 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 alleles characteristic of taxa are randomly distributed among individuals (Allendorf and Leary 1988).

Disease Resistance

The success or failure of an introduction depends on many factors. Moyle and Leidy (1992) state that introduced fishes occasionally replace native species in natural habitats through competition or predation but that most replacements occur in altered environments that provide the introduced fishes an ecological advantage. One way that introduced species can gain an ecological advantage and eliminate native species is through the introduction of diseases (Moyle and Leidy 1992). For example, when the Chinese grass carp (Ctenopharyngodon idella) was introduced into North America it brought with it an Asiatic tapeworm (Bothriocephalus

acheilognathi) (Heckmann et al. 1987). The red shiner (Notropus lutrensis) has subsequently become a carrier of this tapeworm (Heckmann et al. 1987), and its subsequent introduction into the Virgin River, Utah, has corresponded with the decline of the endangered woundfin minnow (Plagopterus argentissimus) (Deacon 1988). The suspected mechanism behind this decline is the competitive superiority of red shiners to woundfin weakened by tapeworm infections (Moyle and Leidy 1992).

Disease and parasite sensitivity to endemic organisms may also be an important characteristic in determining the success or failure of an introduced species. Barbehenn (1969) states that animal hosts are often highly sensitive to parasites and pathogens which infect closely related host species.

Marnell (1981) observed that even though many Yellowstone cutthroat trout fry were stocked in the Quartz Creek drainage in Glacier National Park, there was no evidence of any genetic influence from Yellowstone cutthroat in the trout currently inhabiting the drainage. He hypothesized that the absence of a hybrid influence in that drainage may have been contributed to by competition with other trout, predation by bull trout (Salvelinus confluentus), and the failure of the stocked fish to coexist with the indigenous tapeworm Ceratocephalus sp., as native fish collected from Quartz Lake were heavily infected with this tapeworm, but showed no apparent ill effects.

Marnell et al. (1987) noted that the indigenous tapeworm in Glacier Park (Ceratocephalus sp.) was different than the indigenous tapeworm of the Yellowstone basin (Diphyllobothrium sp.). They further hypothesized that the two cutthroat trout subspecies, having evolved in the presence of

different parasites, developed different means to coexist with the parasites present in their respective habitats.

Selection experiments for increased disease resistance have shown that disease resistance often has a genetic basis. Hayford and Embody (1930), Snieszko et al. (1959), and Wolf (1953) described selection experiments for increased resistance of brook trout to furunculoses and ulcer disease. They further noted that different strains of brook trout also differed in their resistance to these diseases.

McIntyre and Amend (1978) tested 45 full-sib families of sockeye salmon, O. nerka, for the heritability of tolerance to infectious hematopoietic necrosis (IHN). Their results indicated that genetic factors made an important contribution to the differences between survival values for the families. They concluded that the heritability of tolerance to IHN for these fish was about 30%, and that the number of tolerant individuals could be increased by selection.

Buchanan et al. (1983) found that a coastal strain of summer steelhead from the Siletz River in Oregon, where Ceratomyxa shasta does not occur, was highly susceptible to ceratomyxosis, whereas three strains from the Columbia River basin, where the parasite is endemic, were resistant to the organism. They felt that exposure to the parasite of both smolts emigrating in the spring and adults ascending in the summer had resulted in resistance to C. shasta, probably through the process of natural selection. Zinn et al. (1977) also reached similar conclusions. They found that Columbia River basin strains of fall chinook salmon were more resistant to C. shasta than were the coastal strains.

Disease and parasite resistance may also decline in hybrid individuals. Hybrid breakdown or outbreeding depression is generally assumed to result from the break up of coadapted gene complexes, i.e., genetic combinations of two or more loci that somehow enhance each others phenotype (Hedrick 1985). Hemmingsen et al. (1986) crossed a stock of O. kisutch from the Columbia River basin, that are naturally exposed to C. shasta, to two coastal stocks that are not exposed to the parasite. They found that the susceptibility of the progeny from these crosses, when exposed to the parasite, were nearly always intermediate between the susceptibilities of the fish from the parental stocks. They also found that in all cases the progeny from the uncrossed Columbia River basin stock had the highest resistance to the parasite.

Sage et al. (1986) showed that introgressed populations of mice between Mus musculus and M. domesticus had significantly higher numbers of caecal pinworms (Aspiculuris and Syphacia) and a cestode (Hymenolepis) than did either parental type. They suggested that resistance to parasitism was reduced in the hybrid individuals and that the two mice species may have evolved different genes or gene complexes that controlled their resistance to parasitism. Thus, when the mice hybridize, the genes or gene complexes of each species that convey resistance are broken up or lost by chromosomal segregation and recombination, so that resistance in the hybrids is reduced.

Objectives

The South Fork of the Flathead River drainage is considered the "stronghold" of the westslope cutthroat trout within Montana (Liknes and Graham 1988). The Montana Department of Fish, Wildlife and Parks, therefore, wants to replace all the non-native trout populations within the South Fork with westslope cutthroat trout. Before this can be accomplished, however, a survey to determine the genetic composition of the populations within the drainage was required. The objectives of this study were the following:

(1) determine the taxonomic composition of Oncorhynchus populations (i.e. native westslope or introduced fish) from the South Fork of the Flathead River drainage using protein electrophoresis;

(2) test for differences in parasite intensities among fish of different taxonomic groups within populations.

(3) test for differences in frequencies of macroparasites in populations with different taxonomic origins.

MATERIALS AND METHODS

Study Area

The southern end of the South Fork of the Flathead River drainage originates at the head of Youngs and Danaher Creeks. The South Fork of the Flathead River itself begins at the confluence of these creeks (Figure 1). The northern end of the South Fork Flathead River occurs approximately eight kilometers downstream of Hungry Horse Dam; the total drainage encompassing 4,403 square kilometers (Anonymous 1988).

Within the historic range of the westslope cutthroat trout in Montana, the South Fork of the Flathead River drainage is unique in that much of the drainage has largely been undisturbed. Over half of the total drainage lies inside the Bob Marshall Wilderness Complex, including the upper 66 kilometers of the South Fork of the Flathead River (Anonymous 1988). An additional 62.1 square kilometers is contained in the Jewel Basin Hiking Area.

Collection of samples

With the assistance of personnel from the Montana Department of Fish, Wildlife and Parks, and the University of Montana's Genetics Laboratory, 49 lakes and 14 streams in the South Fork of the Flathead River drainage were surveyed (Figures 2, and 3). Lakes known or suspected to contain fish, or those that had a record of fish introductions were surveyed. Of the lakes surveyed, 15 do not currently contain fish (Table 1), but Olar and Twin Lakes have previously been stocked with cutthroat trout by the Montana Department of Fish, Wildlife and Parks, and Crimson Lake and Soldier Lake were known to have had fish prior to their survey (Joe Huston, Montana Department of Fish, Wildlife and Parks, pers. comm.). The

determination of stream selection was less consistent, but in general, they were surveyed on the basis of the presence of headwater lakes containing or having been stocked with non-native fishes, or because the stream itself was stocked with non-native fishes. Many streams and some small lakes within the Bob Marshall Wilderness, however, have still not been surveyed.

Eighty-two samples of trout, totaling 1,908 specimens, were collected by angling, gill netting, and electrofishing. The gill nets used were experimental, 3/4 to 2 inch mesh, monofilament, sinking mountain gill nets, 125 feet in length, and 5 feet in width. The physical and chemical characteristics of the lakes surveyed (i.e. area, depth, pH, total dissolved solids, and standard conductances) were also recorded during the collection of fish.

After collection, fish were transported on ice to the Montana Department of Fish, Wildlife and Parks Region One headquarters in Kalispell, where scale samples were taken, and the fish were weighed, measured, given an identification number, and frozen. Once frozen, they were transported to the University of Montana and stored at -40 or -80 C until tissue samples were removed for protein electrophoresis. Following this sampling, the fish were refrozen and stored for later parasitic examination. Table 2 lists names, sample sizes, locations, dates sampled, and genetic composition for each population.

Sample sizes from individual waters varied, but in general, an effort was made to collect at least 25 fish from each location. If it is assumed that the genes of the parental taxa are randomly distributed among the population (i.e. no linkage disequilibrium) then each gene at each

diagnostic locus will provide independent information about the status of a population. The probability of not detecting some percentage (x) of introduced trout genes in a westslope cutthroat population, therefore, is (1-x) raised to the total number of genes analyzed at the diagnostic loci, which is two times the number of diagnostic loci times the number of fish analyzed. To illustrate, there are generally six diagnostic loci that can be used to distinguish westslope cutthroat genes from rainbow trout genes. With a sample of 25 fish, therefore, the probability of not detecting one percent rainbow trout genes in a randomized hybrid swarm between westslope cutthroat and rainbow trout is $(1 - 0.01)^{300}$, which is one minus the percentage of rainbow trout genes raised to the total number of genes analyzed at the diagnostic loci, that is (2 x 6 x 25 = 300 genes). Thus, the probability of not detecting a one percent contribution of rainbow trout genes in the above population is $(0.99)^{300}$, or 4.9%. Alternately expressed, with a sample of 25 fish, one would expect to detect a one percent contribution of rainbow trout genes in a randomized hybrid swarm between westslope cutthroat and rainbow trout 95.1% of the time.

Because there are 10 diagnostic loci between westslope and Yellowstone cutthroat trout, however, the probability of not detecting a one percent contribution of Yellowstone cutthroat genes in a randomized hybrid swarm between these taxa is $(1 - 0.01)^{500}$, or 0.7%. Thus, with a sample of 25 fish one would expect to detect as little as one percent Yellowstone cutthroat trout genes in a randomized hybrid swarm with westslope cutthroat trout approximately 99% of the time.

Protein Electrophoresis

Horizontal starch gel electrophoresis was used to determine each fish's genotype at 45 enzyme loci encoding 18 enzymes, for proteins present in liver, eye, or muscle tissue (Table 3). Electrophoresis followed the procedures outlined by Utter et al. (1974), Allendorf and Utter (1979) and Leary and Booke (1990). Electrophoretic buffers and enzyme stains were those of Allendorf et al. (1977). Genetic nomenclature conforms with the standards for fish genetics in Shaklee et al. (1990). Loci and alleles are designated as by Leary et al. (1987, 1988). Allele mobilities are determined relative to the standard of 100 for the common allele in the Arlee strain of rainbow trout.

The following enzymes were analyzed, (loci and EC numbers in parentheses): adenylate kinase (AK-1*; AK-2*; 2.7.4.3), alcohol dehydrogenase (ADH*; 1.1.1.1), aspartate aminotransferase (sAAT-1*; sAAT 2*; sAAT-3,4*; 2.6.1.1), creatine kinase (CK-A1*; CK-A2*; CK-B*; CK-C1*; CK-C2*; 2.7.3.2), dipeptidase (PEPA-1*; PEPA-2*; 3.4.-.-), glucose-6-phosphate isomerase (GPI-A*; GPI-B1*; GPI-B2*; 5.3.1.9), glyceraldehyde-3-phosphate dehydrogenase (GAPDH-3*; GAPDH-4*; 1.2.1.12), glycerol-3-phosphate dehydrogenase (G3PDH-1*; G3PDH-2*; 1.1.1.8), L-iditol dehydrogenase (IDDH*; 1.1.1.14), isocitrate dehydrogenase (mIDHP-1*; mIDHP-2*; sIDHP-1,2*; 1.1.1.42), L-lactate dehydrogenase (LDH-A1*; LDH-A2*; LDH-B1*; LDH-B2*; LDH-C*; 1.1.1.27), malate dehydrogenase (sMDH-A1,2*; sMDH-B1,2*; 1.1.1.37), malic enzyme (mMEP-1,2*; sMEP-1*; sMEP-2*; 1.1.1.40), phosphoglucomutase (PGM-1*; PGM-2*; 5.4.2.2), phosphogluconate dehydrogenase (PGDH*; 1.1.1.44), superoxide dismutase (sSOD-1*; 1.15.1.1), tripeptide aminopeptidase (PEPB*; 3.4.-.-), and

xanthine dehydrogenase (XDH1*). The "1" designation at the XDH1* locus results from characterizations done at the phenotypic level.

The gel buffers used included:

AC (Clayton and Tretiak 1972)

Gel buffer: 0.002 M citric acid. pH 6.5

Electrode buffer: 0.04 M citric acid, pH 6.1

Both buffers are pH adjusted with N-(3-aminopropyl)-morpholine

AC+ same as AC with the addition of 0.002 M 2-mercaptoethanal and 0.0001 M NAD to the gel

MF (Market and Faulhaber 1965)

Stock solution: 0.9 M tris, 0.5 M boric acid, 0.02 M EDTA, pH 8.7

Gel buffer: 1:20 dilution of stock solution

Electrode buffer: 1:5 dilution of stock solution

RW (Ridgway et al. 1970)

Gel buffer: 0.03 M tris, 0.005 M citric acid, pH 8.5

Electrode buffer: 0.06 M lithium hydroxide, 0.03 M boric acid, pH 8.1

Gels are made by using 99% gel buffer and 1% electrode buffer

SR (Gall and Bentley 1981)

Gel buffer: 0.05 M tris, 0.009 M citric acid, pH 8.1

Electrode buffer: 0.30 M boric acid, 0.057 M lithium hydroxide pH 8.1

Gels are made by using 99% gel buffer and 1% electrode buffer

Table 4 lists the loci that distinguish the westslope cutthroat, Yellowstone cutthroat, and rainbow trout. In the South Fork of the Flathead River drainage, however, the alleles characteristic of rainbow trout and Yellowstone cutthroat trout at the usually diagnostic loci of CK-A2*, CK-C1*, and sIDHP-1,2* occurred at high frequencies in "pure" populations of westslope cutthroat trout and were, therefore, excluded from the analysis used to determine the relative purities of individual populations. In addition, at the PGM-1* locus Yellowstone cutthroat trout have a fixed null allele while westslope cutthroat have the common rainbow trout allele; allele frequencies at the null allele in Yellowstone cutthroat trout were, therefore, inferred from the square root of the null homozygote frequency. Because this estimation is inaccurate in non-random mating populations, the PGM-1* locus was also excluded from the analysis used to determine the relative purities of hybridized populations containing Yellowstone cutthroat genes. The PEPA-1* locus was also excluded from the above analysis because heterozygotes can be difficult to score.

Where population samples were duplicated, homogeneity of allele frequencies between the samples were tested using contingency table chi-square analysis. The genotypic distributions of loci within populations were measured for deviations from Hardy-Weinberg proportions using the fixation index (F). The fixation index is calculated from the formula, ($F = 1 - (H_o / H_e)$), where H_o is the observed proportion of heterozygotes and H_e is the expected proportion of heterozygotes based on random mating. The values of F range from zero (i.e. Hardy-Weinberg proportions) to one (complete absence of heterozygotes), and the

statistical significance of departures from expected genotypic proportions can be tested by $X^2 = \underline{F}^2 N$, where N is the sample size. There is one degree of freedom with two alleles (Li and Horvitz, 1953). If more than two alleles exist, the Chi-square test for fitness has [k(k-1)-2]/2 degrees of freedom, where k equals the number of alleles present. The significance levels for the contingency table and fixation index chi-squares were also modified according to Cooper (1968), because multiple, simultaneous comparisons were made between samples.

The association of nuclear loci was measured by estimates of gametic disequilibria from the genotypic data by the composite measure of Burrows (Weir, 1979, 1990; Langley et al., 1978; Campton, 1987). This method was chosen to estimate linkage disequilibria because it makes no assumptions regarding the mating structure of the populations (Campton, 1987).

Isoloci

In salmonid fishes, some pairs of loci produce a protein with identical function and electrophoretic mobility. For example, both sAAT-3* and sAAT-4* produce an aspartate aminotransferase present in muscle. The protein produced from the common allele at each of these loci occupies the same position in the gels after electrophoresis. Such pairs of loci are commonly termed isoloci. Their existence can be determined only when one or both loci are polymorphic (genetically variable). In such situations, however, it is not possible to determine at which locus of the pair a variant allele exists. In order to estimate the allele frequencies at the isoloci in westslope cutthroat, Yellowstone cutthroat (sAAT-3,4*, sMDH-A1,2*, and sMDH-B1,2*) and rainbow trout (sAAT-3,4*, sIDHP-1,2*, sMDH-A1,2*, sMDH-B1,2*, and sMEP-1,2*) populations, therefore,

each pair was considered to be a single gene with four instead of two copies per individual.

Parasite Analysis

In this study a subset of the fish analyzed genetically, 413 trout from 15 lakes, were also examined for the presence of macroparasites. Each lake examined was selected on the basis of its genetic characteristics and assigned a hybrid index (HI) value according to the average percentage of westslope cutthroat trout genes present in the sample. The index is calculated as HI = 100($\underline{E}$fi(W alleles)/L), where L is the number of loci and fi(W alleles) is the frequency of the westslope cutthroat trout alleles at the ith locus. Thus, a genetically "pure" population of westslope cutthroat trout would have a score of 100%, while a "pure" Yellowstone cutthroat or rainbow trout population would have a score of zero percent.

Each fish's outer body surface was examined for ectoparasites, including fins, gills, and inner opercular surfaces. After exterior examination, the fish were necropsied and examined for free parasites within the body cavity, and for encysted parasites on the surface of the body cavity and the internal organs. Next, the digestive tract was removed and divided into three regions (i.e. the esophagus and stomach, pyloric caeca, and intestine), and the contents of each region were examined for parasites under a dissecting microscope. Finally, fillets of muscle tissue were taken from each fish and examined for encysted parasites.

Cestode specimens collected were fixed in 10% formalin while trematode and nematode specimens were fixed in a 70% alcohol solution.

Representatives of the parasite specimens collected, were identified by Glenn L. Hoffman (Parasitologist, United States Fish and Wildlife Service, retired) and J.M. Kinsella (Parasitologist, University of Montana).

The Kruskal-Wallis H test (Kruskal and Wallis, 1952) was used to compare parasite intensities among all populations examined, and the Mann Whitney U test (Mann and Whitney, 1947) was used to make 2 x 2 comparisons of parasite intensities between populations, and between taxonomic groups within populations. The parasite intensity of each fish was calculated as the number of parasites it harbored. If more than one species of parasite was present in a population, a parasite intensity for each species was calculated.

