Genetic Analysis of 45 Trout Populations in the Yaak River Drainage, Montana.

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SUMMARY

We used protein electrophoresis to determine the genetic composition of 45 trout populations in the Yaak River drainage, Montana. In the North Fork Yaak drainage, all three populations sampled appear to be genetically pure interior rainbow trout, *Oncorhynchus mykiss*. In the East Fork Yaak drainage, six populations sampled appear to be genetically pure interior rainbow trout, four populations are slightly hybridized with westslope cutthroat trout, *O. clarki lewisi*, and one population, established from hatchery introductions, appears to be genetically pure westslope cutthroat trout. In the West Fork drainage, all six populations sampled appear to be genetically pure westslope cutthroat. In tributaries to the middle and lower Yaak River 10 populations appear to be genetically pure westslope cutthroat, 11 populations are westslope cutthroat by rainbow trout hybrid swarms, and one population is a westslope cutthroat by Yellowstone cutthroat trout hybrid swarm.

The available evidence indicates that interior rainbow and westslope cutthroat trout coexisted in tributaries to the lower Yaak River. The rainbow trout appears to have occupied the lower portions of these streams and the cutthroat trout the headwaters. In contrast, westslope cutthroat trout appear to have been the predominant fish in the West Fork and middle Yaak drainage, while interior rainbow trout appear to have been the predominant fish in the North and East Forks of the Yaak River drainage. In addition, as one proceeds northwards up the drainage the genetic impact of introduced coastal rainbow trout on native populations diminishes.

INTRODUCTION

The waters of western Montana were historically inhabited by two trout species; rainbow trout, *Oncorhynchus mykiss*, and westslope cutthroat trout, *O. clarki lewisi*. Westslope cutthroat trout occurred throughout the region, but evidence for native rainbow trout has come only from populations in two Kootenai River tributaries (Allendorf et al. 1980; Holton 1990). Preliminary evidence indicated that native rainbow trout existed in the Callahan Creek drainage and that hybridized populations between native and introduced hatchery rainbow trout existed in the Yaak River drainage (Allendorf et al. 1980).

Native rainbow trout and westslope cutthroat trout are considered fishes of special concern by the State of Montana (Holton 1990) and sensitive species by the United States Forest Service. Since the beginning of this century, many native trout populations have been extirpated. Degradation of the environment by human exploitation has made many waters unsuitable for the existence of trout. Introduced brook trout, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, have displaced native trout populations (Gresswell 1988). This has probably most often occurred in conjunction with habitat degradation which has made waters more suitable for the introduced than the native species.

Introduction of *Oncorhynchus* taxa into waters outside their natural range has also resulted in the loss of many native populations. These introductions have often resulted in interbreeding between the native and introduced fishes (reviewed by Allendorf and Leary 1988 and papers in Gresswell 1988). This interbreeding has destroyed the genetic integrity of many native populations and has replaced them with numerous hybrid swarms or introgressed populations. That is, populations in which genes from two or more trout taxa are randomly, or nearly so, distributed among individuals. In such situations, no fish in the population is likely to be a genetically pure representative of the hybridizing taxa unless it is a recent immigrant.

Preservation of native trout populations in Montana is now the goal of fish management agencies. Identification of native populations is the initial step of a conservation program. Once identified measures can be taken to ensure the continued viability of the native populations. These populations can also serve as a source of fish or gametes for restoration programs. That is, programs that attempt to re-establish populations of the native taxon in reclaimed waters or to found other populations in previously barren waters within its natural range.

The distribution of potentially pure populations of native rainbow and westslope cutthroat trout in the Yaak River drainage is poorly known. Allendorf et al. (1980) examined only two samples from the lower drainage. Here we report the results of our protein analysis of an additional 45 samples. The results indicate that nine of the samples appear to have come from genetically pure populations of native rainbow trout, 18 apparently came from genetically pure populations of westslope cutthroat trout, of which 17 are native and one is introduced, 17 came from populations in which hybridization between rainbow and westslope cutthroat trout has or is occurring, and the remaining sample came from a hybridized westslope cutthroat by Yellowstone cutthroat trout population.

METHODS

Electrophoresis

From July 1986 through July 1992, 45 samples were obtained from 44 locations within the Yaak River drainage (Table 1, Fig. 1-5). Horizontal starch gel electrophoresis was used to determine the genetic characteristics of each fish at 45 loci (genes) coding for proteins present in muscle, liver, or eye tissue (Table 2). Electrophoresis followed the procedures of Allendorf and Utter (1979) and Leary and Booke (1990). Buffers used to make the gels and stains used to reveal the position of particular enzymes in the gels after electrophoresis followed the protocols of Allendorf et al. (1977). Nomenclature of loci and alleles (form of a gene) follows the recommendations of Shaklee et al. (1990). Allelic mobilities are relative to the product produced by the common allele at each locus in Arlee rainbow trout maintained by the Montana Department of Fish, Wildlife and Parks. This convention is used to facilitate the electrophoretic comparison of salmonid fishes.

Status of the populations

Table 3 lists the loci that distinguish between the westslope cutthroat and rainbow trout, coastal and interior rainbow trout, and westslope cutthroat and Yellowstone cutthroat trout. Such loci are commonly termed diagnostic loci (Ayala and Powell 1972) because the alleles detected at them can be used to determine if a sample came from a genetically pure population of rainbow, westslope cutthroat, or Yellowstone cutthroat trout or a population in which hybridization between these fishes has or is occurring.

Samples from genetically pure populations will possess alleles at all diagnostic loci characteristic of only that fish. First generation hybrids will be heterozygous (possess two different alleles at a locus) at all diagnostic loci for alleles characteristic of the hybridizing trout. When first generation hybrids mate among themselves and individuals of the parental species this initiates the formation of a hybrid swarm. After a few generations, individuals from such populations will have highly variable genetic characteristics. They will be homozygous (possess two copies of the same allele at a locus) at some diagnostic loci and heterozygous at others. Furthermore, the particular loci that are homozygous or heterozygous will differ widely among individuals (e.g. Allendorf and Leary 1988).

Based upon allele frequencies at LDH-B2* and sSOD-1* rainbow trout can be divided into two genetically different groups. Coastal rainbow trout or those native to waters west of the Cascade Mountain Range crest usually possess LDH-B2*100 at frequencies greater than 0.90 and sSOD-1*152 at frequencies greater than 0.15 (Allendorf and Utter 1979). Most hatchery populations of rainbow trout were established from coastal populations. Interior rainbow trout or those native to waters east of the Cascade crest usually possess LDH-B2*100 at frequencies less than 0.80, and often at frequencies much less than this. They also usually lack sSOD-1*152 or possess it at a very low frequency. Samples from genetically pure populations of rainbow trout and with LDH-B2* and sSOD-1* allele frequencies typical of interior rainbow trout were considered to have come from native populations. Samples from rainbow trout populations with allele frequencies intermediate to those typical of interior and coastal rainbow trout were considered to have come from hybridized populations between native and hatchery rainbow trout.

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 rainbow trout (sAAT-3,4*, sIDHP-1,2*, sMDH-A1,2*, sMDH-B1,2*, and sMEP-1,2*) and westslope cutthroat trout (sAAT-3,4*, sMDH-A1,2*, and sMDH-B1,2*) populations, therefore, each pair was considered to be a single gene with four instead of two copies per individual.

RESULTS

Genetically pure interior rainbow trout populations

Alleles characteristic of only rainbow trout were detected at all the diagnostic loci in nine of the 45 samples analyzed (Table 4). With sample sizes of 25 or more individuals, we can detect as little as one percent westslope cutthroat trout genes in a hybrid swarm with rainbow trout 95% of the time, assuming that the genes of the parental taxa are randomly distributed among individuals. All sample sizes from these populations (Table 1 and 4) are near 25 fish except for the upper East Fork Yaak River (N=5) and lower East Fork Yaak River (N=6). With these two exceptions then, we can be reasonably certain that the remaining populations in Table 4 represent pure rainbow trout populations. Furthermore, the allele frequencies at LDH-B2* and sSOD-1* are typical of interior rainbow trout indicating they are native populations (Table 4).

Because of the smaller sample sizes from the two East Fork populations, we can only be 95% certain that westslope cutthroat trout have had no more than a 4% genetic contribution to them. These populations, therefore, might be slightly hybridized with westslope cutthroat trout but we failed to detect this because of sampling error. Until demonstrated otherwise, however, these populations should be managed as pure native rainbow trout.

Hybrid rainbow trout populations

In the samples from Blacktail Creek, Caribou Creek, lower Hellroaring Creek, Meadow Creek, lower Seventeenmile Creek, Solo Joe Creek, and East Fork Yaak River, alleles characteristic of both westslope cutthroat and rainbow trout were detected at at least three diagnostic loci (Table 5). Rainbow trout, however, had a much greater genetic contribution to these hybrid swarms than westslope cutthroat trout.

To determine if the genes from the two species were randomly distributed among individuals in these hybrid swarms, we compared the distribution of the number of westslope cutthroat trout alleles per fish summed over all diagnostic loci to that expected based on a Poisson distribution with a mean equal to the average frequency of westslope cutthroat alleles in the sample. The observed distribution conformed to the expected ($P>0.05$) in the East Fork Yaak and lower Hellroaring samples. Thus, these populations appear to be randomized hybrid swarms that contain no genetically pure rainbow or westslope cutthroat trout.

The number of westslope cutthroat trout alleles per individual significantly differed ($P<0.05$) from the expected random distribution in the five remaining hybrid populations. In four of these (Blacktail, Caribou, lower Seventeenmile, and Solo Joe), there was an excess of fish possessing only rainbow trout alleles at all diagnostic loci and an excess of fish that were heterozygous for alleles characteristic of westslope cutthroat and rainbow trout at three or more diagnostic loci. In the latter fish, all diagnostic loci not heterozygous were homozygous for rainbow trout alleles. The genetic characteristics of these fish, therefore, suggest that most probably represent backcross progeny from matings between rainbow trout and first generation hybrids. These populations, therefore, appear to be nonrandomized hybrid swarms with the majority of the fish being genetically pure rainbow trout or of recent hybrid origin.

The nonrandom distribution of rainbow and westslope cutthroat trout alleles in Meadow Creek is also largely due to a significant excess ($N=15$) of fish homozygous for rainbow trout alleles at all diagnostic loci. The collection also contained two apparent first generation hybrids, one fish homozygous for westslope cutthroat alleles at all diagnostic loci, and seven fish with genetic characteristics expected of matings between westslope cutthroat trout and first generation hybrids. Thus, this population appears to be a nonrandomized hybrid swarm where the majority of fish are genetically pure rainbow trout, others are of recent hybrid origin, and a small proportion may be pure westslope cutthroat trout.

The next question to address is whether coastal or interior rainbow trout have contributed genes to the hybrid swarms. The most accurate estimates of the relative genetic contribution of these fishes to a hybrid swarm would be obtainable if we knew the allele frequencies at LDH-B2* and sSOD-1* in the populations before hybridization. Although this information is unknown, we can obtain qualitatively reliable estimates by making some fairly reasonable assumptions.

We have rarely observed LDH-B2*76 and sSOD-1*152 in westslope cutthroat trout populations. Thus, these alleles are assumed to be absent from the westslope cutthroat trout contributing to the hybrid swarms. In this situation, the frequency of these alleles among the rainbow trout genes in a hybrid swarm is the observed frequency divided by the proportion of rainbow trout alleles averaged over all diagnostic loci. Subsequently, these frequencies will be referred to as "corrected" for the presence of westslope cutthroat trout genes.

Since LDH-B2*76 exists only at low frequency in coastal rainbow trout, we assumed that all these alleles in a hybrid swarm were derived from interior rainbow trout. Violation of this assumption would result in a slight overestimate of the interior rainbow trout genetic contribution.

The final assumption is that the frequency of LDH-B2*76 in interior rainbow trout contributing to a hybrid swarm was equal to its average frequency in the seven large samples from genetically pure populations (Table 4, X = 0.957). The two East Fork of the Yaak River samples were excluded in determining the mean frequency of LDH-B2*76 among the native rainbow populations because the relatively few specimens collected introduces large standard errors in the allele frequency estimates. Although the allele frequencies at this locus significantly differ among the seven samples used (contingency table chi-square; P=0.034) we feel this is the best approximation we can make in trying to determine the genetic contribution of interior rainbow trout to a hybrid swarm when pre-hybridization allele frequencies at this locus are not known. If the frequency of LDH-B2*76 was actually greater than 0.957 in the hybridizing interior rainbow trout, then their genetic contribution to a hybrid swarm would be slightly overestimated. The contribution of interior rainbow trout would be underestimated if the frequency of LDH-B2*76 in them was actually less than 0.957.

With the above assumptions, the proportion of interior rainbow trout genes in a hybrid swarm is the corrected LDH-B2*76 frequency divided by 0.957 times the average rainbow trout genetic contribution. This value subtracted from the average rainbow trout genetic contribution gives the proportion of coastal rainbow trout genes in the population. When the corrected LDH-B2*76 allele frequency was very near or greater than 0.957 we assumed no coastal rainbow trout genetic contribution.