Correlation coefficients were calculated using the statistical package in Minitab (Release 7.2, 1989) and were used to test for relationships between the parasite intensities, hybrid indices, and physical and chemical characteristics of the lakes studied. Usage of the terms, abundance, intensity, and prevalence follow the recommendations of Margolis et al., (1982): abundance is the mean number of parasites per fish examined, intensity is the number of individuals of a particular parasite species in each infected host, and prevalence is the percentage of infected fish.

RESULTS AND DISCUSSION

Nonhybridized Lake Populations of Westslope Cutthroat Trout

Westslope cutthroat trout were unable to gain access to many of the headwater lakes within the South Fork of the Flathead River drainage. Of the 34 lakes that contained fish populations, only seven appeared to harbor pure westslope cutthroat trout populations (Table 5); the polymorphic loci are listed in (Table 6). Of these, only Big Salmon and Doctor Lake are thought to have indigenous populations of fish. No barriers to fish passage exist between these lakes and the South Fork of the Flathead River, and Mountain whitefish (Prosopium williamsoni) and bull trout have been collected in gill net sets from both lakes (Montana Department of Fish, Wildlife and Parks survey data).

The other five lake populations (Cliff, Jenny, Squaw, and Upper and Lower Marshall) are probably not indigenous. No other fish species were collected from these waters, and all are drained by high gradient streams with existing barriers (i.e. falls and chutes). The occurrence of fish within most of these lakes, therefore, can be directly related to the stocking records of the lake. In fact, in gill net survey reports, Domrose (1968, 1970) indicated that Cliff and Jenny Lakes were fishless and recommended that both be stocked with westslope cutthroat trout. His 1968 report also documented the initial stocking of westslope cutthroat trout in Cliff Lake, but Jenny Lake was not officially stocked until 1979 (Montana Department of Fish, Wildlife and Parks fish planting records).

With sample sizes of at least 25 fish from Big Salmon, Cliff, Doctor, Jenny, lower Marshall, and Squaw Lake, there is at least a 95% chance of detecting as little as one percent rainbow trout genes and better than a

99% chance of detecting as little as one percent Yellowstone cutthroat trout genes in these samples. Thus, these populations are almost undoubtedly genetically pure westslope cutthroat trout. Due to the smaller sample size from upper Marshall Lake (N=7), however, it is only possible to be 95% certain of detecting as little as 4.2% rainbow trout or 2.6% Yellowstone cutthroat trout genes in this population. Thus, it is possible that this population may be slightly hybridized with one of the other taxa. Until demonstrated otherwise, however, it should be managed as a pure westslope cutthroat trout population.

Nonhybridized Stream Populations of Westslope Cutthroat Trout

Of the 14 streams sampled, only five appear to harbor pure westslope cutthroat trout populations (Table 5); the polymorphic loci are listed in Table 6. All of these populations appear to be indigenous except possibly for Marshall Creek where a probable barrier occurs below the area of fish collection. The presence of fish above this area, therefore, indicates that fish were either present in the creek before the "barrier" was formed, or that fish were stocked above the "barrier" at some unknown time. Thus, further investigation of this creek's ichthyofauna is required to determine if these fish are indigenous. The presence of other native species would suggest that the westslope are indigenous to this stream, while their absence would suggest that the westslope were introduced.

The presence of a "pure" population in Gordon Creek is also tenuous. It was sampled at two locations, approximately eleven kilometers apart, and the upper sample contained a small percentage of Yellowstone cutthroat trout genes. Four headwater lakes drain into Gordon Creek, and three

(George, Koessler, and Lick) contain Yellowstone cutthroat genes (This paper). George Lake, however, has a falls over 150 meter in height at its outlet, and fish that drift over it probably do not survive. Thus, the remaining two lakes are the likely source of the Yellowstone cutthroat genes present in the upper reach of this creek.

Populations With Uncertain Taxonomic Status

In addition to the populations listed above, alleles characteristic of westslope cutthroat trout were detected at practically all ($\geq$ 99%) of the diagnostic loci in seven other samples analyzed (Table 7); the polymorphic loci are listed in Tables 8 and 9. Two possible explanations exist for this situation. The samples may have come from a hybrid swarm with a very small percentage of non-native genes, or the alleles observed at the diagnostic loci may represent intra-specific genetic variation of westslope cutthroat trout that is identical to the common allele at this locus characteristic of the other taxon (Table 4). Available information on the genetic composition of historical broodstocks, fish stocking records, and lake survey data suggests that for most of these seven waters, the former explanation is the most plausible.

The history of cutthroat trout broodstocks in Montana can be divided into three eras. Before 1957, cutthroat trout stocked were Yellowstone cutthroat with a low probability of some hybridization with westslope cutthroat or rainbow trout (Joe Huston, Montana Department of Fish, Wildlife and Parks, pers. comm.). From 1957 through 1970 most cutthroat trout stocked were westslope cutthroat with a high probability of hybridization with rainbow trout and/or Yellowstone cutthroat trout. After 1970 most cutthroat trout stocked within the westslope cutthroat

trout's range have been pure westslope cutthroat with the possibility of some fish being westslope cutthroat x rainbow trout hybrids in the early 1980's, before the current broodstock in Anaconda was established (Joe Huston, Montana Department of Fish, Wildlife and Parks, pers. comm.).

This information, combined with lake survey data and fish stocking records, suggests that a small percentage of non-native genes probably does exist in the five lake populations listed in Table 7 (Birch, Crater, Fawn, Lower Seven Acres, and Upper Three Eagles). All of these, except for Birch Lake, were reported to be fishless by Domrose (1968, 1970), and all were subsequently stocked with production fish from the 1957 to 1970 era broodstock. The simplest explanation for the apparent presence of non-native genes within these populations, therefore, is that they resulted from the presence of non-native genes within the production fish stocked in those lakes, rather than rare intra-specific genetic variation of westslope cutthroat trout that is identical to the common allele in Yellowstone cutthroat or rainbow trout.

Birch Lake, like the four previous lakes, was probably also historically fishless. It is drained by a high gradient stream that contains numerous barriers to fish passage in its upper sections. The presence of fish in the lake, therefore, can be directly related to the lakes stocking history. The first official fish introduction occurred in 1938, when 15,000 undesignated, but presumed Yellowstone cutthroat trout eggs were stocked in the lake. Following this initial introduction, an additional 63,000 undesignated cutthroat trout fingerlings were stocked between 1939 and 1962; 33,000 of which were stocked prior to 1957 and, therefore, were also predominantly Yellowstone cutthroat trout. Following

these introductions, a combined total of 22,000 fingerlings designated as westslope cutthroat trout were stocked in 1975 (10,000), 1980 (6,000), and 1984 (6,000).

The enzyme analysis of 28 fish collected from this lake indicated that only 1/2 of one percent of the genes present were derived from Yellowstone cutthroat trout. The analysis further suggested that the Yellowstone cutthroat genes present were probably not randomly distributed within the population, as they were all confined to one fish from the sample. Therefore, the random assortment of Yellowstone cutthroat alleles within the sample was tested using the Poisson distribution. The results indicated a significant deviation from what would be expected if the Yellowstone cutthroat genes were randomly distributed within the fish ($X^2 = 6.7$; df=1; $P<0.01$).

Given the large number of Yellowstone cutthroat trout that were stocked within the lake, their low genetic contribution to the present population is puzzling. It suggests that either the early fish stockings were unsuccessful, or that successful reproduction within the lake is limited. Creel census data collected by the Montana Department of Fish, Wildlife and Parks indicates that the early fish introductions were successful. Physical data obtained while collecting fish for protein analysis, however, suggests that available spawning habitat is highly limited. No suitable areas for inlet spawning were present, and only a limited section of the outlet was available ($\leq$ 30 meters) before barriers to fish passage occurred. In addition, the ages of 22 of the 28 fish collected corresponded to the last two stocking dates, further suggesting that reproduction within the lake is limited. Thus, the non-random mating

observed is probably due to a combination of introducing pure hatchery westslope cutthroat into the system and to limited natural reproduction within the lake.

Gorge Creek also probably contains a small percentage of Yellowstone cutthroat genes. Sunburst Lake lies at the head of this drainage and contains an essentially pure population of Yellowstone cutthroat trout (Table 10). The simplest explanation for the presence of Yellowstone cutthroat genes in Gorge Creek, therefore, is to assume that fish are emigrating out of the lake and hybridizing with the fish in the creek.

The Gorge Creek collection was made approximately 13 kilometers from the outlet of Sunburst Lake, and of the 25 fish collected only one contained Yellowstone genes. This fish appeared to be a backcrossed first generation hybrid with a pure westslope cutthroat, suggesting that it was of recent hybrid origin. If fish are in fact emigrating out of Sunburst Lake, then a sample collected from closer to the mouth of the lake should contain a higher percentage of Yellowstone cutthroat genes, and a higher proportion of the fish should show hybridization.

For Deep Creek, however, it is not possible to determine whether a small percentage of Yellowstone cutthroat genes exist within the population, or if intra-specific genetic variation of westslope cutthroat identical to the common allele of Yellowstone cutthroat trout exists. Two variant alleles at two different loci identical to the common Yellowstone cutthroat allele were observed in the population. However, the GPI-A* variant occurs rarely, at low frequencies, in some westslope cutthroat populations. The determination of the status of this population, therefore, relies on the assignment of the remaining variant to either

westslope or Yellowstone cutthroat, and makes an absolute classification of the population difficult.

Introduced Trout Populations

Ten populations within the South Fork of the Flathead River drainage contained non-native trout populations. Brook trout were present in one lake; Yellowstone cutthroat trout were present in two lakes; rainbow trout were present in three lakes and one creek, and introgressed Yellowstone cutthroat by rainbow trout populations occurred in three lakes (Table 10). Of these populations, seven are in the Bob Marshall Wilderness, two are in the Jewel Basin Hiking area, and one occurs between these two areas. Since my surveys, however, the Jewel Lakes within the Jewel Basin Hiking area have been chemically treated with rotenone and currently contain a westslope cutthroat trout population.

No official stocking records exist for six of these waters (Big Salmon Creek, Jewel, Lena, Lick, Necklace chain, and Ross Lake), but unofficial records and letters document the stocking of fish in all but Ross Lake and Big Salmon Creek (Montana Department of Fish, Wildlife and Parks letter from Frank A. Stefanich to George Holton, 1957, and an undated file correspondence obtained by Tom Schurr from Outfitter R.W. Wilhelm). The presence of rainbow trout in the upper reaches of Big Salmon Creek, however, is probably the result of downstream movement of these fish from the headwater lakes within the drainage that contain pure rainbow trout populations (Figure 3). Although the sample size is small (N=2), the population is considered to be pure rainbow trout because upstream migration of westslope cutthroat from Big Salmon lake is blocked by a barrier falls approximately six kilometers above the lake. The

samples were combined into a single Aeneas Creek sample in the following analysis.

Thirty of the 55 fish sampled were homozygous for westslope cutthroat alleles at all the diagnostic loci, and the remaining 25 fish contained alleles from both taxa. At three of the loci (sAAT-1*, CK-A2*, and IDDH*) a significant ($P<0.01$) deficit of heterozygotes exists compared with expected Hardy-Weinberg proportions. The F values for these loci were 0.485, 0.374, and 1.000 respectively, and indicate that the sample does not represent a random mating hybrid swarm.

No records of rainbow trout introductions into Aeneas Creek exist, but rainbow trout and westslope cutthroat x rainbow trout hybrids do occur in the Graves and Jones Creek drainages. The presence of rainbow trout genes in Aeneas Creek, therefore, is probably the result of fish migrating from these waters into Aeneas Creek. This suspected migration is also the likely cause of the non-random mating observed.

Lower Big Hawk Lake

Lower Big Hawk Lake lies at the head end of Jones Creek in the Jewel Basin Special Management Area at an elevation of 1,828 meters. It covers 17.4 surface hectares, and has a maximum depth of 11 meters. Historically fishless (Huston 1991), this lake was first stocked in 1941, with 3,600 fingerling Yellowstone cutthroat trout. After 1941, it was not officially stocked again until 1986, when approximately 5,000 westslope cutthroat fingerlings were introduced. An additional 25,000 westslope fingerlings have also been introduced since 1986.

Enzyme analysis of two trout collections, 48 specimens in 1986, and 49 specimens in 1990, confirmed the presence of a hybrid westslope

cutthroat x Yellowstone cutthroat trout population. The 1986 sample contained 53.6% westslope cutthroat genes and 46.4% Yellowstone cutthroat trout genes, while the 1990 sample contained 82.1% westslope genes and 17.9% Yellowstone cutthroat genes (Table 13). The increase of westslope cutthroat genes in the 1990 sample, however, is attributed to the stocking, and subsequent collection, of pure hatchery westslope within the lake following the 1986 survey, rather than a real decrease in the actual amount of Yellowstone genes present within the lake.

The presence of westslope genes in the population prior to 1986 was surprising because there is no record of their introduction. In analyzing the protein data collected in 1986 we can gain some insight into when westslope cutthroat were likely introduced into the system. The lack of any significant departures from expected Hardy-Weinberg proportions at any of the polymorphic loci, and the detection of all three electrophoretic phenotypes at the diagnostic loci, indicates that the population is randomly mating. The presence of 10 trout that appear to be pure, eight westslope and two Yellowstone cutthroat, and one possible first generation hybrid suggests that some association between loci still exists.

When species that are divergent at many loci mate, non-random associations between alleles at different loci are generated and these associations will persist even after several generations of random mating (Allendorf and Phelps 1981). For unlinked loci in random mating populations, with no selection and non-overlapping generations, the decay of this association is expected to occur at a rate of 50.0% per generation (Crow and Kimura 1970; Brown 1975; Gyllensten et al. 1985), with no statistically detectable linkage between diagnostic loci occurring in

populations that have been hybridizing for six or more generations (Gyllensten et al. 1985). In linked loci, however, the rate of decay and the approach to random association will consequently be delayed.

To test for this association, estimates of gametic disequilibria were derived from genotypic data using the composite method of Burrows. These data indicated that the alleles of the diagnostic loci were not in equilibrium. All 36 pairwise tests of linkage disequilibrium were significant and positive, indicating that the alleles characteristic of each subspecies were still positively associated (Table 14). Thus, although this population was a randomly mating hybrid swarm during the 1986 survey, it had only been randomly mating a short time.

A possible explanation for the presence of westslope genes in the lake prior to 1986 may be found in the Montana Department of Fish, Wildlife and Parks stocking records and in the 1986 survey data collected for upper Big Hawk Lake. Although this lake was officially stocked with westslope cutthroat trout fingerlings on four occasions, in 1967, 1975, 1980, and 1984, only one large fish was temporarily caught in an overnight gill net set. In addition, no other fish were observed during the survey, suggesting that either the introductions were unsuccessful, or that through error, some of the fish intended for upper Big Hawk Lake were stocked in the lower lake. This hypothesis is supported by the physical outline of lower Big Hawk Lake, which is actually two cirque lakes connected through approximately 40 meters of non-flowing channel. This configuration, therefore, may have led to the introduction of westslope fingerlings into the upper half of lower Big Hawk Lake prior to 1986, when the first documented introduction occurred.

Upper Big Hawk Lake

At an elevation of approximately 1,997 meters, upper Big Hawk Lake covers 1.7 surface hectares, and has a maximum depth of 10 meters. No inlets are present and the outlet is small and intermittent, with no potential spawning habitat. During times of discharge, the outlet drains towards lower Big Hawk Lake, but no potential for fish passage appears to exist, indicating that this lake was also historically fishless.

Although no fish were collected for enzyme analysis during the 1986 survey, a remnant trout population was present. Because no potential for reproduction exists, however, it can be assumed that the fish currently present in the lake are principally derived from the introductions of hatchery westslope cutthroat trout that have occurred since 1967. However, since the appropriate protein data are lacking this conclusion should be regarded as tentative.

North Biglow Lake

This lake is 1,860 meters above sea level, covers approximately 9.7 surface hectares, has a maximum depth of 10 meters, and drains a small catchment basin in the Wheeler Creek drainage. The outlet, Biglow Creek, merges with Wheeler Creek about two miles downstream from the lake. Historically fishless (Joe Huston, Montana Department of Fish, Wildlife and Parks, pers. comm.), the lake was stocked only once, in 1960, with 7,875 four inch cutthroat trout from the now closed Hamilton hatchery.

Protein analysis of 25 fish collected in 1984 indicated an introgressed population containing 97.7% westslope cutthroat genes and 2.3% rainbow trout genes (Robb Leary, University of Montana Genetics Laboratory, pers. comm.). Since no rainbow trout were stocked after 1960,

and no fish existed in the lake prior to 1960, the presence of a slightly hybridized westslope cutthroat by rainbow trout population was unexpected, and indicates that the Hamilton broodstock contained rainbow trout genes when the lake was stocked.

Black Lake

Black Lake, in the Jewel Basin Special Management Area, is one of 14 lakes in the Graves Creek drainage. At an elevation of 1,841 meters, it covers approximately 20.4 surface hectares and has a maximum depth of 30 meters. It is connected to Picnic Lakes via an outlet stream, and its outlet drains through lower Black Lake to merge with Graves Creek about 2.5 kilometers and 290 meters below its origin. Spawning is restricted to the first 30 meters of the outlet, before a series of falls and chutes prevent fish passage from below, and to two small gravel fans in the mouths of two intermittent inlets.

Due to an impassable falls in Graves Creek below Handkerchief Lake, the last lake in the drainage, all of the headwater lakes in the drainage were probably historically fishless. Trout were first introduced to Black Lake in 1938, when 15,000 Yellowstone cutthroat eggs and 8,000 fingerlings were stocked. An additional 7,267 fingerling Yellowstone cutthroat were also stocked in 1940. Following these introductions, the lake was stocked with rainbow trout obtained from the Creston National Fish Hatchery some time prior to 1957 (Montana Department of Fish, Wildlife and Parks, Letter from Frank A. Stefanich to George Holton, 1957). Westslope cutthroat trout were not stocked until 1973, when 5,146 fingerlings were introduced. An additional 64,000 westslope fingerlings have been stocked since 1973;

8,000 were stocked in 1979, and 1984, and 48,000 were stocked from 1986 through 1991.