Using the above procedure, it appears that only interior rainbow trout contributed genes to the hybrid swarms in Blacktail Creek, Caribou Creek, lower Hellroaring Creek, and East Fork Yaak River (Table 5). Both coastal and interior rainbow trout apparently contributed genes to the hybrid swarms in Meadow Creek and lower Seventeenmile Creek (Table 5). Interior rainbow trout, however, had a substantially greater contribution to these population than coastal rainbow trout.

The hybrid swarm in Solo Joe Creek does not have as straightforward an interpretation as the others. The relatively low frequency of LDH-B2*76 (Table 5) could indicate a small coastal rainbow trout genetic contribution or an unusually low frequency of this allele in a once pure interior rainbow trout population. We tend to favor the latter interpretation. Solo Joe Creek is an East Fork Yaak River tributary. There are no known rainbow trout introductions in this drainage (Montana Department of Fish, Wildlife, and Parks, Joe Huston, personal communication) and no evidence of coastal rainbow trout genes were detected in the East Fork Yaak sample below the confluence of

Solo Joe Creek. Thus, coastal rainbow trout genes do not appear to have penetrated as far up the Yaak drainage as Solo Joe Creek.

Genetic differences among interior rainbow trout populations

Because there are no known dispersal barriers between the Basin Creek, East Fork Basin Creek, and West Fork Basin Creek sample sites, we tested the possibility that these samples may have come from the same reproductive population. Evidence for this would be supplied by a lack of detectable genetic differences among the samples at polymorphic loci. The allele frequencies at the three polymorphic loci (Table 4) were statistically homogenous (contingency table chi-square, P>0.05) among the samples. Thus, there is no evidence of genetic differences so we combined the samples into a single Basin Creek sample in the following analyses.

The allele frequencies at sIDHP-1,2* and LDH-B2* were heterogenous (P<0.001 and P=0.034 respectively) among the Basin Creek, Boyd Creek, Porcupine Creek, and two North Fork Yaak River samples and indicate that genetic differences exist among the populations. We used the fixation indices of Wright (1978) to estimate the amount of genetic divergence among the populations relative to the theoretical maximum of one when no populations share alleles in common.

For all the inland rainbow trout populations sampled, the total fixation index is only 0.039 indicating relatively little divergence. When this is partitioned into the amount due to divergence among populations within the East and North Fork drainages (0.037) and to differences between populations from the drainages (0.002) most of the divergence is due to the former component. That is, populations within the drainages tend to be as much or more divergent among themselves than when compared to populations from the other drainage.

Genetically pure westslope cutthroat trout populations

Alleles characteristic of only westslope cutthroat trout were detected at all the diagnostic loci between this fish and rainbow trout or Yellowstone cutthroat trout in 18 of the 45 samples analyzed (Table 6). With sample sizes of 25 or more individuals, we can detect as little as a one percent rainbow or Yellowstone cutthroat trout genetic contribution to a hybrid swarm with westslope cutthroat trout 95% of the time. Thus, the populations sampled from Beaver Creek, Fourth of July Creek, French Creek, North Fork Meadow Creek, South Fork Meadow Creek, Pheasant Creek, upper Red Top Creek, upper West Fork Yaak River in Montana (two samples), and the West Fork Yaak River in Canada are almost undoubtedly genetically pure westslope cutthroat trout. In addition, with sample sizes of 19 specimens from upper Seventeenmile and Garver Creek, we have better than a 95% chance of detecting at least 1.5% rainbow trout genes and 1.0% Yellowstone cutthroat trout genes in these populations. We can be relatively certain, therefore, that these populations also represent genetically pure westslope cutthroat trout.

Because of smaller sample sizes, however, we can only be 95% certain that rainbow or Yellowstone cutthroat trout have had no more than a 2.5% or 1%

genetic contribution to the Wampoo Creek and Mt. Henry Lake populations; a 4% or 1.5% genetic contribution to the Koo Koo and upper Pete Creek populations; a 5% or 2% genetic contribution to the lower Pete Creek population, and a 9.5% or 4% genetic contribution to the lower West Fork Yaak River population. These populations, therefore, may be slightly hybridized with rainbow or Yellowstone cutthroat trout but we failed to detect this because of sampling error. Until demonstrated otherwise, however, these populations should be managed as genetically pure westslope cutthroat trout.

Hybrid westslope cutthroat trout populations

In the Yaak River drainage, the sIDHP-1,2*71 allele generally characteristic of rainbow and Yellowstone cutthroat trout occurred at unusually high frequencies in "pure" and hybridized populations of westslope cutthroat trout and was, therefore, excluded from the analysis used to determine the relative purities of individual populations. In the Arbo, Cyclone, Independence, middle Pete, lower Red Top, upper Spread, two lower Spread, and two Turner Creek samples, alleles characteristic of both westslope cutthroat and rainbow trout were detected at at least two diagnostic loci (Table 7). In addition, in the upper Hellroaring Creek sample alleles characteristic of westslope cutthroat and Yellowstone cutthroat trout were detected at all diagnostic loci (Table 8).

Because there are no known barriers between the two Turner Creek samples, and the two lower Spread Creek samples came from the same approximate location, we tested the possibility that these samples were derived from the same reproductive population. The allele frequencies at the polymorphic loci (Table 7) between the two Turner Creek samples were statistically homogenous (contingency table X^2=10.776, df=7, P=0.149). Thus, there was no evidence of genetic differences so we combined the Turner Creek samples in the following analysis. In contrast, allele frequencies were statistically heterogeneous (contingency table X^2= 37.4, df=13, P=0.0004) between the lower Spread Creek samples. Thus, these samples were treated independently in the following analysis.

In order to determine if the genes from the two taxa were randomly distributed among individuals in these hybrid swarms, we compared the distribution of the number of rainbow trout and Yellowstone cutthroat trout alleles per fish summed over all diagnostic loci to that expected based on a Poisson distribution with a mean equal to the average frequency of these alleles in each sample. The observed distribution of rainbow trout alleles per individual conformed (P>0.05) to the expected random distribution in the 1984 lower Spread Creek sample, the upper Spread Creek sample, and the Turner Creek sample. Thus, these populations appear to be randomized hybrid swarms with a predominant westslope contribution that contain no genetically pure rainbow or westslope cutthroat trout. The observed distribution of Yellowstone cutthroat trout alleles per individual also conformed to the expected random distribution in the upper Hellroaring Creek sample. This population, therefore, appears to be a randomized hybrid swarm with an approximately equal Yellowstone-westslope contribution and no genetically pure Yellowstone or westslope cutthroat trout.