Ninety-three trout were collected for electrophoresis during five sampling trips to Black Lake and enzyme analysis of the first two samples collected in 1986 confirmed that hybridization between all three taxa previously stocked in the lake had occurred. The initial 27 fish collected in July contained 91.1% westslope cutthroat genes, 6.3% rainbow genes, and 2.6% Yellowstone cutthroat trout genes while 15 fish collected in August contained 76.1% westslope genes, 22.8% rainbow trout genes and 1.1% Yellowstone cutthroat genes (Table 15). Contingency chi-square analysis indicated that there was a significant difference in allele frequencies between the samples (X^2=26.77, df=15, P=0.031) so each sample was treated independently.

Of the 27 fish collected in July, 23 were homozygous for westslope alleles at all of the diagnostic loci, three had alleles from all three taxa, and one was a rainbow x Yellowstone cutthroat trout hybrid. Nine of the 15 fish collected in August were also homozygous for westslope alleles; four were heterozygous for both westslope and rainbow alleles at one or more loci, and two had alleles from all three taxa. At the LDH-B2* and mMEP-1* loci in the 27 fish sample and the CK-A2* and IDDH* loci in the 15 fish sample, a significant (P=0.006) deficiency of heterozygotes exists compared with expected Hardy-Weinberg proportions. The F values for these loci were 1.000, 1.000, 0.700, and 1.000 respectively, and indicates that these samples were not collected from a random mating hybrid swarm.

The inclusion of recently introduced hatchery westslope in the collections is the most plausible explanation for the non-random mating observed in each sample, and age and growth data support this hypothesis. Thirty-two fish, from both samples, were homozygous for westslope alleles at all diagnostic loci, 23 of which were two-years old. This age corresponds to the most recent introduction of hatchery westslope. Unequal contributions of hatchery fish in each collection also probably accounts for the significant difference in allele frequencies observed between the samples.

Two additional small samples were collected from Black Lake in 1987 and 1990. In 1987, two post-spawning adults were collected from the outlet. One appeared to be a pure rainbow trout, and the other was a slightly hybridized rainbow trout x Yellowstone cutthroat trout. In 1990, five more fish were collected for analysis. Four were homozygous for westslope alleles at all the diagnostic loci, and the other was a slightly hybridized rainbow trout x Yellowstone cutthroat trout. Although small, these samples also indicate a non-random mating population in Black Lake.

The last collection of fish from Black Lake was made in 1991. Enzyme analysis of 44 fish detected 98.6% westslope genes and 1.4% rainbow trout genes, but no Yellowstone genes. Forty-two of these fish were homozygous for the westslope allele at all diagnostic loci, and two were heterozygous for both westslope and rainbow alleles at three of the diagnostic loci. Unlike the two samples collected in 1986, however, this sample conforms to expected Hardy-Weinberg proportions and appears to have been collected from a random mating population. The genetic characteristics of the two hybridized fish, however, suggest that they may represent backcross

progeny from matings between westslope cutthroat and first generation hybrids.

To determine if the genes from the two species were randomly distributed among the individuals in this sample, a comparison was made of the distribution of the number of rainbow trout alleles per fish summed over all diagnostic loci to that expected based on a Poisson distribution with a mean equal to the frequency of rainbow trout alleles averaged over all loci. The number of rainbow trout alleles per individual did significantly differ (X^2=12.48, df=2, P<0.005) from that expected based on a random distribution, and indicates that the sample was not collected from a random mating population.

The lack of any significant deviations from expected Hardy-Weinberg proportions, and the non-random distribution of rainbow trout alleles observed within the sample, indicates that most of the fish collected in 1991 were from hatchery introductions. It also suggests that the population structure within the lake has been largely influenced by the hatchery introductions, and that successful natural reproduction in Black Lake is low.

Blackfoot Lake

Blackfoot Lake, in the Jewel Basin Special Management Area, is also in the Graves Creek drainage. It is 1,698 meters above sea level, covers approximately 6.9 surface hectares, and has a maximum depth of seven meters. It is connected to North and South Twin Lakes via their outlet stream, and its outlet joins with the Jewel and Black Lake outlets to form Graves Creek. Its reproductive capacity is judged to be good, with available spawning habitat present in both of its inlets and its outlet.

Historically fishless, the lake was stocked with 8,000 fingerling cutthroat in 1938; 2,100 fingerling cutthroat in 1965; 2,500 fingerling westslope cutthroat in 1982, and with 15,000 fingerling westslope cutthroat from 1986 through 1991. The cutthroat stocked in 1938 were undoubtedly Yellowstone cutthroat, but those stocked in 1965 were probably westslope cutthroat. In addition, Blackfoot Lake, like Black Lake, was also stocked with rainbow trout obtained from the Creston National Fish Hatchery some time prior to 1957.

One hundred adult trout and 42 fry were collected for enzyme analysis during four sampling trips to Blackfoot Lake; 24 fish were collected in 1986, 12 in 1987, 34 in 1990, and 30 adults and 42 fry in 1991. Rainbow and westslope cutthroat genes were present in all samples (Table 15), but no Yellowstone genes were detected in any of the samples, indicating that their introduction was not successful.

Analysis of the samples indicates that a non-random mating population exists in the lake. Of 24 fish collected in 1986, 18 were homozygous for rainbow trout alleles, and six were homozygous for westslope cutthroat alleles at all the diagnostic loci. In the 1987 sample, eight of the 12 fish collected were homozygous for rainbow trout alleles, and four were homozygous for westslope cutthroat alleles. Domrose (1968), also observed a similar situation in 13 fish he collected from an overnight gill net set. From visual observations, he detected no obvious evidence of hybridization between the taxa, and classified the fish as 12 pure rainbow trout and one pure westslope cutthroat trout.

Analysis of the fish collected in 1990 and 1991, however, did detect hybridization. Of 34 fish collected in 1990, 22 appeared to be pure

westslope, 10 appeared to be pure rainbow, and two were heterozygous for westslope and rainbow alleles at all the diagnostic loci, indicating that they were probably first generation hybrids. In 1991, 30 additional adults and 42 fry were also collected. Of the adults, 23 appeared to be pure westslope, four appeared to be pure rainbow, and three were heterozygous at one or more loci for both westslope and rainbow trout alleles. Only muscle tissue could be analyzed from the fry, but 32 appeared to be pure westslope, one appeared to be pure rainbow, and nine were heterozygous at the diagnostic loci detectable in muscle tissue, suggesting that they were also first generation hybrids. Thus, although hybridization between these taxa has occurred, it appears to have only recently begun.

Clayton Lake

This lake is also in the Jewel Basin Special Management Area. At an elevation of 1,823 meters, it covers 25.5 surface hectares, and has a maximum depth of 30 meters. Spawning habitat is available in the southern inlet and the outlet, but it is restricted to the first 100 meters of the outlet before a series of falls prevent fish from returning to the lake, and to about 20 meters of the inlet.

Due to numerous barriers (falls and chutes) in the upper sections of Clayton Creek, the lake was probably historically fishless prior to the introduction of 20,000 undesignated, but presumed, Yellowstone cutthroat trout eggs in 1926. Subsequent to this introduction, 62,000 additional Yellowstone cutthroat eggs and 25,250 fingerlings were stocked through 1953. In addition to the introduced Yellowstone cutthroat trout, 12,000 rainbow trout fingerlings were also stocked in 1928. The first

introduction of westslope cutthroat occurred in 1982, when 8,000 fingerlings were stocked. Between 1986 and 1989 another 34,000 westslope cutthroat fingerling were stocked in the lake.

Three samples of fish for enzyme analysis were collected from Clayton Lake; 14 were collected in 1985, 29 in 1986, and 32 in 1989. Enzyme analysis of these samples confirmed hybridization between westslope and Yellowstone cutthroat trout, but did not detect any rainbow trout genes, and suggests that their introduction was unsuccessful. In 1985, 87.8% of the alleles were derived from westslope cutthroat; in 1986, 73.0% of the alleles were derived from westslope cutthroat, and in 1989, 92.7% of the alleles were westslope cutthroat trout alleles (Table 13). Contingency table chi-square analysis indicated that there were significant differences in allele frequencies between the samples (X^2=76.973, df=18, P<0.001), so each sample was treated independently.

In the 1985 sample, 12 of the 14 specimens collected were homozygous for westslope alleles at all diagnostic loci, while the remaining two were homozygous for Yellowstone cutthroat alleles at at least five of the eight diagnostic loci. In the 1986 sample, 20 of the 29 specimens were homozygous for westslope alleles, while nine had predominantly Yellowstone cutthroat alleles at the diagnostic loci. In the 1990 sample, 27 of the 32 specimens were homozygous for westslope alleles; three were heterozygous for Yellowstone alleles at one diagnostic locus; one was heterozygous for westslope alleles at three diagnostic loci, and one was homozygous for Yellowstone alleles.

Significant (P<0.005) deficits of heterozygotes existed compared with expected Hardy-Weinberg proportions at four of the diagnostic loci in the

1985 sample, and at six of the diagnostic loci in the 1986 and 1989 samples. These results indicate that the samples were not collected from a random mating population; a result not unexpected given the recent stockings of pure hatchery westslope cutthroat trout into Clayton Lake.

The collection of backcrossed, westslope x Yellowstone hybrids in the 1985 and 1986 samples, however, was unexpected. If in fact westslope were not introduced until 1982, no backcrossed specimens should have been collected. Three possible explanations exist for this situation; the lake had a resident population of westslope cutthroat prior to the introduction of Yellowstone cutthroat trout; an undocumented introduction of westslope cutthroat occurred, or a mix of cutthroat trout types were stocked in the past.

It seems unlikely that fish were present in Clayton Lake prior to their introduction in 1926. No other taxa have been documented from the lake, and downstream populations are currently unable to gain access to the lake because of barriers present in the outlet stream. Thus, one of the latter two explanations appear more likely but it is not possible to determine with certainty which is correct.

Clayton Creek

Originating as the outlet to Clayton Lake, Clayton Creek has an average gradient of approximately 118 meters per kilometer over its seven kilometer course to Hungry Horse Reservoir. In 1949 a single introduction of 10,000 two inch cutthroat trout, presumably the Yellowstone subspecies, were stocked in the creek.

Seventy-eight trout were collected for enzyme analysis during three sampling trips to Clayton Creek. Specimens from two samples, 25 fish in

1983, and 26 fish in 1990, were collected from the same approximate location in the lower reach of the creek, but the third sample of 27 fish, also obtained in 1990, was collected from an upstream location. Analysis of the samples confirmed hybridization between westslope and Yellowstone cutthroat. In 1983, 6.7% of the genes in the population were of Yellowstone cutthroat trout origin, while in 1990, 7.0% of the genes in the lower sample and 4.7% of the genes in the upper sample were of Yellowstone cutthroat trout origin (Table 17). Because allele frequency differences between the samples were not significantly different (X^2=44.907, df=32, P=0.065), the samples were combined into a single Clayton Creek sample in the following analysis.

Fifty of the 78 fish analyzed were homozygous for westslope cutthroat alleles at all the diagnostic loci, while the remaining 28 fish contained genes from both taxa at one or more loci. A significant (P<0.007) deficit of heterozygotes existed at two of the diagnostic loci (IDDH*, and PEPB*) compared to Hardy-Weinberg proportions. The F values for these loci were 0.410, and 0.307 respectively, and indicate that the sample was not derived from a random mating hybrid swarm. Periodically, the creek population is undoubtedly exposed to adult and juvenile migrants from the lake, and the inclusion of some of these fish within the samples probably accounts for the non-random mating observed.

Doris Lake #2

Doris Lake #2 is one of four headwater lakes in the Fawn Creek drainage. At an elevation of 1,960 meters above sea level, it covers 2.2 surface hectares, has a maximum depth of nine meters, and drains approximately 100 meters to Doris Lake #3. No inlets are present, and the

outlet is small and intermittent with only a limited potential for reproduction in its first 15 meters. Additional spawning may also occur along the west shoreline in a small spring fed area, but the overall reproductive success within the lake is probably low.

Historically fishless, the first reported introduction of trout in Doris lake #2 occurred in 1967, when 2,360 two inch westslope cutthroat were stocked. An additional 7,110 westslope fingerlings were later stocked between 1969 and 1985. Enzyme analysis of thirty-two fish collected in 1986 confirmed hybridization between westslope cutthroat and rainbow trout; 97.3% of the alleles at the four loci used to determine the relative genetic contributions from these two taxa were of westslope cutthroat trout origin (Table 15). Thirty-one of the 32 fish sampled were homozygous for westslope alleles at all four diagnostic loci, while one specimen was homozygous for rainbow trout alleles at three diagnostic loci, and heterozygous for a westslope cutthroat and a rainbow trout allele at the other diagnostic locus. Obviously, this sample was not derived from a random mating hybrid swarm. The population is largely westslope cutthroat trout, with a slight hybrid influence from rainbow trout.

Since there are no documented introductions of rainbow trout in the lake, the presence of rainbow trout genes in the population was unexpected. Two possible explanations exist for this situation. Some of the cutthroat stocked in the lake prior to 1986 may have been slightly hybridized with rainbow trout, or there was an undocumented introduction of rainbow trout in the lake. Given that the only fish of definite hybrid origin was predominantly rainbow trout at the diagnostic loci, it is

unlikely that the rainbow trout genes present were derived from the introduction of hybridized fish; rather it suggests that an undocumented introduction of rainbow trout occurred in the lake.

Age and growth data obtained from the 1986 sample may lend support for this view. In 1985, 1,000 westslope cutthroat fingerlings were stocked in Doris Lake #2, and all of the specimens collected in 1986 were determined to be one year old (Joe Huston, Montana Department of Fish, Wildlife and Parks, pers., comm.). This suggests that the majority of specimens collected were from the 1985 hatchery introduction and, therefore, may indicate that the fish present in the lake prior to the 1985 introduction contained a large percentage of rainbow trout genes, an unlikely situation if in fact the rainbow trout genes were derived from hatchery introductions.

Doris Lake #3

At an elevation of 1,948 meters, Doris Lake #3 covers approximately 1.6 surface hectares, has a maximum depth of five meters, and drains approximately five kilometers to the South Fork of the Flathead River below Hungry Horse Dam. As in Doris #2, spawning habitat in Doris #3 is restricted; limited to about 15 meters of the inlet and to the first 15 meters of the outlet. Historically fishless the first reported introduction of trout into Doris Lake #3 also occurred in 1967 when 2,360 two-inch westslope cutthroat trout were stocked. An additional 5,560 westslope cutthroat trout fingerlings were also stocked between 1977 and 1985.

Enzyme analysis of 26 specimens collected in 1986 indicated hybridization between westslope cutthroat and rainbow trout; 98.1% of the

alleles at the four diagnostic loci appeared to be of westslope cutthroat trout origin (Table 15). Twenty-three of the 26 fish analyzed were homozygous for westslope cutthroat alleles at the diagnostic loci, while two fish were heterozygous and one was homozygous for the allele characteristic of rainbow trout at the GPI-A* locus. However, because the GPI-A* variant characteristic of rainbow trout is present at a low frequency in the current westslope broodstock and occurs rarely in wild populations of westslope, the variation observed can not conclusively be assigned. The presence of rainbow trout genes in Doris Lake #2, however, suggests that the variation observed at this locus in Doris Lake #3, is in fact rainbow trout variation.

George Lake

George Lake is one of two lakes at the head of George Creek in the Bob Marshall Wilderness. Situated just below a smaller fishless lake, George Lake lies at an elevation of 2,170 meters, covers approximately 49 surface hectares, and is over 60 meters deep. Spawning is available in about 100 meters of the outlet, before a 150 meter falls occurs, and in the mouths of three small inlets. In addition, limited spawning habitat may also be available in a few spring areas along the lake's North shore. Historically fishless, George Lake was first stocked with an unspecified number of Yellowstone cutthroat trout in the mid 1930's (Letter from Robert Schumacher, Montana Department of Fish, Wildlife and Parks District One Fisheries Manager, to Robert K. Bergman, 1971). Additional introductions occurred in 1965, when 5,200 cutthroat trout fingerlings were stocked, and between 1988 and 1990 when 24,000 westslope fingerlings were stocked.

Two separate collections of trout were made from George Lake. Twenty-seven fish were collected in 1987, and 28 fish were collected in 1990. Enzyme analysis of both samples confirmed hybridization between westslope and Yellowstone cutthroat trout; in 1987, 66.7% of the alleles at the eight diagnostic loci were of Yellowstone cutthroat origin, and in the 1990 sample, 55.8% of the alleles at the diagnostic loci were characteristic of Yellowstone cutthroat trout (Table 13).

Twenty-six of the 27 fish examined in 1987 contained alleles from both taxa, and the remaining specimen was homozygous for westslope alleles at all the diagnostic loci. All three electrophoretic phenotypes were detected at all the diagnostic loci, and no significant deviations from expected Hardy-Weinberg proportions were observed at any of the diagnostic loci, suggesting that the sample was collected from a random mating population.

In the 1990 sample, twenty-two of the 28 fish examined possessed alleles from both taxa. All three electrophoretic phenotypes were detected at all the diagnostic loci, and no deviations from expected Hardy-Weinberg proportions were observed at any loci. Thus, this sample also appears to be drawn from a random mating population. In this sample, however, three specimens appeared to be pure Yellowstone and three appeared to be pure westslope. The three "Yellowstone" specimens were probably actually hybrids that happened to possess only Yellowstone alleles at the diagnostic loci by chance alone, but some or all of the three "westslope" specimens could have originated from the 1988 year class of hatchery westslope stocked in the lake, as all three were determined to be two years old.

Although the population is randomly mating, it has not been that way for an appreciable length of time. Twenty-two of 28 pairwise tests for gametic disequilibria in 1987, and 27 of 28 pairwise tests for gametic disequilibria in 1990, were significant and positive (Table 14), and indicated that the alleles characteristic of each subspecies were still positively associated. The increases in the pairwise disequilibria values observed in the 1990 sample, and the overall increase in the number of significant pairwise tests between the two samples also suggests that some recently introduced hatchery fish were collected in the 1990 sample.

Graves Creek

Graves Creek begins at the confluence of the Black and Blackfoot Lake outlet streams. It drops an average of 56 meters per kilometer over its nine kilometer course to Hungry Horse Reservoir, flowing through Handkerchief Lake about one and one half kilometers above the reservoir. Due to the falls below Handkerchief Lake, however, Graves Creek was probably historically fishless prior to the introduction of trout into the drainage. A total of 60,000 Yellowstone cutthroat trout eggs and 77,266 fingerlings were stocked in Graves Creek between 1929 and 1951.

Ninety-four trout, from two stream locations, were collected for analysis during three sampling trips to Graves Creek. The first two collections, 27 specimens in 1983, and 26 in 1989, were from the same approximate location, but the 1991 sample (N=41) was collected inside the Jewel Basin Special Management Area approximately three kilometers upstream from the previous samples.

Enzyme analysis of all three samples confirmed hybridization between westslope cutthroat, Yellowstone cutthroat and rainbow trout (Table 16).

In the 1983 sample, 80.1% of the alleles were from westslope; 17.6% were from rainbow, and 2.3% were from Yellowstone cutthroat. In the 1989 sample, 83.2% of the alleles were from westslope; 15.4% were from rainbow, and 1.5% were from Yellowstone cutthroat. In the 1991 sample collected from the upstream location, however, only 56.4% of the alleles were from westslope, while 42.5% were from rainbow, and 1.1% were from Yellowstone cutthroat. The differences in allele frequencies among the samples were significant (X^2=136.774, df=38, P<0.001) so each sample was treated independently.

Significant (P<0.006) deviations from expected Hardy-Weinberg proportions were observed at three of eight diagnostic loci (GPI-A*, IDDH*, and mMEP-1*) in the 1983 sample; one of ten polymorphic loci (CK-A2*) in the 1989, and in two of the diagnostic loci (sAAT-1* and IDDH*) in the 1990 sample. Thus, these samples were not collected from random mating hybrid swarms. Emigration of stocked fish out of the headwater lakes of the Graves Creek drainage provides the most plausible explanation for the apparent non-random mating observed in the samples. Over 100,000 westslope fingerlings have been introduced into the headwaters of the drainage in the last ten years, and well over 300,000 fish have been stocked in the drainage as a whole.

Handkerchief Lake

Handkerchief Lake is 1,170 meters above sea level, covers approximately 13 surface hectares, and is approximately 23 meters deep. Historically fishless, an initial introduction of 10,000 Yellowstone cutthroat trout eggs was made into this lake in 1936. Subsequently, 79,500 additional Yellowstone fingerlings were stocked between 1948 and

1957, and 45,000 westslope fingerlings were stocked between 1986 and 1990. In addition, the lake also supports an introduced Arctic grayling (Thymallus arcticus) population.

Thirty-one trout were collected for analysis during two sampling trips to the lake; 15 specimens were collected in 1986, and 16 were collected in 1991. Enzyme analysis of these specimens confirmed hybridization between westslope cutthroat, Yellowstone cutthroat and rainbow trout (Table 16). In 1986, 92.7% of the alleles were from westslope; 5.2% were from rainbow, and 2.1% were from Yellowstone cutthroat. In the 1991 sample, however, only 65.8% of the alleles were from westslope, while 33.0% were from rainbow, and 1.2% were from Yellowstone cutthroat.

In the 1986 sample, nine of the specimens collected were homozygous for westslope alleles at the diagnostic loci, and six were heterozygous for alleles characteristic of at least two of the taxa at one or more of the diagnostic loci. In the 1991 sample, six specimens were homozygous for westslope alleles; nine were heterozygous for alleles characteristic of at least two of the taxa, and one was homozygous for rainbow trout alleles at all diagnostic loci. Significant ($P<0.006$) departures from expected Hardy-Weinberg proportions were also observed at two of the diagnostic loci in the 1986 sample (GPI-A* and mMEP-1*), and in the LDH-B2* locus in the 1991 sample, and indicates that the samples were not derived from a random mating population. The non-random mating observed is probably due to the recent introductions of hatchery westslope cutthroat into Handkerchief lake, and to the immigration of Graves Creek fish into the lake. The downstream movement of the Graves Creek fish

probably being caused by the increased introductions of westslope cutthroat trout into the headwater lakes of Graves Creek.

Jones Creek

Jones Creek, which begins at the confluences of the outlets from lower Big Hawk Lake and Pilgrim Lake, has an average drop of 170 meters per kilometer and flows approximately four kilometers before joining Aeneas Creek. Enzyme analysis of two samples collected from the same approximate location, 25 specimens in 1983 and 26 specimens in 1989, confirmed hybridization between westslope cutthroat and Yellowstone cutthroat trout.

In the 1983 sample, 91.7% of the diagnostic alleles were characteristic of westslope cutthroat, while in 1989, 94.7% of those alleles were of westslope cutthroat trout origin (Table 17). Contingency table chi-square analysis, however, indicated that the change in allele frequencies between the samples was not significant (X^2=23.298, df=16, P=0.106) so the samples were combined into a single Jones Creek sample in the following analysis.

Twenty-nine of the 51 fish analyzed were homozygous for westslope cutthroat alleles at all the diagnostic loci, while the remaining 22 fish were heterozygous for both westslope and Yellowstone alleles at one or more of the loci. The population also appears to be randomly mating as no significant departures from expected Hardy-Weinberg proportions were detected at any of the polymorphic loci. Although there is no record of Yellowstone cutthroat trout introductions in Jones Creek, lower Big Hawk Lake, a headwater lake to Jones Creek, does contain Yellowstone cutthroat trout genes. The presence of Yellowstone genes in Jones Creek, therefore,

is probably the result of emigration of fish from lower Big Hawk Lake into the creek.

Koessler Lake

Koessler Lake covers approximately 34 surface hectares, is 1,832 meters above sea level and over 60 meters deep. Spawning habitat is available in the first 200 meters of the outlet and in the mouths of two inlets. Its outlet merges with Doctor Creek about one kilometer from the lake, and although Doctor Creek contains a native fish fauna, a series of falls and chutes in the Koessler Lake outlet appears to have prevented fish from gaining access to the lake. Thus, the lake was probably historically fishless until sometime between 1928 and 1930 when it was stocked with an unknown number of Yellowstone cutthroat trout fingerlings (Montana Department of Fish, Wildlife and Parks file correspondence). Subsequently, an additional 5,200 presumed westslope cutthroat trout fingerlings were stocked in 1965.

Enzyme analysis of 26 specimens collected in 1987 confirmed hybridization between westslope cutthroat and Yellowstone cutthroat trout; 52.9% of the alleles at the diagnostic loci were of Yellowstone cutthroat trout origin (Table 13). All 26 specimens examined contained electrophoretic alleles from both taxa, and all three electrophoretic phenotypes were detected at all marker loci. In addition, none of the 11 polymorphic loci deviated significantly from Hardy-Weinberg proportions and indicates that the sample was collected from a random mating population.

Linkage disequilibrium data collected from this sample also suggests that the population has been randomly mating for several generations.

Only two of 28 estimates between the diagnostic loci are statistically significant (Table 14), and of the 28 estimates, 10 show negative associations between the alleles characteristic of each taxa. The two significant estimates, however, are in the direction that would be predicted by the hybrid origin of these fish. Since westslope cutthroat trout were not introduced until 1965, the two significant estimates probably do indicate that a small amount of linkage disequilibria still exists within the population.

Margaret Lake

Margaret Lake is a headwater lake to Forest Creek. It covers approximately 25.9 surface hectares, is 1,733 meters above sea level, and has a maximum depth of 23 meters. No inlets are present and available spawning habitat is restricted to approximately 35 meters of the outlet before a series of falls prevent spawning and juvenile fish that pass over them from returning to the lake. When lake levels are low, however, access to the outlet appears to be blocked by a log jam; consequently outlet spawning may not occur in some years.

Trout were first stocked in Margaret Lake in 1948, when 9,600 three inch Yellowstone cutthroat trout were introduced. Following this introduction no other trout were put in the lake until 1982 when 8,000 westslope cutthroat fingerlings were stocked. Additional introductions of westslope cutthroat fingerlings occurred in 1985, when 6,000 were stocked, and in 1986 when 3,000 were stocked.

Thirty-eight trout were collected for enzyme analysis during two sampling trips to Margaret lake; 26 specimens were collected in 1985, and 12 specimens were collected in 1991. Analysis of these fish indicated

that relatively few Yellowstone cutthroat trout genes still existed in the population (Table 13). Twenty-five of the 26 specimens collected in 1985, and all 12 specimens collected in 1991, were homozygous for westslope alleles at all the diagnostic loci. The remaining fish was homozygous for alleles characteristic of Yellowstone cutthroat trout at four diagnostic loci, and heterozygous for alleles characteristic of both westslope cutthroat and Yellowstone cutthroat trout at three diagnostic loci.

The lack of an appreciable genetic contribution from Yellowstone cutthroat trout in either sample suggests that only a small percentage of Yellowstone cutthroat genes still persists in the lake. However, as in Clayton Lake, the collection of a backcrossed, westslope cutthroat x Yellowstone cutthroat hybrid in the 1985 sample was unexpected, and indicates that westslope cutthroat trout genes were present in the lake prior to their first documented introduction in 1982. Again, three possible explanations exist for this situation; the lake may of had a resident population of westslope cutthroat; an undocumented introduction of westslope cutthroat may have occurred, or a mix of cutthroat trout types may have been stocked in the past.

Although it is unknown if fish were present in Margaret Lake prior to 1948, it does seem unlikely. Domrose (1968) did not collect any apparent westslope cutthroat trout in a survey of the lake in 1967; numerous barriers to upstream fish passage are present in the outlet; only cutthroat trout have been documented from the lake, and available spawning habitat is limited. Thus, as in Clayton Lake, the latter two explanations appear more likely but it is not possible to determine with certainty which is correct.

Lower Pilgrim Lake

Lying inside the Jewel Basin Special Management Area, Pilgrim Lake is 1,940 meters above sea level, and is located in the headwaters of the Jones Creek drainage above a series of impassible falls and chutes. It covers approximately 13.4 surface hectares, and has a maximum depth of 41 meters. Available spawning habitat appears to be restricted to the mouth of its inlet and periodically to a short distance of its outlet. The outlet was dry during the August 1986 survey, however, and as a result it may be unavailable for reproduction in some years.

No record of fish introductions exists for lower Pilgrim Lake, but enzyme analysis of 22 fish collected in 1986 confirmed hybridization between westslope cutthroat and rainbow trout; 94.7% of the alleles at four diagnostic loci were characteristic of westslope cutthroat trout (Table 15). Fifteen of the 22 fish analyzed were homozygous for westslope alleles at all diagnostic loci, while seven fish contained rainbow trout alleles at one or more of the diagnostic loci. In addition, there were no significant deviations from expected Hardy-Weinberg proportions at any of the polymorphic loci. Thus, this sample was apparently drawn from a random mating hybrid swarm, and it is unlikely that any individual within the population is genetically pure. Although no documented record of fish introductions exists, the presence of a low percentage of rainbow trout genes in the sample confirms that the lake has been stocked in the past.

Wheeler Creek

Flowing into Hungry Horse Reservoir, Wheeler Creek has an average gradient of 60 meters per kilometer over its 14.5 kilometer course. A native fish fauna historically occurred in the lower six kilometers of the

creek, but two barrier falls approximately six and seven kilometers above the creek's mouth blocked access to the upper portion of the drainage. A total of 22,400 Yellowstone eggs and 60,000 fingerlings were stocked in the creek between 1938 and 1950, but it is unknown if any of these introductions occurred above the falls. The introduction of Yellowstone cutthroat and westslope cutthroat trout fingerlings into Tom Tom Lake, a headwater lake to Wheeler Creek, however, did provide cutthroat trout with access to the upper reaches of the creek. In 1941, 3,600 Yellowstone cutthroat fingerlings were introduced into Tom Tom Lake, and between 1985 and 1990, 6,000 westslope cutthroat fingerlings were introduced into the lake.

One-hundred and six specimens, from three locations, were collected for protein analysis during four sampling trips to Wheeler Creek. Three samples, collected in 1983 (N=25), 1984 (N=25), and 1991 (N=19) were from the same area below the falls; a seven fish sample, also collected in 1991, came from the area between the falls, and two 15 fish samples collected in 1990, were taken from different locations above the falls.

Enzyme analysis of all three samples collected below the falls confirmed hybridization between westslope and Yellowstone cutthroat trout. In the 1983 and 1984 samples, 1.3% of the alleles were characteristic of Yellowstone cutthroat, while in 1991, 5.9% of the alleles were characteristic of Yellowstone cutthroat (Table 17). No significant differences in allele frequencies were observed between the diagnostic loci in the 1983 and 1984 samples (X^2=7.674, df=6, P=0.263), but a significant increase in the frequency of Yellowstone alleles was observed

in the 1991 sample compared to the combined 1983-1984 sample (X^2=20.364, df=9, P=0.0158).

Twenty-two of the 25 fish were homozygous for westslope alleles in the 1983 sample; 20 of the 25 fish were homozygous for westslope alleles in the 1984 sample, and 15 of the 19 fish were homozygous for westslope alleles in the 1991 sample. The remaining fish from these samples contained alleles characteristic of Yellowstone cutthroat at at least one diagnostic locus. The collection of one specimen in 1991 that contained Yellowstone alleles at all eight diagnostic loci, and the significant deficiency of heterozygotes observed at the IDDH* locus in the 1983 sample and the mMEP-1* locus in the 1991 sample, indicates that the samples were not collected from a random mating population.

The three samples collected from above the falls were also not drawn from a random mating population. In the upper sample, collected nearest to Tom Tom Lake, 13 fish were homozygous for Yellowstone alleles and two fish were homozygous for westslope alleles. In the middle sample, one fish was homozygous for Yellowstone alleles, and 14 fish were heterozygous for westslope and Yellowstone alleles at all diagnostic loci, indicating that they were first generation hybrids. Finally, in the seven fish sample collected from between the falls, all the fish were homozygous for westslope alleles at the diagnostic loci.

The level of hybridization observed in the samples collected from below the falls indicates that although the Yellowstone cutthroat trout stocked in Wheeler Creek and Tom Tom Lake have hybridized with the indigenous westslope, their contribution has been minimal. Because Wheeler Creek was historically fishless above the falls, however,

Yellowstone cutthroat have had a much larger genetic contribution to these populations.

Wildcat Lake

Wildcat Lake, also in the Jewel Basin Special Management Area, drains into Hungry Horse Reservoir via Wildcat Creek. It is 1,780 meters in elevation, covers 15.8 surface hectares, and has a maximum depth of approximately 30 meters. Historically fishless, the lake was initially stocked with 15,000 Yellowstone cutthroat trout in 1938. An additional 20,196 Yellowstone cutthroat were stocked between 1939 and 1953, and 35,296 westslope cutthroat trout were stocked between 1965 and 1988.

Enzyme analysis of two trout collections, 20 specimens in 1985, and 39 specimens in 1988, confirmed the presence of a westslope cutthroat x Yellowstone cutthroat trout population. In the 1985 sample, 96.9% of the alleles were characteristic of westslope cutthroat, and in the 1988 sample, 97.7% of the alleles were characteristic of westslope cutthroat (Table 13). The diagnostic alleles also appear to be randomly distributed among the individuals within the population; both samples conform to expected Hardy-Weinberg proportions. In the 1985 sample, 14 of the specimens were homozygous for westslope alleles at eight diagnostic loci and six were heterozygous for both westslope and Yellowstone alleles at one or more of the loci. In the 1988 sample, 32 specimens were homozygous for westslope alleles at all diagnostic loci and seven specimens were heterozygous for both westslope and Yellowstone alleles at at least one of the diagnostic loci.

Given the large number of Yellowstone cutthroat trout stocked in Wildcat Lake, the low percentage of Yellowstone genes observed in the

samples is surprising. It suggests that either reproduction within the lake is restricted, or that the early fish stockings were unsuccessful. Creel census data collected by the Montana Department of Fish, Wildlife and Parks indicates that the early fish introductions were successful. Physical data gathered during the collection of samples, however, suggests that available spawning habitat is limited to a short distance of the outlet, before the gradient becomes too steep for fish to navigate, and to the mouth of one small intermittent inlet. Thus, the low percentage of Yellowstone genes observed in the samples suggests that successful natural reproduction in this lake is low.

Wildcat Creek

Beginning as the outlet of Wildcat Lake, Wildcat Creek joins Wounded Buck Creek about eight kilometers below the lake, and has an average gradient of 50 meters per kilometer. Enzyme analysis of two samples collected from the same approximate location, 15 specimens in 1984 and 38 specimens in 1988, confirmed hybridization between westslope and Yellowstone cutthroat trout.

In the 1984 sample, 89.6% of the diagnostic alleles were characteristic of westslope, and in 1989, 97.9% of the diagnostic alleles were characteristic of westslope cutthroat trout (Table 17). Although there is a significant difference in allele frequencies between the samples (X^2=46.921, df=14, P<0.001), the distribution of alleles among individuals within each sample appears to be random, as all polymorphic loci conform to expected Hardy-Weinberg proportions. Thus, although a significant decrease in the percentage of Yellowstone alleles was observed

between the samples, the population still appears to be a random mating hybrid swarm.

Although there is no record of trout introductions in Wildcat Creek, Wildcat Lake was stocked with Yellowstone cutthroat trout and currently contains a westslope cutthroat x Yellowstone cutthroat trout population. The presence of Yellowstone genes in Wildcat Creek, therefore, is probably the result of emigration of fish from Wildcat Lake into the creek.

PARASITE ANALYSIS

Metazoan parasites belonging to five genera (one fluke, two tapeworms, and two roundworms) were collected from the 413 trout necropsied. Fourteen of the 15 lakes examined for macroparasites harbored at least one genera (Table 18). Crepidostomum farionis (Muller, 1784) was recovered from 13 populations, Cystidicoloides salvelini (Skinker, 1931) and Cyathocephalus truncatus (Pallus, 1781) were each recovered from three populations, and Cystidicola stigmatura (Fischer, 1798) and Diphyllobothrium ditremum (Creplin, 1825) were each recovered from one population (Table 18). For each sample, the prevalence and abundance of each parasite species recovered, ordered by the sample's hybrid index (HI), is listed in Table 19.