The number of rainbow trout alleles per individual significantly differed ($P<0.05$) from the expected random distribution in the Arbo, Cyclone, Independence, middle Pete, lower Red Top, and the 1991 lower Spread Creek sample. These samples, therefore, were not collected from randomized hybrid swarms. Of these populations, only Arbo Creek contained a nearly equal proportion of westslope cutthroat and rainbow trout genes. The other populations were predominantly westslope cutthroat trout (Table 7).

In the Arbo and Independence Creek samples, most of the fish collected were of definite hybrid origin. There was, however, a significant excess ($N=6$ and $N=8$) of fish in each sample that had only westslope cutthroat trout alleles at all diagnostic loci. These hybrid swarms, therefore, mainly contain fish of hybrid origin, but some may still be genetically pure westslope cutthroat trout.

The nonrandom distribution of alleles observed in the middle Pete and lower Spread Creek populations was largely due to an excess of fish possessing only westslope cutthroat trout alleles at all diagnostic loci. In lower Spread Creek, there was also an excess of fish with genetic characteristics indicative of matings between rainbow trout and first generation hybrids. Thus, these populations appear to be nonrandomized hybrid swarms with the majority of the fish being either genetically pure westslope cutthroat trout or of recent hybrid origin.

Unlike the previous populations, Cyclone and lower Red Top Creek appear to contain pure individuals from both species. In each population there was an excess of fish that had only westslope cutthroat (16 and 21, respectively) or rainbow trout (3 and 2) alleles at all diagnostic loci. The remaining fish in each sample were of definite hybrid origin, and their genetic characteristics suggested that most were of recent hybrid origin. Thus, these populations contain mainly pure westslope cutthroat trout and a small proportion of hybrids and rainbow trout.

We next determined the proportional contribution of coastal and interior rainbow trout genes in these hybrid swarms using previously described procedures. For Cyclone and Independence Creek, it appears that only interior rainbow trout contributed genes to the hybrid swarms (Table 7). For Arbo, middle Pete, lower Red Top, and the 1991 lower Spread Creek samples, however, it appears that both coastal and interior rainbow trout contributed genes to the hybrid swarms (Table 7). Interior rainbow trout contributed a greater proportion of genes in the Arbo and lower Red Top Creek hybrid swarms, but the hybrid swarms in middle Pete and lower Spread Creek had approximately equal contributions of genes from interior and coastal rainbow trout.

Since LDH-B2*76 was not detected in either the Turner or upper Spread Creek hybrid swarms it appears that only coastal rainbow trout have contributed genes to these populations (Table 7). Given the average frequency of rainbow trout genes in these populations, it is unlikely ($P<0.05$) the samples would not contain this allele if the fish had hybridized with interior rainbow trout having average LDH-B2*76 frequencies for the drainage.

Genetic differences among westslope cutthroat trout populations

Again, using the fixation indices of Wright (1978), we estimated the amount of genetic divergence among the 17 native westslope populations (the Mt. Henry populations being eliminated because it was established form hatchery introductions) relative to the theoretical maximum of one when no populations share alleles in common. For the native westslope cutthroat trout populations sampled, the total fixation index is 0.707 indicating a large amount of divergence. When this is partitioned into the amount due to divergence among populations within the West Fork and lower Yaak drainages (0.658) and to differences between populations from the drainages (0.049) most of the divergence is due to the former component. That is, within the drainages there tends to be as much or more divergence among populations as there is when comparisons are made between drainages. This situation is common among westslope cutthroat trout populations (Allendorf and Leary, 1988).

DISCUSSION

Distribution of Oncorhynchus genes in the Yaak River drainage

Interior rainbow trout genes appear to predominate in the North and East Forks of the Yaak drainage (Figure 3). All three samples from the North Fork Yaak drainage and six of eleven samples from the East Fork Yaak drainage appear to be from genetically pure populations of interior rainbow trout.

Of the remaining samples from the East Fork of the Yaak drainage, four came from interior rainbow trout populations that were slightly hybridized with westslope cutthroat (Figure 5), while the Mt. Henry Lake sample came from an introduced pure westslope cutthroat trout population (Figure 4). In addition, the hybrid swarms in this drainage all exist below the confluence of the Mt. Henry Lake outlet and Basin Creek. This suggests that the Mt. Henry Lake population is the main or sole source of hybridization between rainbow and westslope cutthroat trout in this portion of the Yaak drainage.

Westslope cutthroat trout genes appear to predominate in the West Fork Yaak drainage and in the middle Yaak drainage between Spread Creek and the confluence of the East and North Forks of the Yaak River (Figure 4). All six samples from the West Fork Yaak drainage and three of seven samples from the middle Yaak drainage appear to have come from genetically pure populations of westslope cutthroat trout. In addition, the only sample from the South Fork of the Yaak River drainage, Beaver Creek, also came from a genetically pure westslope cutthroat trout population.

The remaining four samples from the middle Yaak drainage came from westslope cutthroat trout populations that were slightly hybridized with rainbow trout. The upper Spread Creek and Turner Creek populations represent westslope cutthroat by coastal rainbow trout hybrid swarms that contain a low percentage of rainbow genes. The middle Pete Creek and lower Spread Creek populations represent hybrid swarms that mainly contain westslope cutthroat genes, and approximately equal proportions of interior and coastal rainbow trout genes.

In the lower Yaak River drainage westslope cutthroat trout genes also appear to predominate, but both coastal and interior rainbow trout genes are common (Figures 4 & 5). Yellowstone cutthroat trout genes also occur in one of the populations in this portion of the drainage (Figure 5).

Six of 14 samples collected from tributaries to the lower Yaak River (Fourth of July, North Fork Meadow, South Fork Meadow, upper Red Top, upper Seventeenmile, and Wampoo Creek) appear to have come from genetically pure populations of westslope cutthroat trout. In addition, except for Wampoo Creek, all these populations occur in the headwaters of tributaries to the lower Yaak River.

The remaining eight samples collected from the lower Yaak drainage came from hybridized populations. The Arbo Creek population represents a hybrid swarm with an appreciable proportion of genes from westslope cutthroat trout, interior rainbow trout, and coastal rainbow trout. The upper Hellroaring Creek population represents a hybrid swarm with an approximately equal proportion of genes from Yellowstone cutthroat and westslope cutthroat trout.

The Cyclone, Independence, and lower Red Top populations represent hybrid swarms that mainly contain westslope cutthroat trout genes and a moderate percentage of rainbow trout genes. The Cyclone and Independence Creek populations appear to be solely hybridized with interior rainbow trout, but both interior and coastal rainbow trout appear to have contributed genes to the lower Red Top Creek population.