C. farionis occurs as an adult in the intestine of salmonids, and is acquired by fish feeding on infected ephemeropteran insects (mayfly nymphs) and gammarid amphipods. C. salvelini occurs as an adult in the stomach and intestine of salmonids, and is acquired by fish feeding on infected gammarid amphipods and to a lesser extent, infected Ephemeroptera. C. truncatus is found as an adult primarily in the pyloric

caeca of salmonids and is transmitted to fish through the ingestion of infected gammarid amphipods. C. stigmatura is found as an adult primarily in the swim bladder of fish, although the Tom Tom Lake specimens were recovered from stomachs, and is also transmitted through the ingestion of infected gammarid amphipods. D. ditremum occurs as a plerocercoid, either encysted in the viscera or unencysted in the body cavity of salmonid fishes, and is acquired through the ingestion of infected copepods. Additional information on the life cycles and distributions of these parasites is presented by Hoffman (1967).

Among the samples examined, only four (Blackfoot Lake 1986; Blackfoot Lake 1990; Big Hawk Lake 1990; Tom Lake 1990) contained at least two distinct taxonomic groups of trout that could be used to test for differences in parasite intensities. Of these, however, only the Big Hawk Lake and 1990 Blackfoot Lake samples could be used to test for differences in parasite intensities between hybridized fish and pure parental types. In the Big Hawk Lake sample, 19 westslope cutthroat trout and 30 westslope cutthroat x Yellowstone cutthroat trout were collected, and in the 1990 Blackfoot Lake sample, 22 westslope cutthroat, 10 rainbow trout, and two first generation hybrids were collected. Because of the small number of hybrids present in the 1990 Blackfoot Lake sample the results of the Mann-Whitney U tests comparing the parasite intensities between them and the parental taxa are tentative. In the remaining samples, only pure parental taxa were collected. The 1986 Blackfoot Lake sample contained six westslope cutthroat trout and 18 rainbow trout, and the 1990 Tom Lake sample contained 13 westslope cutthroat trout and 19 Yellowstone cutthroat trout.

Mann-Whitney U tests used to compare the parasite intensities of the different taxonomic groups within each lake revealed no significant differences between the groups. This suggests that the levels of resistance to parasitism for the parasites detected do not differ among the taxa examined. It also suggests that the hybrids do not exhibit a form of outbreeding depression and support a larger number of parasites than do their parental hosts.

Molnar et al. (1984) observed similar results between the parental taxa of carp and their hybrids, but other investigators have shown significant differences in parasite abundance between hybrids and parental taxa. The direction of these differences, however, are not consistent. Some investigators (Halvorsen 1969; Sage et al. 1986; Dupont and Crivelli 1988; Whitham 1989; Moulia et al. 1991) have found significantly higher parasite intensities in hybrids, while others have found intermediate levels (Drake 1981; Aguilar and Boecklen 1992; Le Brun et al. 1992), and still others have found lower levels (Heaney and Timm 1985; Boecklen and Spellenberg 1990). Thus, while hybridization and the resulting recombination of the genome appears to be an important component in determining the parasite intensities of some hybrids, the magnitude of its affect on resistance to parasitism appears to vary among organisms.

In systems where the same genes or gene complexes regulate resistance to the same parasite or group of parasites, the recombination of the parental genome may not significantly alter parasite resistance in the hybrids. Boecklen and Spellenberg (1990) suggest that the distribution of parasites in host hybrid zones will vary according to the systems examined, and that the patterns of parasitism are likely to be affected by

the particular combination of parental species involved, and by the parasite species present.

Following this analysis, the Kruskal-Wallis H test was used to determine if significant differences in parasite intensities occurred among populations harboring C. farionis, C. truncatus, and C. salvelini. In each case, significant heterogeneity among the samples was detected (C. farionis, H corrected for ties = 178.86; df = 15; P=0.000; C. truncatus, H corrected for ties = 46.67; df = 2; P=0.000; C. salvelini, H corrected for ties = 14.8; df = 2; P=0.001). No among population comparisons were made utilizing C. stigmatura and D. ditremum because each helminth was observed in only one population.

Because the Kruskal-Wallis H test indicated that there were significant differences in parasite intensities among the populations examined, the Mann-Whitney U test was used to compare the parasite intensities between sites taken two at a time. The results of these comparisons are given in Tables 20 and 21. As can be seen, significant differences in parasite intensities occur within and between the different taxonomic groups sampled. That is, significant differences in parasite intensities occurred between populations with the same taxonomic origins, as well as between populations of different taxonomic origin.

The lack of any consistent relationship between taxonomic status and parasite abundances among these populations suggests that the differences observed are due to nongenetic factors, i.e. ecological and intrinsic parameters. Differences in physical and chemical characteristics, population densities, availability of intermediate hosts, parasite life

cycles, fish age, and dates of collection can all influence the parasite intensities of fish from the different lakes examined.

Marcogliese and Cone (1991) found depth, and to a lesser extent area, to be important factors in determining parasite assemblage structure. They suggested that limnetic intermediate hosts are probably more abundant in larger, deeper lakes as opposed to shallower lakes, and that salmonids in deeper lakes may consume relatively more zooplankton since access to benthos is probably more difficult. The shift from more benthic food items in shallower lakes, to more zooplankton utilization in the deeper lakes, therefore, contributes to different parasite assemblages within these systems.

Albert and Curtis (1991) have documented significant changes in the prevalence and abundance of parasites following a decrease in the population density of brook trout. They hypothesized that the increase in parasite prevalence and abundance occurred because the fish remaining were better able to exploit the plankton and benthic invertebrates that were the intermediate hosts of the parasites present in the lake. These same investigators also observed a significant increase in the prevalence and abundance of C. farionis from June to August of each study year, indicating that time of collection also generated differences in parasite intensities.

Alternatively it can be envisioned how differences in the other parameters listed could also influence parasite prevalence and abundance among the populations examined. For example, because all of the parasites recovered in this study have heteroxenous life cycles, differences in the

abundance of intermediate hosts between populations could generate significant differences in parasite prevalence and abundance between them.

To better determine if the genotypes of the populations examined were influencing parasite abundance tests for correlations between the hybrid indices and parasite abundances of the populations were made. For each of the three parasite species detected from multiple samples, there was no significant correlation between the genotypes of the trout examined and the parasite abundance observed (C. farionis, r_s = -0.139, P = 0.548; C. salvelini, r_s = -0.089, P = 0.701, C. truncatus, r_s = 0.251, P = 0.273). Thus, the non-native and hybridized populations examined do not appear to be any more susceptible to parasitism than are the native westslope cutthroat trout populations.

Detecting no apparent correlation between parasite abundance and taxonomic status, other possible associations between parasite abundance and lake depth, lake area, elevation, collection date, pH, standard conductance, and total dissolved solids were tested for. No significant correlations were observed between these factors and the abundance of C. truncatus, but significant correlations were observed between mean parasite abundance and total dissolved solids and standard conductance for C. farionis (r_s = 0.485 and 0.454, P = 0.026 and 0.039 respectively) and between mean parasite abundance and lake depth and area for C. salvelini (r_s = 0.802 and 0.709, P = 0.000 and 0.000 respectively).

As previously noted, other investigators have also shown depth and area to be important components in determining parasite assemblage structure. The significant relationship observed between parasite abundance and standard conductance and parasite abundance and total

dissolved solids suggests that these factors may also be important in determining parasite abundances. Higher concentrations of total dissolved solids and higher standard conductances probably indicate higher nutrient levels. Lakes with higher nutrients levels probably support more of the mayfly nymphs that serve as intermediate hosts for C. farionis, and their increased abundance may lead to significant differences in parasite abundances among populations.

Although no information was collected pertaining to fish population densities or the availability of intermediate hosts, it seems likely that these factors have also contributed to the differences in parasite abundances observed among the populations examined. For example, although no differences in C. farionis abundance were observed between the different fish taxa examined within years from Blackfoot Lake, a significant increase in its abundance did occur between years (Mann-Whitney U Test = 531.5, P = 0.004). Because the time of collection, taxonomic status, and physical and chemical characteristics remained comparable between the samples, it seems likely that an increase in fish abundance, created by the introduction of hatchery westslope cutthroat trout into the system, and or an increase in the usage or availability of C. farionis's intermediate hosts contributed to the increase.

RECOMMENDATIONS

Native westslope cutthroat trout were unable to gain access to many of the headwater lakes in the South Fork of the Flathead River drainage. Only Big Salmon Lake and Doctor Lake harbor indigenous fish populations. The remaining lakes surveyed were drained by high gradient streams with existing barriers that apparently prohibited fish from accessing them. The trout found in these waters, therefore, are either introduced westslope cutthroat, non-native trout, or hybrids whose origins can generally be traced to one or more introductions.

Once these non-native and hybridized populations were established, however, they became a continual source of fish and gametes to downstream systems. Through their movements they have colonized stream sections previously barren of fish and initiated hybridization with other indigenous populations of westslope cutthroat trout. Thus, these populations represent a considerable threat to the genetic integrity of the native trout populations within the drainage, and steps to ensure their removal or replacement with native trout are highly recommended.

Of the waters surveyed, 10 currently harbor non-native Yellowstone cutthroat trout, rainbow trout, or brook trout populations, while 20 harbor hybridized westslope cutthroat trout populations. The restoration of this many populations will require substantial effort by the Montana Department of Fish, Wildlife and Parks and should encompass several management strategies. In some waters the chemical removal of fish is recommended, while in other waters the replacement of non-native genes with westslope cutthroat genes via hybridization is recommended.

Specifically, in waters where the percentage of non-native genes (> 30%) and the potential for downstream migration is high, chemical removal is recommended. Although it is possible to replace the non-native genes in these populations with westslope cutthroat trout genes through hybridization, the number of introductions and the time required to replace them utilizing this management strategy will be substantial. Theoretically, in a closed system with nonoverlapping generations, random mating, equal parental contributions, and equal competition between the resident and introduced fish, each introduction of westslope cutthroat would reduce the percentage of non-native genes contributed to the next generation by one half. However, because at least four generations exist in each population (three year classes of immature fish and one combined group of mature fish) at least four introductions are required to effectively reduce the percentage of non-native genes within the population by one half. Thus, if the above assumptions are not violated, the replacement of a non-native population with a westslope population (i.e. > 99.0% westslope cutthroat trout) utilizing hybridization will require approximately 26 introductions. In natural systems with overlapping generations, and where unequal competition, unequal parental contributions, and assortive matings are likely to occur, however, the actual amount of time and number of introductions required to effectively purge or "swamp out" the non-native genes may be much higher.

Thus, the chemical removal of the fish in Big Salmon Creek above barrier falls 23, Big Hawk Lake, Blackfoot Lake, Graves Creek, Handkerchief Lake, Koessler Lake, Lena Lake, Lick Lake, Smokey and Necklace Lakes, Ross Lake, Sunburst Lake, Tom Tom Lake, Woodward Lake, and

Wheeler Creek above the lower falls is highly recommended. These waters harbor non-native trout populations or contain hybrid populations with a high percentage of non-native genes and pose a considerable threat to downstream populations. The chemical removal of the populations of rainbow trout in the Big Salmon Lake drainage (i.e. Smokey and Necklace Lakes, Lena Lake, Woodward Lake, and Big Salmon Creek) and the Brook trout in Ross Lake, however, should receive the highest priority. The hybridization of the indigenous westslope cutthroat trout population in Big Salmon Lake and the possible spread of brook trout throughout the South Fork would represent significant set backs to the establishment of a native fishery in the drainage.

After the chemical treatment of these waters, it is recommended that the waters harboring Yellowstone cutthroat trout (Lick Lake, Sunburst Lake, Tom Tom Lake, and Wheeler Creek) be treated, followed by the hybrid populations in the Graves Creek drainage (Blackfoot Lake, Graves Creek, and Handkerchief Lake) and Koessler Lake and Big Hawk Lake. It is further recommended that fish not be reintroduced into some of these waters. The establishment of fish populations in these systems has undoubtedly altered their historical aquatic biota, thus the removal of fish may allow some of the indigenous amphibian and invertebrate fauna to recolonize these waters.

In the waters where the percentage on non-native genes is low (< 30%), yearly or periodic introductions of hatchery westslope cutthroat trout should be sufficient to "swamp out" the non-native genes in relatively few generations. Waters where this type of management is

recommended include North Biglow Lake, Black Lake, Clayton Lake, Doris Lake #2 and #3, Margaret Lake, Pilgrim Lake, and Wildcat Lake.

This management strategy is also recommended for George Lake and Pyramid Lake. Although George Lake contains a high percentage of Yellowstone cutthroat genes and Pyramid Lake harbors a Yellowstone cutthroat trout population, there appears to be little danger of these fish migrating downstream. The immediate establishment of westslope cutthroat trout populations in these waters, therefore, is less urgent than in the other waters that contain a high percentage of non-native genes and migration corridors.

No direct action may be required to reduce the percentage of non-native genes in the Aeneas, Clayton, Gordon, Jones, and Wildcat Creek populations. Currently, the headwater lakes in these drainages harbor non-native and hybridized populations, and these fish provide a continual source of non-native genes to the creeks. The establishment of westslope cutthroat trout populations in the lakes, therefore, may be all that is required to effectively reduce the percentage of non-native genes in these creeks. Thus, direct action to reduce the percentage of non-native genes in these creeks is not recommended until it has been determined whether the establishment of westslope cutthroat trout in the lakes has also significantly reduced the percentage of non-native genes in the creeks.

SUMMARY

Westslope cutthroat trout are a species of special concern in Montana, currently inhabiting only about 2.5% of their historic range. A major factor contributing to their decline has been hybridization with introduced Yellowstone cutthroat trout and rainbow trout. In some instances, however, these introduced fish have failed to become established, and it has been hypothesized that an increased sensitivity to endemic parasites may have contributed to these failures. Thus, this study was designed to determine the distribution and extent of hybridization of the westslope cutthroat trout in the South Fork of the Flathead River drainage, and to determine if non-native and hybridized trout populations have higher parasite intensities than native trout populations.

Forty-nine lakes and 14 streams known or suspected of harboring fish were surveyed. Fifteen lakes were found to be fishless, but samples were collected from 48 other waters (Table 2). The taxonomic status of these populations was determined using horizontal starch gel electrophoresis.

Essentially pure populations of westslope cutthroat trout (> 99%) occurred in 12 lakes and seven streams (Tables 5 and 7). Introgressed populations of westslope cutthroat trout existed in 13 lakes and seven streams (Table 11), and non-native populations of trout existed in nine lakes and one stream (Table 10). Thus, only 39% of the waters surveyed in the South Fork of the Flathead River drainage harbored essentially pure populations of westslope cutthroat trout, while 41% harbored hybridized populations and 20% harbored non-native taxa.

Fish from 15 lakes were also examined for macroparasites. Metazoan parasites belonging to five genera were recovered. Crepidostomum farionis was present in 13 lakes, Cyathocephalus truncatus and Cystidicoloides salvelini were each present in three lakes, and Cystidicola stigmatura and Diphyllobothrium ditremum each occurred in one lake (Tables 18 and 19).

The non-native and hybridized populations do not appear to be more susceptible to parasitism than the native westslope cutthroat trout populations. Although significant differences in parasite intensities were observed between populations, Mann-Whitney U tests used to compare the parasite intensities of westslope cutthroat with other taxonomic groups present in the same lakes revealed no significant differences between the groups. In addition, no significant correlation between the percentage of westslope cutthroat genes and the abundance of the parasites present within the populations existed. The differences in the parasite intensities observed between the populations, therefore, appear to have been generated by environmental factors.

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Table 1

Fishless lakes in the South Fork of the Flathead River drainage. Note: T = township, R = range, and S = section.

Name	Location			Sample Date
	T	R	S	
Aeneas Lake	28N	18W	32	7/25/86
Crimson Lake	18N	14W	23	8/26/87
Devine Lake	17N	14W	10	9/23/88
Doris Lake #1	29N	18W	32	7/22/86
Olar Lakes (2)	23N	16W	15	9/17/87
Otis Lake	18N	14W	16	8/26/87
Palisade Lake	22N	15W	6	7/14/87
Picnic Lakes (2)	28N	18W	30	7/31/86
Pilgrim Lake (upper)	27N	18W	15	8/15/86
Upper Seven Acres Lake	28N	18W	7	7/29/86
Soldier Lake	26N	16W	33	6/19/86
Twin Lakes (2)	28N	18W	19	7/31/86

Note: Crimson, Doris #1, Olar lakes, Upper Seven Acres, Soldier, and both Twin lakes have been stocked with production fish from the current westslope cutthroat trout broodstock. Palisade lake has also reportedly been unofficially stocked since its survey.

Table 2

Samples, number sampled, locations (township, range, section) and taxonomic status of the populations sampled from the South Fork of the Flathead River drainage. W = pure westslope cutthroat trout, Y = pure Yellowstone cutthroat, R = pure rainbow trout, B = pure brook trout, and WxY, WxR, RxY, and WxRxY indicate hybridization between the taxa listed. Sample locations not designated as creeks in the table are from lakes. The star (*) indicates that no known introduction of fish exists for that water.

Sample		N	Location T	R	S	Date Collected	Taxonomic Status
1. Aeneas Creek		31	27N	18W	3D	8/31/83	W x R
Aeneas Creek	(b)	24				8/11/89	W x R
2. Big Hawk Lake		48	28N	18W	14	7/03/86	W x Y
Big Hawk Lake	(b)	49				8/07/90	W x Y
*3. Big Salmon		19	21N	14W	3	7/22/88	W
Big Salmon	(b)	26				3/1&29/92	W
*4. Big Salmon Creek		2	20N	15W	10	7/09/87	R
5. Birch		28	28N	18W	32	7/25/86	W x Y
6. Biglow (north)		25	26N	18W	1	9/05/84	W x R
7. Black		27	28N	18W	30	7/31/86	W x R x Y
Black	(b)	15				9/04/86	W x R x Y
Black	(c)	2				6/23/87	R x Y
Black	(d)	5				8/02/90	W x R x Y
Black	(e)	44				9/04/91	W x R
8. Blackfoot		24	28N	18W	19	8/01/86	R x W
Blackfoot	(b)	12				6/23/87	R x W
Blackfoot	(c)	34				8/02/90	W x R
Blackfoot	(d)	30				9/04/91	W x R
Blackfoot (YOY)	(e)	42				9/04/91	W x R
9. Clayton		14	28N	18W	16	7/08/85	W x Y
Clayton	(b)	29				7/08/86	W x Y
Clayton	(c)	32				8/15/89	W x Y
10. Lower Clayton Creek		26	28N	18W	3B	8/31/83	W x Y x R
Lower Clayton Creek	(b)	25				9/16/90	W x Y
Upper Clayton Creek		27	28N	18W	8D	8/08/90	W x Y
11. Cliff		25	28N	18W	28	7/28/86	W
12. Crater		26	27N	18W	8	7/16/86	W x R
13. Danaher Creek		26	19N	12W	4,5&9	6/27/89	W
*14. Deep Creek		25	29N	17W	28	9/16/86	W x Y
15. Doris #2		32	29N	19W	6	7/22/86	W x R
16. Doris #3		26	29N	19W	6	7/22/86	W x R
17. Doctor		25	19N	15W	14	7/23/87	W
18. Fawn		28	30N	19W	31	7/23/86	W x R
19. George		27	19N	15W	26	8/02/87	Y x W
George	(b)	28				9/12/90	Y x W
20. Upper Gordon Creek		10	19N	14W	7	7/23/87	W x Y
Lower Gordon Creek		26	19N	13W	5	8/02/89	W
21. Gorge Creek		25	24N	15W	35C	9/05/88	W x Y

Table 2 - continued

Sample		N	Location T	R	S	Date Collected	Taxonomic Status
22. Graves Creek		27	28N	18W	35A	8/31/83	W x R X Y
Graves Creek		26				8/10/89	W x R x Y
Graves Creek		41	28N	18W	21D	9/16/91	W x R
23. Handkerchief		15	28N	18W	36	6/20/86	W x R x Y
Handkerchief	(b)	16				9/06/91	W x R x Y
24. Jenny		26	29N	19W	18	7/23/86	W
25. Jewel		10	28N	18W	19	9/30/85	R
*26. Jones Creek		25	27N	18W	12C	8/31/83	W x Y
Jones Creek	(b)	26				8/11/89	W x Y
27. Koessler		26	19N	15W	15	7/24/87	Y x W
28. Lena		27	20N	15W	25	7/09/87	R
29. Lick		35	19N	15W	9	7/23/87	Y
30. Margaret		26	27N	17W	19	8/25/85	W x Y
Margaret	(b)	12				9/05/91	W
*31. Lower Marshall		27	18N	14W	19	9/22/88	W
*32. Upper Marshall		7	18N	14W	19	9/23/88	W
*33. Marshall Creek		25	18N	14W	13	8/26/87	W
34. Mid Creek		26	23N	14W	4	7/03/88	W
*35. Lower Necklace		8	20N	15W	17	7/09/87	R
*36. Lower Pilgrim		22	26N	18W	1	8/14/86	W x R
37. Pyramid		12	18N	14W	3	8/05/87	Y x R
*38. Ross		22	17N	14W	11	9/23/88	B
39. Lower Seven Acres		26	28N	18W	27	7/29/86	W x R
40. S.F. Flathead River		35	23N	14W	4,9&16	7/03/88	W
41. Squaw		26	27N	18W	5	7/15/86	W
42. Sunburst		25	23N	16W	23	7/03/87	Y x R
Sunburst	(b)	14				8/02/91	W x Y
43. Upper Three Eagles		26	27N	18W	10	8/14/86	W x Y
44. Tom Tom		11	27N	18W	27	8/20/85	Y
Tom Tom	(b)	14				8/08/86	Y
Tom Tom (YOY)	(c)	11				9/18/90	W x Y
Tom Tom (1+)	(d)	12				9/18/90	W x Y
Tom Tom (adults)	(e)	32				9/18/90	Y x W
45. Upper Wheeler Creek		15	27N	18W	27A	9/19/90	Y x W
Upper Wheeler Creek		15	27N	18W	25A	9/19/90	Y x W
Middle Wheeler Creek		7	27N	17W	32A	9/05/91	W
Lower Wheeler Creek		25	27N	17W	22C	8/31/83	W x Y
Lower Wheeler Creek	(b)	25				8/07/84	W x Y
Lower Wheeler Creek	(c)	19				9/05/91	W x Y
46. Wildcat		20	28N	19W	12	9/25/85	W x Y
Wildcat	(b)	39				8/24/88	W x Y
*47. Wildcat Creek		15	28N	18W	6D	8/17/84	W x Y
Wildcat Creek	(b)	38				10/05/88	W x Y
48. Woodward		2	20N	15W	18	7/09/87	R x Y

Note: In hybridized populations, the taxon with the greatest genetic contribution is listed first.

Table 3

Enzymes and loci examined. Tissues: E = eye, L = liver, M = muscle. Buffer indicates the buffer system or systems that gave the best resolution for each enzyme.

Enzyme	Loci	Tissue	Buffer
Adenylate kinase	AK-1*, AK-2*	M	AC
Alcohol dehydrogenase	ADH*	L	RW
Aspartate aminotransferase	sAAT-1*, sAAT-2*	L	AC, RW
	sAAT-3,4*	M	AC, RW
Creatine kinase	CK-A1*, CK-A2*	M	RW
	CK-B*, CK-C1*, CK-C2*	E	SR
Dipeptidase	PEPA-1*, PEPA-2*	E	SR
Glucose-6-phosphate isomerase	GPI-A*	E	SR
	GPI-B1*, GPI-B2*	M	RW
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH-3*, GAPDH-4*	E	AC+
Glycerol-3-phosphate dehydrogenase	G3PDH-1*, G3PDH-2*	L	AC
Isocitrate dehydrogenase	mIDHP-1*, mIDHP-2*	M	AC+
	sIDHP-1,2*	L	AC
L-Iditol dehydrogenase	IDDH*	L	RW
L-Lactate dehydrogenase	LDH-A1*, LDH-A2*	M	RW
	LDH-B1*, LDH-B2*, LDH-C*	E	SR
Malate dehydrogenase	sMDH-A1,2*	L	AC
	sMDH-B1,2*	M	AC+
Malic enzyme	mMEP-1*, mMEP-2*, sMEP-1*	M	AC
	sMEP-2*	L	AC
Phosphoglucomutase	PGM-1*, PGM-2*	M	AC, RW
Phosphgluconate dehydrogenase	PGDH*	M	AC
Superoxide dismutase	sSOD-1*	L	RW
Tripeptide aminopeptidase	PEPB*	E	SR
Xanthine dehydrogenase-like	XDH1*	L	RW

Table 4

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

	Characteristic Alleles		
Locus	Westslope	Yellowstone	Rainbow
sAAT-1	200,250	165	100
CK-A2	84,100	84	100,76
CK-C1	100,38	38	100,38
GPI-A	92,100	100	100
IDDH	40,100	100	100,200,40
mIDHP-1	100	~75	100
sIDHP-1,2	86,100,40,71,114	71	100,71,40,114
mMEP-1	88	null	null
sMEP-1	100	90	100,75
sMEP-2	100	110	100
PEPA-1	100	101	100,115,90
PEPB	100	135	100,135
PGM-1	100,null	null	100,null

Table 5

Samples of twelve putative westslope cutthroat trout populations from the South Fork of the Flathead River drainage.

Sample	N	Location T	R	S	Date Collected
1. Big Salmon Lake	19	21N	14W	3	7/22/88
Big Salmon Lake	26				3/1&29/92
2. Cliff Lake	25	28N	18W	28	7/28/86
3. Danaher Creek	26	19N	12W	4,5&9	6/27/89
4. Doctor Lake	25	19N	15W	14	7/23/87
5. Lower Gordon Creek	26	19N	13W	5	8/02/89
6. Jenny Lake	26	29N	19W	18	7/23/86
7. Lower Marshall Lake	27	18N	14W	19	9/22/88
8. Upper Marshall Lake	7	18N	14W	19	9/23/88
9. Marshall Creek	25	18N	14W	13	8/26/87
10. Mid Creek	26	23N	14W	4	7/03/88
11. S.F. Flathead River	35	23N	14W	4,9&16	7/03/88
12. Squaw Lake	26	27N	18W	5	7/15/86

Table 6

Intra-specific variation at the polymorphic loci in the twelve putative populations of westslope cutthroat trout from the South Fork of the Flathead River drainage.

		Allele frequencies			
		Big Salmon Lake			
Locus	Alleles	(1987)	(1992)	Cliff Lake	Doctor Lake
sAAT-1	200	0.947	0.942	1.000	1.000
	250	0.053	0.058	-	-
sAAT-3,4	100	1.000	1.000	1.000	1.000
	77	-	-	-	-
	63	-	-	-	-
CK-A2	84	0.921	0.981	1.000	1.000
	100	0.079	0.019	-	-
CK-C1	100	0.579	0.580	0.760	0.820
	38	0.421	0.420	0.240	0.180
GAPDH-4	100	1.000	1.000	1.000	1.000
	null	-	-	-	-
sIDHP-1	86	0.842	0.942	1.000	0.860
	71	0.158	0.058	-	0.140
sIDHP-2	100	0.632	0.788	0.480	0.940
	40	0.368	0.212	0.520	0.060
LDH-B1	100	1.000	1.000	1.000	1.000
	133	-	-	-	-
LDH-C	100	0.974	1.000	1.000	1.000
	95	0.026	-	-	-
sMDH-A1,2	100	1.000	0.981	1.000	1.000
	40	-	0.019	-	-
PGM-2	100	1.000	1.000	1.000	1.000
	85	-	-	-	-

Table 6 - continued

Locus	Alleles	Allele frequencies: Danaher Creek	South Fork Flathead River	Lower Gordon Creek	Jenny Lake
sAAT-1	200	0.942	0.971	0.962	1.000
	250	0.058	0.029	0.038	-
sAAT-3,4	100	1.000	1.000	1.000	1.000
	77	-	-	-	-
	63	-	-	-	-
CK-A2	84	1.000	0.924	1.000	1.000
	100	-	0.076	-	-
CK-C1	100	0.565	0.833	0.692	0.860
	38	0.435	0.167	0.308	0.140
GAPDH-4	100	1.000	0.957	1.000	1.000
	null	-	0.043	-	-
sIDHP-1	86	1.000	0.912	1.000	1.000
	71	-	0.088	-	-
sIDHP-2	100	0.763	0.485	0.780	0.442
	40	0.237	0.515	0.220	0.558
LDH-B1	100	1.000	1.000	1.000	1.000
	133	-	-	-	-
LDH-C	100	1.000	1.000	1.000	1.000
	95	-	-	-	-
sMDH-A1,2	100	0.981	1.000	0.933	1.000
	40	0.019	-	0.067	-
PGM-2	100	1.000	1.000	1.000	1.000
	85	-	-	-	-

Table 6 - continued

Locus	Alleles	Allele frequencies: Lower Marshall Lake	Upper Marshall Lake	Marshall Creek	Mid Creek	Squaw Lake
sAAT-1	200	1.000	1.000	1.000	1.000	1.000
	250	-	-	-	-	-
sAAT-3,4	100	1.000	1.000	0.471	1.000	1.000
	77	-	-	0.519	-	-
	63	-	-	0.010	-	-
CK-A2	84	0.981	1.000	1.000	0.808	1.000
	100	0.019	-	-	0.192	-
CK-C1	100	0.963	1.000	1.000	0.808	0.750
	38	0.037	-	-	0.192	0.250
GAPDH-4	100	1.000	1.000	1.000	1.000	1.000
	null	-	-	-	-	-
sIDHP-1	86	1.000	1.000	1.000	1.000	1.000
	71	-	-	-	-	-
sIDHP-2	100	0.630	0.286	1.000	0.481	0.558
	40	0.370	0.714	-	0.519	0.442
LDH-B1	100	1.000	1.000	0.269	1.000	1.000
	133	-	-	0.731	-	-
LDH-C	100	1.000	1.000	1.000	1.000	0.962
	95	-	-	-	-	0.038
sMDH-A1,2	100	1.000	1.000	1.000	0.962	1.000
	40	-	-	-	0.038	-
PGM-2	100	0.981	1.000	1.000	1.000	1.000
	85	0.019	-	-	-	-

Table 7

Samples collected from the South Fork of the Flathead River that are greater than 99.0% pure westslope cutthroat trout. W x Y indicates hybridization between westslope and Yellowstone cutthroat, and W x R indicates hybridization between westslope cutthroat and rainbow trout.

Sample	N	Location T	R	S	Date Collected	Taxonomic Status
1. Birch Lake	28	28N	18W	32	7/25/86	W x Y
2. Crater Lake	26	27N	18W	8	7/16/86	W x R
3. Deep Creek	25	29N	17W	28	9/16/86	W x Y
4. Fawn Lake	26	30N	19W	31	7/23/86	W x R
5. Gorge Creek	25	23N	15W	2	9/05/88	W x Y
6. Lower Seven Acres Lake	26	28N	18W	27	7/29/86	W x R
7. Upper Three Eagles Lake	26	27N	18W	10	8/14/86	W x Y

Table 8

Allele frequencies at the polymorphic loci in populations containing greater than 99% westslope cutthroat trout genes and less than 1% Yellowstone cutthroat trout genes from the South Fork of the Flathead River drainage.

		Allele frequencies			
Locus	Alleles	Birch Lake	Deep Creek	Gorge Creek	Upper Three Eagles Lake
sAAT-1	200	0.982	1.000	0.980	0.962
	250	-	-	-	0.038
	165	0.018	-	0.020	-
sAAT-3,4	100	0.991	1.000	1.000	1.000
	90	0.009	-	-	-
CK-C1	100	0.650	1.000	*	0.962
	38	0.350	-	*	0.038
GPI-A	92	1.000	0.980	0.980	1.000
	100	-	0.020	0.020	-
lDDH	40	1.000	1.000	0.980	1.000
	100	-	-	0.020	-
mIDHP-1	100	0.982	1.000	1.000	0.981
	-75	0.018	-	-	0.019
sIDHP-1	86	0.982	1.000	1.000	0.981
	71	-	-	-	0.019
	null	0.018	-	-	-
sIDHP-2	100	0.571	0.220	0.120	0.500
	40	0.429	0.780	0.880	0.500
sMEP-2	100	1.000	1.000	0.980	1.000
	110	-	-	0.020	-
PEPB	100	1.000	0.980	0.980	1.000
	135	-	0.020	0.020	-
Percent westslope		0.995	0.996	0.990	0.992
Percent Yellowstone		0.005	0.004	0.010	0.008

Note: The star (*) indicates that protein data was not obtained for that locus.

Table 9

Allele frequencies at the polymorphic loci in populations containing greater than 99% westslope cutthroat and less than 1% rainbow trout genes from the South Fork of the Flathead River drainage.

		Allele frequencies		
Locus	Alleles	Crater Lake	Fawn Lake	Lower Seven Acres Lake
sAAT-1	200	0.804	1.000	0.981
	250	-	-	0.019
	null	0.196	-	-
sAAT-3,4	100	1.000	1.000	0.981
	77	-	-	0.019
CK-A2	84	1.000	1.000	0.962
	100	-	-	0.038
CK-C1	100	0.700	0.768	0.900
	38	0.300	0.232	0.100
GPI-A	92	0.962	0.982	1.000
	100	0.038	0.018	-
sIDHP-1,2	86	0.500	0.491	0.500
	71	-	0.009	-
	100	0.346	0.277	0.269
	40	0.154	0.223	0.231
LDH-C	100	1.000	0.982	0.962
	95	-	0.018	0.038
sMEP-2	100	1.000	1.000	0.962
	110	-	-	0.038
sSOD-1	100	0.962	1.000	1.000
	152	0.038	-	-
Percent westslope		0.994	0.994	0.994
Percent rainbow		0.006	0.006	0.006

Table 10

Samples of non-native fish species collected from the South Fork of the Flathead River drainage. R = pure rainbow trout, Y = pure brook trout, B = pure brook trout, and Y x R indicates the presence of a hybridized trout population. The species with the largest genetic contribution to the hybrid population is listed first.

Sample	N	Location T	R	S	Date Collected	Taxonomic Status
1. Big Salmon Creek	2	20N	15W	10	7/09/87	R
2. Jewel Lake	10	28N	18W	19	9/30/85	R
3. Lena Lake	27	20N	15W	25	7/09/87	R
4. Lick Lake	35	19N	15W	9	7/25/87	Y
5. Lower Necklace Lake	8	20N	15W	17	6/09/87	R
6. Pyramid Lake	12	18N	14W	3	8/05/87	Y x R
7. Ross Lake	22	17N	14W	11	9/23/88	B
8. Sunburst Lake	25	23N	16W	23	7/03/97	Y x R
9. Tom Tom Lake	25	27N	18W	27	8/08/86	Y
10. Woodward Lake	2	20N	15W	18	7/09/87	R x Y

Note: The brook trout from Ross Lake were not electrophoretically analyzed.

Table 12

Allele frequencies at the diagnostic loci between westslope cutthroat and rainbow trout in hybridized creek populations in the South Fork of the Flathead River drainage.

		Allele frequencies	
Locus	Alleles	1983 Aeneas	1989 Aeneas
sAAT-1	200	0.935	1.000
	250	0.048	-
	100	0.016	-
CK-A2	84	0.823	0.875
	100	0.177	0.125
GPI-A	92	0.871	0.896
	100	0.129	0.104
IDDH	40	0.968	1.000
	100	0.032	-
sIDHP-1,2	86	0.323	0.282
	71	0.177	0.198
	40	0.194	0.198
	100	0.306	0.322
mMEP-1	88	0.984	1.000
	null	0.016	-
Percent westslope		0.926	0.954
Percent rainbow		0.074	0.046

Table 13

Allele frequencies at the diagnostic loci between westslope cutthroat and Yellowstone cutthroat trout in hybridized lake populations of these fishes in the South Fork of the Flathead River drainage.