The lower Hellroaring, Meadow, and lower Seventeenmile populations represent hybrid swarms that mainly contain interior rainbow trout genes. Lower Hellroaring Creek is hybridized solely with westslope cutthroat. Meadow Creek contains an appreciable proportion of westslope cutthroat genes and a small percentage of coastal rainbow trout genes, while lower Seventeenmile Creek contains an appreciable proportion of coastal rainbow trout genes, and a small percentage of westslope cutthroat trout genes. These and the previous data suggest that interior rainbow trout and westslope cutthroat trout both naturally existed in these creeks. The latter fish apparently occupied the upper waters of the creeks and the interior rainbow trout the lower waters. Considering all the data, it seems that as one moves northwards up the Yaak drainage coastal rainbow trout have had a decreasing genetic impact on the native trout populations.

In Idaho, westslope cutthroat and interior rainbow trout (steelhead) naturally coexisted in the Clearwater River and Salmon River drainages (Hanson 1977; Griffith 1988; Rieman and Apperson 1989). The two species, however, were never observed to be sympatric in the mainstem rivers. Westslope cutthroat trout were confined to the upper mainstems with rainbow trout below them. A similar distributional pattern was observed in tributaries where both species coexisted. Rainbow trout were always confined to the lower portion of the drainage and westslope cutthroat trout to the upper drainage. The general impression, therefore, has been that rainbow trout entered these river systems after westslope cutthroat trout and displaced the cutthroat to headwater areas unless they were isolated above dispersal barriers.

Our data suggest that in the Yaak River drainage native rainbow and westslope cutthroat trout had a more complex spatial distribution, at least in the tributaries, than in the Idaho drainages. In the lower tributaries, distributional patterns appear to be similar to those in Idaho. Rainbow trout occupied the lower waters and westslope cutthroat trout the headwaters. In the middle Yaak drainage, however, the lower reaches of the tributaries appear to have mainly been occupied by westslope cutthroat trout as none of the samples were collected above dispersal barriers. Historically, interior rainbow trout may never have entered these streams. In the upper Yaak drainage, westslope cutthroat trout occupied the West Fork of the Yaak River and its headwater tributaries, while rainbow trout occupied the North and East Forks of the Yaak River and their headwater tributaries. In Idaho, such waters historically were occupied by westslope cutthroat trout.

Hybridization

There are two possible explanations for the small amount of hybridization observed between interior rainbow and westslope cutthroat trout in four East Fork Yaak River drainage populations: East Fork Yaak River, Caribou Creek, Blacktail Creek, and Solo Joe Creek. It may represent a small and sporadic amount of hybridization between native rainbow and westslope cutthroat trout, or it may represent recent hybridization between native rainbow and introduced hatchery westslope cutthroat trout.

We tend to favor the latter hypothesis. According to stocking records (Joe Huston, personal communication) the only location in the East Fork Yaak drainage where hatchery westslope cutthroat trout have been introduced is upper Mt. Henry Lake in 1971, 1978, 1983, and 1987. This lake drains into Basin Creek below the confluence of the East and West Forks where our samples were obtained. The Mt. Henry Lake population is, therefore, the likely source of the westslope cutthroat trout genes observed in the East Fork Yaak drainage. The introduced fish have probably emigrated out of the lake and hybridized with the native fish in the lower reaches of Basin Creek. From here hybridization has probably proceeded downstream to the East Fork Yaak River and from there spread to the lower reaches of Caribou, Solo Joe, and Blacktail Creek where the samples were obtained.

The data provide some circumstantial support for this scenario. In Caribou Creek and the East Fork of the Yaak River, the westslope cutthroat genes were largely confined to one fish in each sample, while in Blacktail Creek and Solo Joe Creek, the westslope cutthroat trout genes were largely confined to two fish in each sample. These populations, therefore, appear to have only recently become hybridized with westslope cutthroat trout and this is consistent with the history of westslope introductions into Mt. Henry Lake. Furthermore, there appears to be a relationship between sampling date and the percentage of westslope cutthroat trout genes present in the hybridized populations. That is, the more recent a population was sampled the higher its percentage of westslope cutthroat trout genes.

This suggests that emigration and hybridization between the westslope cutthroat introduced into Mt. Henry Lake and the native interior rainbow trout is an ongoing process. It further suggests that the amount and extent of hybridization in the drainage will continue to increase as long as westslope cutthroat trout are present in Mt. Henry Lake. If our suspicion is correct, then without restoration efforts only those rainbow populations in the East Fork Yaak drainage above barriers are not threatened by future hybridization. Thus, we feel it is important to quickly obtain more information addressing the possibility of hatchery westslope genes emigrating out of Mt. Henry Lakes. This can best be done by sampling Basin Creek below the confluence of the Mt. Henry Lakes outlet with Basin Creek. Finding a hybridized population in this area of Basin Creek would lend strong support to the hypothesis that the lake stockings have initiated hybridization between rainbow and westslope cutthroat trout in the drainage. Given this situation, the elimination of the Mt. Henry Lake population would be highly recommended.

In the middle Yaak drainage, hybridization between native westslope cutthroat and rainbow trout appears to have primarily been initiated by the introduction of hatchery rainbow trout into the main Yaak River. Three of the creeks sampled from the middle Yaak drainage contain rainbow - westslope cutthroat trout hybrid swarms. Although none of these creeks are known to have been stocked with rainbow trout, all the populations contain some coastal rainbow trout genes.

Westslope cutthroat and coastal rainbow trout genes were randomly distributed among the fish in the upper Spread and Turner Creek populations, suggesting that they have been hybrid swarms for an appreciable amount of time. The genes from westslope cutthroat, coastal rainbow, and interior rainbow trout were not randomly distributed among the fish in the lower Spread and middle Pete Creek populations. This suggests that these populations have only recently become hybridized, or that genes from the different fishes are emigrating into the populations. Some data support this contention. In 1987 Pete Creek appeared to be pure westslope cutthroat trout but in 1991 evidence of hybridization was detected. Analysis of fish collected from lower Spread Creek in 1984, indicated that the coastal rainbow and westslope cutthroat genes in this population were randomly distributed among individuals. In 1991, the sample showed an increase in the proportion of rainbow genes (both coastal and interior) and a nonrandom distribution. This indicates a continual infusion of rainbow genes into the area either due to immigration of pure or hybrid fish.

In the lower Yaak drainage, there are eight hybridized populations, and of these only Arbo Creek has documented introductions of hatchery rainbow and westslope cutthroat trout. Hybridization in Arbo Creek, therefore, can probably be attributed, at least partially, to the introduction of these fish. In 1931, its headwater lake, Wee Lake, was stocked with rainbow trout and the main Yaak in the vicinity of Arbo Creek was stocked with rainbow trout in 1955, 1961, 1964, and 1966. Thus, coastal rainbow trout genes probably invaded the system from above and below. In 1976, westslope cutthroat trout were stocked into Arbo Creek. This could have initiated hybridization between rainbow and westslope cutthroat trout in the system. The possibility that hybridization preceded the hatchery introduction because of native westslope cutthroat trout, however, cannot be excluded with the available data. In fact, given the high proportion of westslope cutthroat trout genes in the population the latter may be more likely than assuming they all arose from a single hatchery introduction.

Although none of the remaining populations have documented records of trout introductions the hybridization in them is probably also due to introductions in the Yaak drainage. The hybridization observed in upper Hellroaring Creek confirms that at some point this creek was stocked with Yellowstone cutthroat trout. Protein data from the other hybridized populations sampled in the lower Yaak drainage also suggest that in Hellroaring, Meadow, and Seventeenmile Creek, both the interior rainbow and westslope cutthroat trout naturally coexisted. Native westslope cutthroat occupying the headwaters and interior rainbow trout occupying the lower reaches of the creeks. Hybridization between them probably rarely if ever occurred because of spatial and possibly temporal differences in spawning. Furthermore, the westslope cutthroat trout in the upper creeks may have been isolated from the native rainbow trout because of a dispersal barrier.

The most likely scenario to explain the hybridization observed in these creeks is that introduced coastal rainbow trout or their descendants entered these systems from the main Yaak. This resulted in hybridization between the introduced and native rainbow trout. Occasionally westslope cutthroat trout would emigrate to the area from above, but because of premating reproductive isolating mechanisms hybridization seldom occurred between them and the native rainbows. Once the latter had extensively hybridized with the introduced rainbows or their descendants, the premating reproductive isolating mechanisms broke down. Thus, hybridization was initiated between rainbow and westslope cutthroat trout in the creek. This is also probably still occurring because some of the fish in the samples appeared to be of recent hybrid origin. Through time, therefore, we expect the percentage of westslope cutthroat trout genes in these populations to increase.

In Cyclone, Independence, and lower Red Top Creek, it appears that both westslope cutthroat and interior rainbow trout historically occupied these creeks. The presence of coastal rainbow trout genes in lower Red Top Creek suggests that hybridization in this creek may have been initiated by coastal rainbow trout. Due to the apparent absence of coastal rainbow trout genes in the Cyclone and Independence Creek populations, however, we can not rule out the possibility that interior rainbow and westslope cutthroat trout may have sporadically hybridized in the lower reaches of these creeks.

In summary, hybridization between rainbow and westslope cutthroat trout in the Yaak drainage appears to mainly be due to the introduction of hatchery fish. In the upper drainage, it seems to have been initiated by the fairly recent introduction of hatchery westslope cutthroat trout. In the middle and lower portion of the drainage, with the exceptions of Turner, upper Hellroaring and Arbo Creek, most of the hybridization is probably attributable to the introductions of coastal rainbow trout that occurred in the main Yaak between 1934 and 1969. Due to a barrier falls at the mouth of Turner Creek, the coastal rainbow trout genes observed there are probably derived from an undocumented rainbow trout introduction, while the hybridization observed in upper Hellroaring Creek undoubtedly results from an undocumented introduction of Yellowstone cutthroat trout. The hybridization in Arbo Creek, however,

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Table 1

Name, status (W = westslope, R = rainbow, W x R = westslope - rainbow hybrids, R x W = rainbow - westslope hybrids, W x Y = westslope - Yellowstone hybrids), location (township, range, section), sample size (N), and collection date of 45 trout samples from the Yaak River drainage, Montana.

Name	Taxonomic Status	Location			N	Date
		T	R	S		
1. Arbo Creek	W x R	33N	33W	13	30	15 Sep 87
2. Wampoo Creek	W	33N	33W	4&5	12	18 Sep 91
3. Seventeenmile Creek (lower)	R x W	34N	33W	27	26	Sep 87
4. Seventeenmile Creek (upper)	W	33N	32W	9	19	Sep 87
5. Fourth of July Creek	W	34N	33W	30	25	18 Sep 91
6. Independence Creek	W x R	34N	33W	15C	25	16 Sep 91
7. Cyclone Creek	W x R	34N	33W	6	25	18 Sep 91
8. Red Top Creek (lower)	W x R	35N	33W	31	25	17 Sep 91
9. Red Top Creek (upper)	W	34N	34W	11	25	17 Sep 91
10. Meadow Creek	R x W	35N	33W	19	25	13 Sep 91
11. South Fork Meadow Creek	W	35N	34W	22	25	16 Sep 91
12. North Fork Meadow Creek	W	35N	34W	13	25	16 Sep 91
13. Hellroaring Creek (lower)	R x W	35N	33W	18	24	13 Sep 91
14. Hellroaring Creek (upper)	Y x W	36N	34W	35	27	11 Sep 91
15. Spread Creek (lower)	W x R	35N	33W	3	25	11 Sep 91
16. Spread Creek (lower)	W x R	35N	33W	3	10	26 Sep 84
17. Spread Creek (upper)	W x R	36N	33W	19	26	9 Sep 91
18. Pheasant Creek	W	35N	33W	12C	26	5 Sep 91
19. Pete Creek (lower)	W	36N	32W	29	6	Sep 87
20. Pete Creek (middle)	W x R	36N	32W	19	10	5 Sep 91
21. Pete Creek (upper)	W	37N	33W	36	7	5 Sep 91
22. Beaver Creek	W	36N	31W	34C	25	5 Sep 91
23. Turner Creek	W x R	36N	31W	23C	25	9 Sep 91
24. Turner Creek	W x R	36N	31W	25	27	20 Sep 90
25. French Creek	W	37N	32W	35	26	22 Aug 91
26. West Fork Yaak River	W	37N	32W	35	3	Sep 87
27. West Fork Yaak River	W	(Canada)			25	30 Sep 91
28. West Fork Yaak River	W	37N	32W	6	25	16 Sep 91
29. Garver Creek	W	37N	32W	18	19	23 Aug 91
30. West Fork Yaak River	W	37N	33W	22	25	16 Sep 91
31. Koo Koo Creek	W	37N	31W	20	7	22 Aug 91
32. East Fork Yaak River	R	37N	31W	23	6	22 Aug 91
33. Blacktail Creek	R x W	37N	30W	17	25	21 Aug 91
34. East Fork Yaak River	R x W	37N	30W	29	22	15 Sep 87
35. Solo Joe Creek	R x W	37N	30W	32	27	19 Sep 90
36. Caribou Creek	R x W	37N	30W	22	24	19 Jul 86
37. Mt. Henry Lake	W	36N	30W	17A	12	7 Jul 92
38. Basin Creek	R	36N	30W	16D	28	18 Sep 90
39. West Fork Basin Creek	R	36N	30W	21	28	18 Sep 90
40. East Fork Basin Creek	R	36N	30W	21	27	18 Sep 90
41. Porcupine Creek	R	36N	30W	13	24	19 Sep 90
42. East Fork Yaak River	R	37N	29W	31	5	21 Aug 91
43. North Fork Yaak River	R	37N	31W	10	26	20 Sep 90
44. North Fork Yaak River	R	(Canada)			24	10 Oct 91
45. Boyd Creek	R	37N	32W	1A	25	6 Sep 91