		Allele frequencies				
		Lower Big Hawk Lake		Clayton Lake		
Locus	Alleles	(1986)	(1990)	(1985)	(1986)	(1989)
sAAT-1	200	0.594	0.781	0.929	0.804	0.914
	250	-	0.042	-	-	0.048
	165	0.406	0.177	0.071	0.196	0.048
	100	-	-	-	-	-
CK-C1	100	0.435	0.745	0.692	0.625	*
	38	0.565	0.255	0.308	0.375	*
GPI-A	92	0.521	0.844	0.857	0.759	0.889
	100	0.479	0.156	0.143	0.241	0.111
IDDH	40	0.552	0.812	0.857	0.724	0.935
	100	0.448	0.188	0.143	0.276	0.065
mIDHP-1	100	0.570	0.827	0.893	0.741	0.935
	-75	0.430	0.173	0.107	0.259	0.065
sIDHP-1	86	0.208	0.735	0.643	0.679	*
	71	0.781	0.265	0.357	0.321	*
	100	0.010	-	-	-	*
mMEP-1	88	0.543	0.796	*	0.724	0.919
	null	0.457	0.204	*	0.276	0.081
sMEP-1	100	0.521	0.806	0.857	0.724	0.895
	90	0.479	0.194	0.143	0.276	0.105
sMEP-2	100	0.583	0.844	0.893	0.741	0.935
	110	0.417	0.156	0.107	0.259	0.065
PEPA-1	100	*	0.878	0.893	0.814	0.935
	101	*	0.122	0.107	0.186	0.065
PEPB	100	0.400	0.816	0.857	0.625	0.952
	135	0.600	0.184	0.143	0.375	0.048
PGM-1	100	0.569	0.798	0.929	0.509	0.935
	null	0.431	0.202	0.071	0.491	0.065
Percent westslope		0.536	0.821	0.878	0.730	0.927
Percent Yellowstone		0.464	0.179	0.122	0.270	0.073

Table 13 - continued

Locus	Alleles	Allele frequencies: George Lake (1987)	George Lake (1990)	Koessler Lake	Margaret Lake	Wildcat Lake (1985)	Wildcat Lake (1988)
sAAT-1	200	0.310	0.411	0.580	0.981	0.925	0.910
	250	-	-	-	-	-	0.038
	165	0.690	0.589	0.420	0.019	0.075	0.026
	100	-	-	-	-	-	0.026
CK-C1	100	0.350	0.481	0.400	0.773	0.694	0.629
	38	0.650	0.519	0.600	0.227	0.306	0.371
GPI-A	92	0.310	0.446	0.420	0.962	0.975	1.000
	100	0.690	0.554	0.580	0.038	0.025	-
IDDH	40	0.190	0.518	0.320	0.962	0.950	0.936
	100	0.810	0.482	0.680	0.038	0.050	0.064
mIDHP-1	100	0.310	0.411	0.480	0.981	0.975	0.974
	-75	0.690	0.589	0.520	0.019	0.025	0.026
sIDHP-1	86	0.200	0.232	0.460	0.760	0.800	0.974
	71	0.800	0.768	0.540	0.240	0.200	0.026
	100	-	-	-	-	-	-
mMEP-1	88	*	0.411	*	1.000	1.000	1.000
	null	*	0.589	*	-	-	-
sMEP-1	100	0.430	0.536	0.600	0.981	1.000	1.000
	90	0.570	0.464	0.400	0.019	-	-
sMEP-2	100	0.350	0.375	0.440	0.962	0.950	0.962
	110	0.650	0.625	0.560	0.038	0.050	0.038
PEPA-1	100	0.570	0.518	0.730	0.962	1.000	0.840
	101	0.430	0.482	0.270	0.038	-	0.160
PEPB	100	0.430	0.429	0.460	0.962	0.975	0.974
	135	0.570	0.571	0.540	0.038	0.025	0.026
PGM-1	100	0.310	0.518	0.520	0.962	1.000	0.840
	null	0.690	0.482	0.480	0.038	-	0.160
Percent westslope		0.333	0.442	0.471	0.974	0.969	0.977
Percent Yellowstone		0.667	0.558	0.529	0.026	0.031	0.023

Note: Star (*) as in table 8.

Table 14

Pairwise composite gametic disequilibria for diagnostic loci in hybrid swarms of cutthroat trout. Values are the chi-square distributed statistic Q with sign of D (df = 1).

Loci		Lower Big Hawk Lake		George Lake		Koessler Lake
		1986	1990	1987	1991	1987
sAAT-1	GPI-A	17.86***	23.76***	7.42**	19.24***	1.799
	IDDH	30.65***	20.53***	4.29*	9.19**	0.330
	mIDHP-1	29.94***	25.73***	9.21**	16.75***	3.058
	sIDHP-1	11.79***	23.09***	4.28*	12.35***	0.167
	mMEP-1	9.53**	30.26***	--	10.78**	--
	sMEP-1	19.69***	22.46***	0.38	14.61***	1.684
	sMEP-2	20.10***	11.61***	7.30**	19.54***	6.409**
	PEPB	24.89***	15.42***	9.26**	14.85***	6.545**
GPI-A	IDDH	18.03***	22.76***	6.46*	14.27***	1.893
	mIDHP-1	20.04***	17.44***	6.69**	11.64***	-0.008
	sIDHP-1	15.14***	19.29***	6.34*	8.15**	-0.303
	mMEP-1	15.20***	20.98***	--	11.64***	--
	sMEP-1	22.15***	18.38***	-0.06	13.61***	-0.016
	sMEP-2	25.50***	29.84***	21.12***	20.00***	3.484
	PEPB	15.22***	36.23***	10.31**	12.46***	0.605
IDDH	mIDHP-1	25.84***	14.66***	8.62**	7.89**	-0.359
	sIDHP-1	16.78***	19.27***	4.36*	3.43	-0.207
	mMEP-1	13.55***	17.41***	--	10.24**	--
	sMEP-1	15.62***	25.04***	8.18**	15.36***	-0.059
	sMEP-2	21.67***	17.66***	7.92**	13.07***	-0.531
	PEPB	20.07***	18.10***	5.36*	13.44***	-0.372
mIDHP-1	sIDHP-1	11.95***	11.57***	3.20	8.21**	1.021
	mMEP-1	18.51***	29.53***	--	10.15**	--
	sMEP-1	22.64***	13.97***	1.16	10.00**	3.463
	sMEP-2	19.11***	13.16***	6.68**	16.77***	2.829
	PEPB	21.37***	13.85***	4.75*	10.15**	3.757
sIDHP-1	mMEP-1	15.23***	12.25***	--	13.30***	--
	sMEP-1	14.79***	11.16***	0.09	5.75*	-0.284
	sMEP-2	12.13***	6.34*	7.54**	10.09**	-0.006
	PEPB	22.32***	11.40***	5.07*	12.62***	2.917
mMEP-1	sMEP-1	14.06***	16.06***	--	12.54***	--
	sMEP-2	12.84***	10.00**	--	10.60**	--
	PEPB	16.06***	16.08***	--	12.74***	--
sMEP-1	sMEP-2	8.05**	8.91**	-0.01	12.98***	3.575
	PEPB	18.82***	14.19***	2.92	15.92***	1.531
sMEP-2	PEPB	12.03***	27.35***	12.26**	15.01***	2.829

*P<0.05, **P<0.01, ***P<0.001

Table 15

Allele frequencies at the diagnostic loci between westslope cutthroat and rainbow trout in hybridized lake populations in the South Fork of the Flathead River drainage. YOY = Young of the Year

		Allele frequencies				
		Blackfoot Lake				YOY
Locus	Alleles	(1986)	(1987)	(1990)	(1991)	(1991)
sAAT-1	200	0.239	0.333	0.676	0.767	*
	250	-	-	-	0.050	*
	100	0.761	0.667	0.324	0.183	*
CK-A2	84	0.229	0.333	0.676	0.817	0.890
	100	0.771	0.667	0.324	0.183	0.110
GPI-A	92	0.250	0.333	0.676	0.800	0.890
	100	0.750	0.667	0.324	0.200	0.110
IDDH	40	0.250	0.333	0.676	0.800	*
	100	0.750	0.667	0.324	0.200	*
sIDHP-1,2	86	0.125	0.167	0.338	0.308	*
	71	0.115	0.020	0.118	0.109	*
	40	0.156	0.188	0.235	0.258	*
	100	0.604	0.625	0.309	0.325	*
mMEP-1	88	0.222	0.333	0.676	0.883	0.890
	null	0.778	0.667	0.324	0.167	0.110
Percent westslope		0.250	0.333	0.676	0.813	0.890
Percent rainbow		0.750	0.667	0.324	0.187	0.110

Table 16

Allele frequencies at the diagnostic loci between westslope cutthroat, Yellowstone cutthroat, and rainbow trout in hybridized populations in the South Fork of the Flathead River drainage.

		Allele frequencies				
		Black Lake				
Locus	Alleles	(1986)	(1986)	(1987)	(1990)	(1991)
sAAT-1	200	0.870	0.833	-	0.800	0.943
	250	-	-	-	-	0.034
	165	0.037	-	-	-	-
	100	0.056	0.167	1.000	0.200	0.023
	null	0.037	-	-	-	-
CK-A2	84	0.926	0.667	0.250	0.800	0.989
	100	0.074	0.333	0.750	0.200	0.011
CK-C1	100	0.870	0.867	1.000	0.900	0.830
	38	0.130	0.133	-	0.100	0.170
GPI-A	92	0.907	0.833	-	0.800	1.000
	100	0.093	0.167	1.000	0.200	-
IDDH	40	0.907	0.733	-	0.800	0.977
	100	0.093	0.267	1.000	0.200	0.023
mIDHP-1	100	0.944	1.000	0.750	1.000	1.000
	-75	0.056	-	0.250	-	-
sIDHP-1,2	86	0.472	0.433	-	0.400	0.420
	71	0.019	0.017	-	0.050	0.080
	40	0.204	0.233	0.380	0.200	0.267
	100	0.306	0.317	0.500	0.350	0.233
	114	-	-	0.120	-	-
mMEP-1	88	0.926	0.733	-	0.800	0.989
	null	0.0741	0.267	1.000	0.200	0.011
sMEP-1	100	1.000	1.000	1.000	0.900	1.000
	90	-	-	-	0.100	-
sMEP-2	100	0.926	0.933	1.000	1.000	1.000
	110	0.074	0.067	-	-	-
PEPA-1	100	1.000	1.000	1.000	1.000	1.000
	101	-	-	-	-	-
PEPB	100	1.000	1.000	1.000	1.000	1.000
	135	-	-	-	-	-
PGM-1	100	1.000	1.000	1.000	1.000	1.000
	null	-	-	-	-	-
Percent westslope		0.911	0.761	-	0.800	0.986
Percent rainbow		0.063	0.228	0.937	0.180	0.014
Percent Yellowstone		0.026	0.011	0.063	0.020	0.011

Table 16 - continued

Locus	Alleles	Allele frequencies: Graves Creek (1983)	Graves Creek (1989)	Graves Creek (1991)	Handkerchief Lake (1986)	Handkerchief Lake (1991)
sAAT-1	200	0.704	0.808	0.585	0.933	0.544
	250	0.111	0.096	-	-	0.031
	165	0.019	0.038	-	-	0.031
	100	0.167	0.058	0.067	0.067	0.344
	null	-	-	-	-	-
CK-A2	84	0.815	0.750	0.650	0.967	0.667
	100	0.185	0.250	0.350	0.033	0.333
CK-C1	100	*	0.712	0.915	0.633	0.719
	38	*	0.288	0.085	0.367	0.281
GPI-A	92	0.778	0.827	0.549	0.900	0.687
	100	0.222	0.173	0.451	0.100	0.313
IDDH	40	0.796	0.808	0.488	0.833	0.719
	100	0.204	0.192	0.512	0.167	0.281
mIDHP-1	100	1.000	1.000	0.988	0.967	0.969
	-75	-	-	0.012	0.033	0.031
sIDHP-1,2	86	0.185	0.269	0.262	0.217	0.281
	71	0.231	0.154	0.140	0.233	0.031
	40	0.222	0.240	0.189	0.200	0.203
	100	0.361	0.327	0.409	0.350	0.485
	114	-	0.010	-	-	-
mMEP-1	88	0.815	0.788	0.634	0.933	0.688
	null	0.185	0.212	0.366	0.067	0.312
sMEP-1	100	0.759	0.981	1.000	0.967	1.000
	90	0.241	0.019	-	0.033	-
sMEP-2	100	0.963	0.981	1.000	0.967	1.000
	110	0.037	0.019	-	0.033	-
PEPA-1	100	0.963	1.000	1.000	1.000	1.000
	101	0.037	-	-	-	-
PEPB	100	0.963	1.000	1.000	1.000	1.000
	135	0.037	-	-	-	-
PGM-1	100	0.963	1.000	1.000	1.000	1.000
	null	0.037	-	-	-	-
Percent westslope		0.801	0.832	0.564	0.927	0.658
Percent rainbow		0.176	0.154	0.425	0.052	0.330
Percent Yellowstone		0.023	0.015	0.011	0.021	0.012

Note: Star (*) as in table 8.

Table 17

Allele frequencies at the diagnostic loci between westslope cutthroat and Yellowstone cutthroat trout in hybridized creek populations in the South Fork of the Flathead River drainage, * as in table 8.

		Allele frequencies			
		Clayton Creek			
Locus	Alleles	(1983)	(1990)	(1990)	Gordon Creek
sAAT-1	200	0.962	0.926	0.900	0.900
	250	0.019	0.037	0.020	0.100
	165	0.019	0.037	0.080	-
CK-C1	100	0.923	0.685	0.760	0.833
	38	0.077	0.315	0.240	0.167
GPI-A	92	0.885	0.944	0.880	0.950
	100	0.115	0.056	0.120	0.050
IDDH	40	0.942	0.963	0.920	1.000
	100	0.058	0.037	0.080	-
mIDHP-1	100	0.885	0.944	0.960	1.000
	-75	0.115	0.056	0.040	-
sIDHP-1	86	0.808	0.926	0.840	0.900
	71	0.192	0.074	0.160	0.100
mMEP-1	88	0.981	0.963	0.960	1.000
	null	0.019	0.037	0.040	-
sMEP-1	100	0.942	0.944	0.920	1.000
	90	0.058	0.056	0.080	-
sMEP-2	100	0.865	0.963	0.920	1.000
	110	0.135	0.037	0.080	-
PEPA-1	100	1.000	0.926	0.920	1.000
	101	-	0.074	0.080	-
PEPB	100	0.981	0.944	0.960	0.950
	135	0.019	0.056	0.040	0.050
PGM-1	100	0.962	1.000	0.960	1.000
	null	0.038	-	0.040	-
Percent westslope		0.933	0.953	0.930	0.987
Percent Yellowstone		0.067	0.047	0.070	0.013

Table 17 - continued

		Allele frequencies			
		Jones Creek		Wildcat Creek	
Locus	Alleles	(1983)	(1989)	(1984)	(1988)
sAAT-1	200	0.720	0.731	0.800	0.618
	250	0.240	0.173	0.067	0.368
	165	0.040	0.096	0.133	0.014
CK-C1	100	*	0.750	0.900	*
	38	*	0.250	0.100	*
GPI-A	92	0.900	0.923	0.867	0.947
	100	0.100	0.077	0.133	0.053
IDDH	40	0.880	0.942	0.867	0.987
	100	0.120	0.058	0.133	0.013
mIDHP-1	100	0.920	1.000	0.900	1.000
	-75	0.080	-	0.100	-
sIDHP-1	86	0.580	0.538	0.900	0.921
	71	0.420	0.462	0.100	0.079
mMEP-1	88	0.940	0.981	0.933	1.000
	null	0.060	0.019	0.067	-
sMEP-1	100	0.900	0.942	0.967	1.000
	90	0.100	0.058	0.033	-
sMEP-2	100	0.940	0.981	0.900	0.947
	110	0.060	0.019	0.100	0.053
PEPA-1	100	1.000	1.000	0.900	1.000
	101	-	-	0.100	-
PEPB	100	0.900	0.904	0.867	0.961
	135	0.100	0.096	0.133	0.039
PGM-1	100	0.940	1.000	1.000	1.000
	null	0.060	-	-	-
Percent westslope		0.918	0.947	0.902	0.972
Percent Yellowstone		0.082	0.053	0.098	0.028

Table 17 - continued

		Allele frequencies					
		Wheeler Creek					
Locus	Alleles	(1983)	(1984)	(1991)	(1990)	(1990)	(1991)
sAAT-1	200	0.940	0.900	0.948	0.133	0.467	0.929
	250	0.060	0.080	0.026	-	-	0.071
	165	-	0.020	0.026	0.867	0.533	-
CK-C1	100	0.900	0.840	0.789	0.107	0.500	0.714
	38	0.100	0.160	0.211	0.893	0.500	0.286
GPI-A	92	0.960	0.980	0.895	0.133	0.467	1.000
	100	0.040	0.020	0.105	0.867	0.533	-
IDDH	40	0.960	1.000	0.974	0.133	0.467	1.000
	100	0.040	-	0.026	0.867	0.533	-
mIDHP-1	100	1.000	1.000	0.947	0.133	0.467	1.000
	-75	-	-	0.053	0.867	0.533	-
sIDHP-1	86	0.800	0.958	0.710	0.133	0.467	1.000
	71	0.200	0.042	0.290	0.867	0.533	-
mMEP-1	88	1.000	1.000	0.957	0.133	0.467	1.000
	null	-	-	0.053	0.867	0.533	-
sMEP-1	100	1.000	0.940	0.947	0.133	0.467	1.000
	90	-	0.060	0.053	0.867	0.533	-
sMEP-2	100	1.000	1.000	0.947	0.133	0.467	1.000
	110	-	-	0.053	0.867	0.533	-
PEPA-1	100	1.000	1.000	0.974	0.133	0.467	1.000
	101	-	-	0.026	0.867	0.533	-
PEPB	100	0.980	1.000	0.895	0.133	0.467	1.000
	135	0.020	-	0.105	0.867	0.533	-
PGM-1	100	1.000	1.000	0.770	0.133	0.467	1.000
	null	-	-	0.230	0.867	0.533	-
Percent westslope		0.987	0.987	0.941	0.133	0.467	1.000
Percent Yellowstone		0.013	0.013	0.059	0.867	0.533	-

Table 18

Presence (+) or Absence (-) of Metazoan parasites recovered from 15 lake populations examined from the South Fork Flathead River drainage. Note, CF = Crepidostomum farionis, CS = Cystidicoloides salvelini, CT = Cyathocephalus truncatus, CST = Cystidicola stigmatura, and DD = Diphyllobothrium ditremum.