Table 3

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

Locus	Westslope	Yellowstone	Coastal Rainbow	Interior Rainbow
sAAT-1*	200,250	165	100	100
CK-A2*	84,100	84	100,76	100
CK-C1*	100,38	38	100,38	100
GPI-A*	92,100	100	100	100
IDDH*	40,100	100	100,200,40	100,200,40
mIDHP-1*	100	-75	100	100
sIDHP-1,2*	86,100,40,71,114	71	100,71,40,114	100,71,40,114
LDH-B2*	100,112,76,24	100	100,76	76,100
mMEP-1*	88	null	null	null
sMEP-1*	100	90	100,75	100,75
sMEP-2*	100	110	100	100
PEPA-1*	100	101	100,115,90	100,115,90
PEPB*	100	135	100,135	100,135
PGM-1*	100,null	null	100,null	100,null
sSOD-1*	100	100	100,152	100,152

Table 4
Allele frequencies at the polymorphic loci in native rainbow trout populations in the Yaak River drainage, Montana. All other loci analyzed but not listed here were genetically invariant for the allele characteristic of rainbow trout. The number designations below the East and North Fork of the Yaak River samples correspond to the sample numbers listed in Table 1.

		Samples and Allele Frequencies								
Locus	Alleles	E. Fk. Basin Creek	W. Fk. Basin Creek	Basin Creek	Boyd Creek	Porcupine Creek	E. Fk. Yaak River (31)	E. Fk. Yaak River (33)	N. Fk. Yaak River (41)	N. Fk. Yaak River (44)
GPI-B2*	100	1.000	1.000	1.000	1.000	0.979	1.000	1.000	1.000	1.000
	null	-	-	-	-	0.021	-	-	-	-
mIDHP-2*	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.981	1.000
	140	-	-	-	-	-	-	-	0.019	-
sIDHP-1,2*	100	0.500	0.509	0.500	0.500	0.500	0.500	0.500	0.635	0.500
	71	0.500	0.482	0.500	0.190	0.469	0.500	0.333	0.231	0.479
	40	-	0.009	-	0.310	0.031	-	0.167	0.134	0.021
LDH-B2*	100	0.056	0.089	0.036	-	0.104	0.200	-	0.019	-
	76	0.944	0.911	0.964	1.000	0.896	0.800	1.000	0.981	1.000
LDH-C*	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.981	1.000
	95	-	-	-	-	-	-	-	0.019	-
sMDH-B1,2*	100	0.991	1.000	1.000	1.000	1.000	1.000	1.000	0.981	1.000
	83	-	-	-	-	-	-	-	0.019	-
	125	0.009	-	-	-	-	-	-	-	-

Table 5

Alleles frequencies at the diagnostic loci between rainbow trout and westslope cutthroat trout, and at the two loci that differentiate coastal and interior rainbow trout in seven rainbow-westslope cutthroat trout hybrid swarms in the Yaak River drainage, Montana. At the six diagnostic loci, the allele characteristic of westslope cutthroat trout is listed first. At the last two loci, the allele characteristic of coastal rainbow trout is listed first and values in parentheses indicate allele frequencies in rainbow trout corrected for hybridization. The number designation below the East Fork of the Yaak River sample corresponds to the sample number listed in Table 1.

		Samples and Allele Frequencies						
Locus	Alleles	Blacktail Creek	Caribou Creek	Lower Hellroaring Creek	Meadow Creek	Lower Seventeenmile Creek	Solo Joe Creek	East Fork Yaak River (32)
sAAT-1*	200	0.040	0.021	0.021	0.160	0.038	0.037	-
	100	0.960	0.979	0.979	0.840	0.962	0.963	1.000
CK-A2*	84	0.020	-	0.063	0.240	0.019	0.019	0.023
	100	0.980	1.000	0.937	0.760	0.981	0.981	0.977
GPI-A*	92	0.060	0.021	0.125	0.140	0.019	0.019	0.023
	100	0.940	0.979	0.875	0.860	0.981	0.981	0.977
IDDH*	40	0.080	0.021	0.021	0.140	0.019	0.056	0.023
	100	0.920	0.979	0.979	0.860	0.981	0.944	0.977
sIDHP-1,2*	86	-	-	-	0.070	0.010	-	-
	100	0.520	0.500	0.552	0.510	0.577	0.528	0.511
	71	0.440	0.500	0.406	0.400	0.404	0.389	0.489
	40	0.040	-	0.042	0.020	0.010	0.083	-
mMEP-1*	88	0.040	-	0.042	0.140	0.038	0.019	0.045
	null	0.960	1.000	0.958	0.860	0.962	0.981	0.955
Average westslope		0.040	0.011	0.045	0.160	0.026	0.025	0.019
Average rainbow		0.960	0.989	0.955	0.840	0.974	0.975	0.981
LDH-B2*	100	0.080 (0.042)	0.042 (0.031)	0.063 (0.019)	0.260 (0.119)	0.288 (0.269)	0.148 (0.126)	0.068 (0.050)
	76	0.920 (0.958)	0.958 (0.969)	0.937 (0.981)	0.740 (0.881)	0.712 (0.731)	0.852 (0.874)	0.932 (0.950)
sSOD-1*	152	- (-)	- (-)	0.167 (0.175)	0.100 (0.120)	0.058 (0.060)	- (-)	- (-)
	100	1.000 (1.000)	1.000 (1.000)	0.833 (0.825)	0.900 (0.880)	0.942 (0.940)	1.000 (1.000)	1.000 (1.000)
Average coastal		-	-	-	0.063	0.229	0.080	-
Average interior		0.960	0.989	0.955	0.773	0.744	0.890	0.981

Table 6

Allele frequencies at the polymorphic loci in populations of westslope cutthroat trout in the Yaak River drainage, Montana. All other loci analyzed but not listed here were genetically invariant for the allele characteristic of westslope cutthroat trout.