	Parasites recovered				
Sample	CF	CS	CT	CST	DD
Big Hawk Lake	+	+	+	-	-
Black Lake	+	-	+	-	-
Blackfoot Lake (1986)	+	-	-	-	-
Blackfoot Lake (1990)	+	-	-	-	-
Fawn Lake	+	-	-	-	-
George Lake	+	-	-	-	-
Jewel Lake	+	-	-	-	+
Koessler Lake	+	+	-	-	-
Lena Lake	+	-	-	-	-
Lick Lake	+	+	-	-	-
Marshall Lake (lower)	-	-	-	-	-
Marshall Lake (upper)	+	-	-	-	-
Necklace Lake	+	-	-	-	-
Pilgrim Lake	-	-	+	-	-
Pyramid Lake	+	-	-	-	-
Tom Tom Lake (1986)	+	-	-	+	-
Tom Tom Lake (1990)	+	-	-	+	-

Table 19

Prevalence (%) and abundance (mean number per fish) of Crepidostomum farionis, Cyathocephalus truncatus, Cystidicoloides salvelini, Cystidicola stigmatura and Diphyllobothrium ditremum in relation to the lake samples hybrid index (HI). P = Prevalence, A = Abundance.

			C. farionis		C. truncatus		C. salvelini		C. stigmatura		D. ditremum	
Sample	HI%	N	P	A	P	A	P	A	P	A	P	A
Lower Marshall	100.0	27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Upper Marshall	100.0	7	71.4	32.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fawn	99.4	28	39.3	12.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pilgrim	94.7	22	0.0	0.0	100.0	21.7	0.0	0.0	0.0	0.0	0.0	0.0
Big Hawk	82.1	49	46.9	7.9	20.4	0.7	6.0	0.1	0.0	0.0	0.0	0.0
Black	76.1	15	60.0	5.0	60.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0
Blackfoot (1990)	67.6	34	100.0	68.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Koessler	47.1	26	100.0	56.5	0.0	0.0	42.3	2.1	0.0	0.0	0.0	0.0
George (1990)	44.2	28	39.3	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tom Tom (1990)	40.6	32	3.3	0.1	0.0	0.0	0.0	0.0	6.3	0.1	0.0	0.0
Blackfoot (1986)	25.0	24	79.2	39.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jewel	0.0	30	36.7	8.1	0.0	0.0	0.0	0.0	0.0	0.0	76.7	12.8
Lena	0.0	27	22.2	8.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Necklace	0.0	8	62.5	35.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lick	0.0	35	2.9	0.1	0.0	0.0	21.9	0.4	0.0	0.0	0.0	0.0
Pyramid	0.0	12	100.0	32.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tom Tom (1986)	0.0	24	8.3	1.1	0.0	0.0	0.0	0.0	6.0	0.1	0.0	0.0

Table 20

Mann-Whitney U tests comparing the parasite intensities of Crepidostomum farionis between populations.
Note: Populations (numbers in parenthesis) are the same in both axes.

Lake Populations Taxonomic Status	(1) W	(2) W	(3) W	(4) R	(5) R	(6) R	(7) Y	(8) Y	(9) Y	(10) Y	(11) WxY	(12) WxY	(13) WxY	(14) WxR	(15) WxR
(1) Marshall Lake L.	___														
(2) Marshall Lake U.	***	___													
(3) Fawn Lake	**	NS	___												
(4) Lena Lake	*	*	NS	___											
(5) Necklace Lake	***	NS	NS	*	___										
(6) Jewel Lake	**	*	NS	NS	NS	___									
(7) Pyramid Lake	***	NS	***	***	NS	***	___								
(8) Lick Lake	NS	***	***	*	***	***	***	___							
(9) Tom Tom L. 1986	NS	*	NS	NS	*	NS	***	NS	___						
10) Tom Tom L. 1990	NS	***	***	*	***	**	***	NS	NS	___					
11) Koessler Lake	***	*	***	***	NS	***	NS	***	***	***	___				
12) George Lake	**	*	NS	NS	NS	NS	***	***	NS	***	***	___			
13) Big Hawk L. 1990	***	NS	NS	NS	NS	NS	***	***	*	***	***	NS	___		
14) Blackfoot L. 1986	***	NS	**	***	NS	***	NS	***	***	***	NS	***	***	___	
15) Blackfoot L. 1990	***	*	***	***	*	***	**	***	***	***	NS	***	***	NS	___
16) Black Lake 1986	***	NS	NS	NS	NS	NS	***	***	*	***	***	NS	NS	*	***

NS not significant * P < .050 ** P < .010 *** P < .001

W = westslope cutthroat trout; R = rainbow trout; Y = Yellowstone cutthroat trout

W x R = westslope cutthroat by rainbow trout populations

W x Y = westslope cutthroat by Yellowstone cutthroat trout populations

W x Y x R = westslope cutthroat by Yellowstone cutthroat by rainbow trout populations

Table 21

Mann-Whitney U tests comparing the parasite intensities of Cyathocephalus truncatus between populations 1-3 (above the diagonal), and Cystidicoloides salvelini between populations 4-6 (below the diagonal).

Population	(1)	(2)	(3)	(4)	(5)	(6)
Genetic status	WxY	WxRxY	WxR	WxY	WxY	Y
(1) Big Hawk Lake	___	**	***			
(2) Black Lake		___	***			
(3) Pilgrim Lake			___			
(4) Big Hawk Lake				___		
(5) Koessler Lake				***	___	
(6) Lick Lake				*	NS	___

NS = Not Significant * P < 0.050 ** P < 0.010 *** P < 0.001

Y = Yellowstone cutthroat trout

W x R = westslope cutthroat x rainbow trout

W x Y = westslope cutthroat x Yellowstone cutthroat trout

W x Y x R = westslope cutthroat x Yellowstone cutthroat x rainbow trout

FIGURE 1. Map of the South Fork of the Flathead River drainage.

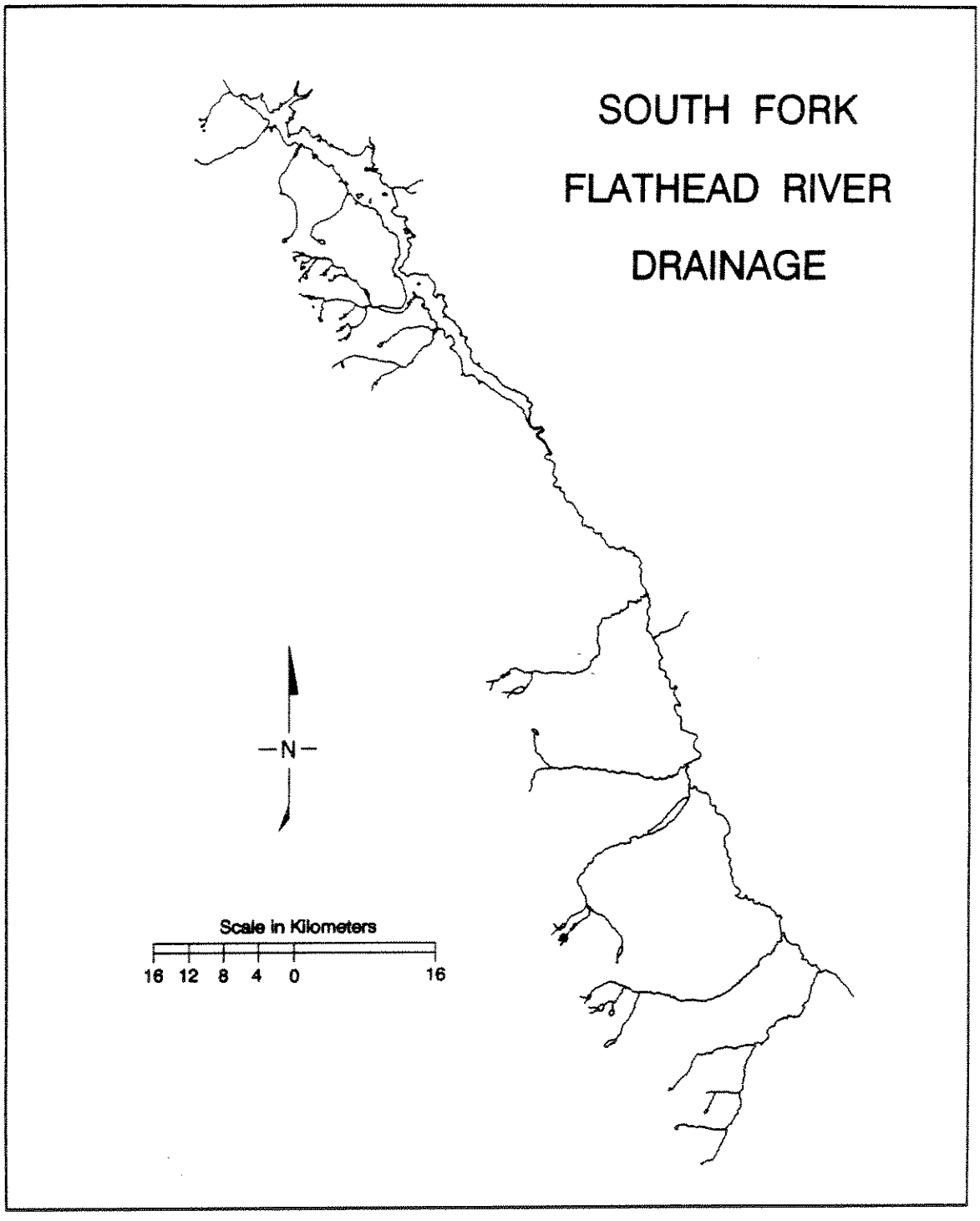

SOUTH FORK
FLATHEAD RIVER
DRAINAGE
N
Scale in Kilometers
16 12 8 4 0 16

FIGURE 2. Map depicting the Northern half of the study area with location sample sites.

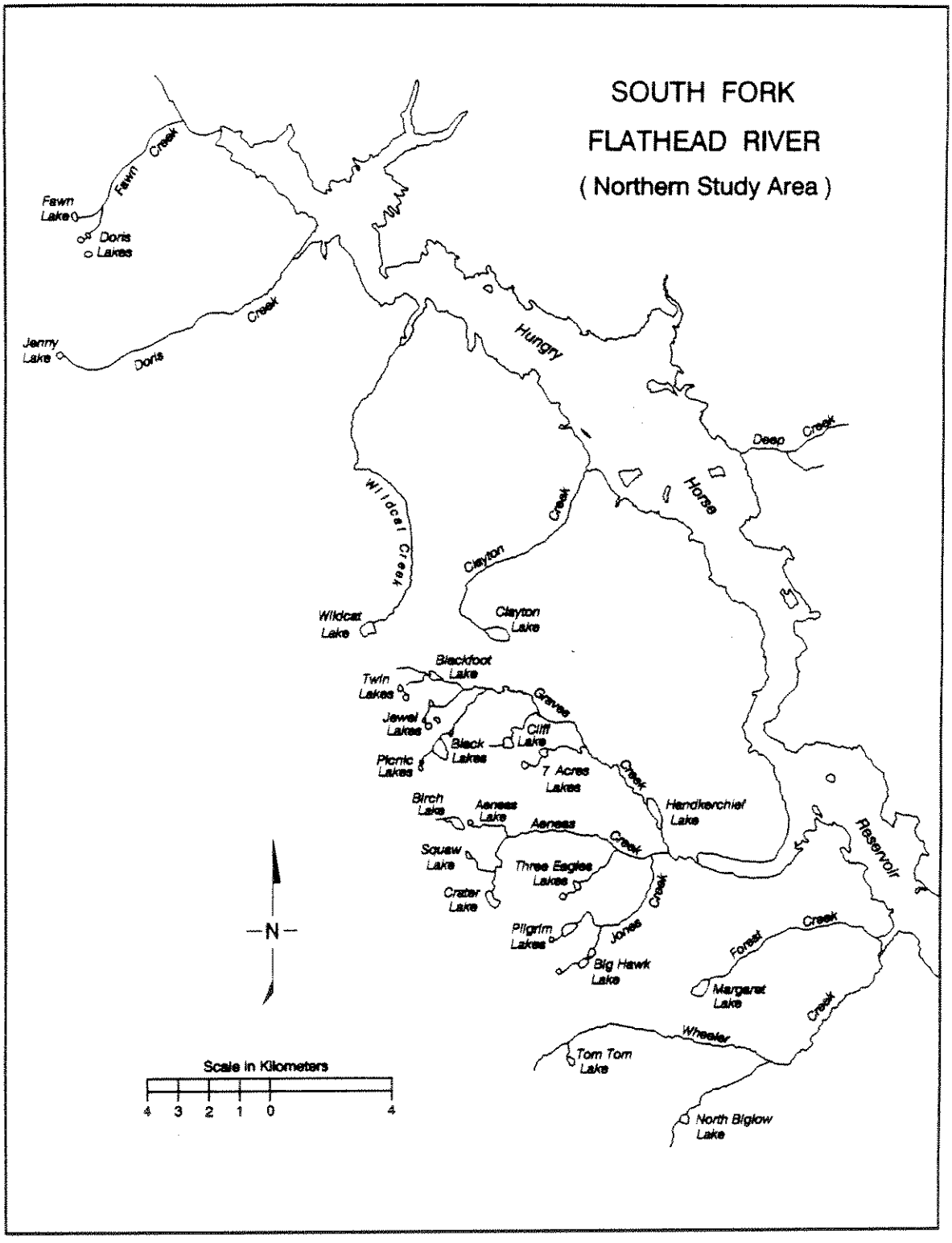
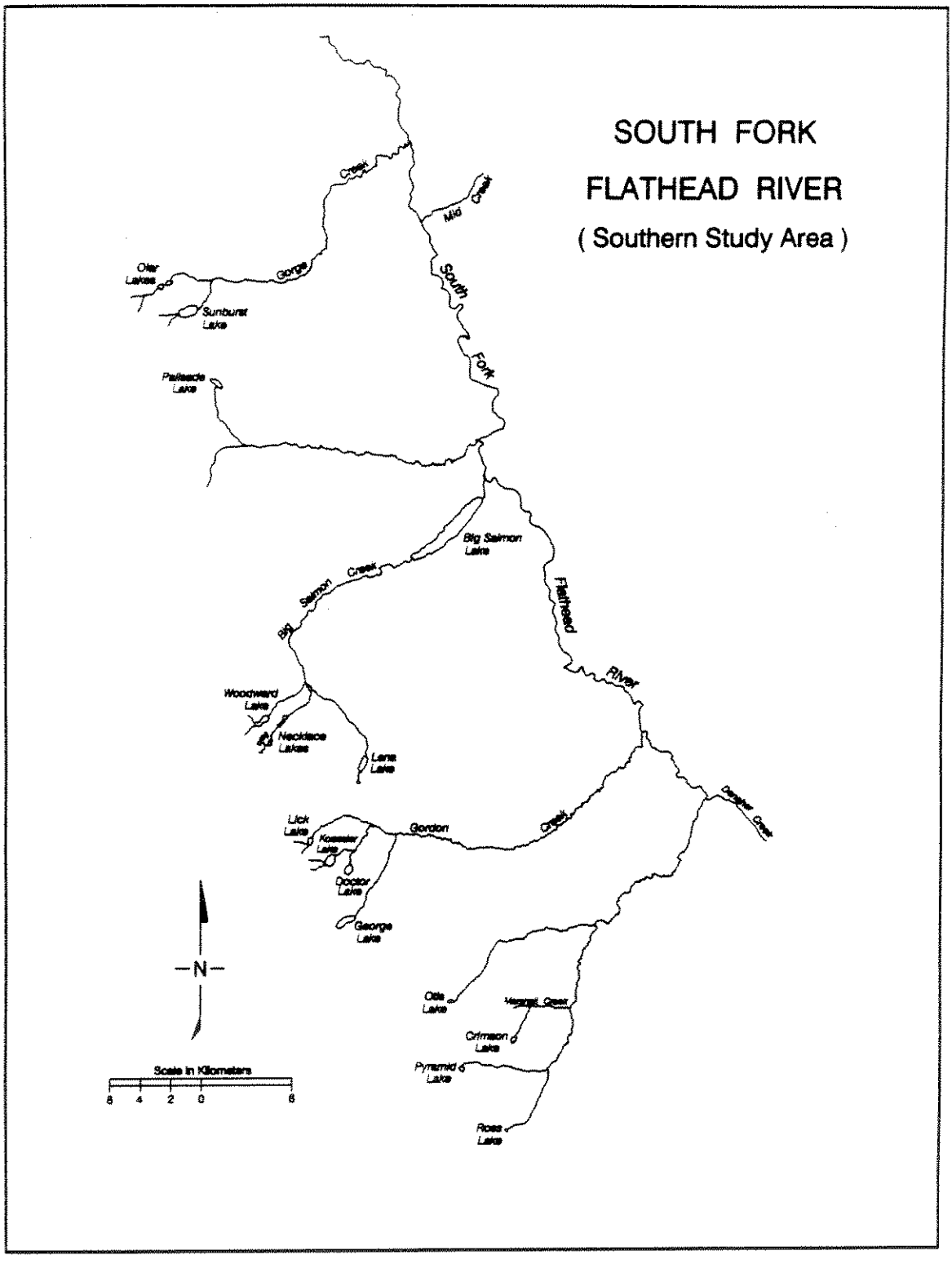

SOUTH FORK
FLATHEAD RIVER
(Northern Study Area)
Fawn Creek
Fawn Lake
Doris Lakes
Jenny Lake
Doris Creek
Hungry
Deep Creek
Horse
Wildcat Creek
Clayton Creek
Wildcat Lake
Clayton Lake
Blackfoot Lake
Twin Lakes
Graves
Jewel Lakes
Cliff Lake
Black Lakes
Picnic Lakes
7 Acres Lakes
Creek
Handkerchief Lake
Birch Lake
Aeneas Lake
Aeneas Creek
Souaw Lake
Three Eagles Lakes
Crater Lake
Pilgrim Lakes
Jones Creek
Big Hawk Lake
Forest Creek
Margaret Lake
Wheeler Creek
Tom Tom Lake
North Bigkow Lake
Reservoir
N
Scale in Kilometers
4 3 2 1 0 4

FIGURE 3. Map depicting the Southern half of the study area with location sample sites.


SOUTH FORK
FLATHEAD RIVER
(Southern Study Area)
Mid Creek
Gorge Creek
Otter Lakes
Sunburst Lake
South Fork
Palisade Lake
Big Salmon Lake
Big Salmon Creek
Flathead River
Woodward Lake
Necklace Lakes
Lens Lake
Lick Lake
Kossler Lake
Doctor Lake
George Lake
Gordon Creek
Dougher Creek
Otis Lake
Crimson Lake
Pyramid Lake
Ross Lake
N
Scale in Kilometers
8 4 2 0 8