		Samples and Allele Frequencies				
Locus	Alleles	Beaver Creek	French Creek	Koo Koo Creek	Fourth of July Creek	Garver Creek
sAAT-1*	200	*	1.000	1.000	0.940	0.895
	250	*	-	-	0.060	0.105
CK-C1*	100	1.000	1.000	1.000	1.000	1.000
	38	-	-	-	-	-
GPI-B1*	100	1.000	1.000	1.000	1.000	1.000
	null	-	-	-	-	-
sIDHP-1*	86	0.680	-	1.000	1.000	0.579
	71	0.320	1.000	-	-	0.421
sIDHP-2*	100	0.900	1.000	1.000	1.000	1.000
	40	0.100	-	-	-	-
LDH-A2*	100	1.000	1.000	1.000	1.000	1.000
	24	-	-	-	-	-
LDH-C*	100	1.000	1.000	1.000	1.000	1.000
	95	-	-	-	-	-
sMDH-B1,2*	100	1.000	1.000	1.000	1.000	1.000
	83	-	-	-	-	-
PGDH*	100	1.000	-	1.000	1.000	1.000
	110	-	1.000	-	-	-
PGM-2*	100	1.000	-	1.000	1.000	0.974
	85	-	1.000	-	-	0.026

Table 6 continued

Locus	Alleles	West Fork Yaak River (34)	West Fork Yaak River (35)	West Fork Yaak River (36)	West Fork Yaak River (43)
sAAT-1*	200	1.000	0.060	-	0.040
	250	-	0.940	1.000	0.960
CK-C1*	100	1.000	1.000	1.000	1.000
	38	-	-	-	-
GPI-B1*	100	1.000	1.000	1.000	1.000
	null	-	-	-	-
sIDHP-1*	86	0.667	0.280	0.520	0.580
	71	0.333	0.720	0.480	0.420
sIDHP-2*	100	1.000	1.000	1.000	1.000
	40	-	-	-	-
LDH-A2*	100	1.000	1.000	1.000	1.000
	24	-	-	-	-
LDH-C*	100	1.000	1.000	1.000	1.000
	95	-	-	-	-
sMDH-B1,2*	100	1.000	1.000	1.000	1.000
	83	-	-	-	-
PGDH*	100	1.000	1.000	1.000	1.000
	110	-	-	-	-
PGM-2*	100	1.000	0.920	0.880	0.900
	85	-	0.080	0.120	0.100

Note: The star (*) at the AAT-1* locus in the Beaver creek sample indicates that no information was unattainable at that locus. The number designation below the samples correspond to the sample numbers listed in Table 1.

Table 7

Allele frequencies at the diagnostic loci between westslope cutthroat trout and rainbow trout and at the two loci that differentiate coastal and interior rainbow trout in ten westslope cutthroat-rainbow trout hybrid swarms in the Yaak River drainage, Montana. The table follows the conventions of Table 5.

		Samples and Allele Frequencies				
Locus	Alleles	Arbo Creek	Cyclone Creek	Independence Creek	Middle Pete Creek	Lower Red Top Creek
sAAT-1*	200	0.533	0.800	0.860	0.950	0.080
	250	-	-	-	-	0.800
	100	0.467	0.200	0.140	0.050	0.120
CK-A2*	84	0.600	0.840	0.760	0.700	0.880
	100	0.400	0.160	0.240	0.300	0.120
GPI-A*	92	0.500	0.800	0.780	0.750	0.880
	100	0.500	0.200	0.220	0.250	0.120
IDDH*	40	0.550	0.760	0.780	0.850	0.860
	100	0.450	0.240	0.220	0.150	0.140
sIDHP-1,2*	86	0.183	0.350	0.240	0.250	0.340
	114	0.017	-	-	-	-
	100	0.467	0.510	0.490	0.575	0.540
	71	0.125	0.100	0.220	0.175	0.120
	40	0.208	0.040	0.050	-	-
mMEP-1*	88	0.633	0.820	0.800	0.750	0.880
	null	0.367	0.180	0.200	0.250	0.120
Average westslope		0.563	0.804	0.796	0.800	0.876
Average rainbow		0.437	0.196	0.204	0.200	0.124
LDH-B2*	100	0.850 (0.657)	0.800 (-)	0.740 (-)	0.900 (0.500)	0.900 (0.194)
	76	0.150 (0.343)	0.200 (1.000)	0.260 (1.000)	0.100 (0.500)	0.100 (0.806)
sSOD-1*	152	0.133 (0.304)	0.040 (0.204)	0.140 (0.686)	- (-)	- (-)
	100	0.867 (0.696)	0.960 (0.796)	0.860 (0.314)	1.000 (1.000)	1.000 (1.000)
Average coastal		0.157	-	-	0.096	0.020
Average interior		0.280	0.196	0.204	0.104	0.104

Table 7 continued

Locus	Alleles	Spread Creek (15)	Spread Creek (16)	Spread Creek (17)	Turner Creek (22)	Turner Creek (23)
sAAT-1*	200	0.760	0.900	0.865	1.000	1.000
	100	0.240	0.100	0.135	-	-
CK-A2*	84	0.820	0.800	0.942	1.000	1.000
	100	0.180	0.200	0.058	-	-
GPI-A*	92	0.700	1.000	0.864	0.981	0.960
	100	0.300	-	0.154	0.019	0.040
IDDH*	40	0.800	1.000	0.885	1.000	0.980
	100	0.200	-	0.115	-	0.020
sIDHP-1,2*	86	0.210	0.425	0.337	0.398	0.860
	114	0.010	-	-	-	-
	100	0.510	0.525	0.500	0.593	0.040
	71	0.250	0.025	0.163	0.009	0.100
	40	0.020	0.025	-	-	-
mMEP-1*	88	0.780	1.000	0.923	0.963	0.980
	null	0.220	-	0.077	0.037	0.020
Average westslope		0.772	0.940	0.892	0.957	0.984
Average rainbow		0.228	0.060	0.108	0.043	0.016
LDH-B2*	100	0.880 (0.474)	1.000 (1.000)	1.000 (1.000)	0.875 (1.000)	0.880 (1.000)
	76	0.120 (0.526)	- (-)	- (-)	- (-)	- (-)
	24	- (-)	- (-)	- (-)	0.130 (-)	0.120 (-)
sSOD-1*	152	- (-)	- (-)	- (-)	- (-)	- (-)
	100	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)
Average coastal		0.125	0.060	0.108	0.043	0.016
Average interior		0.103	-	-	-	-

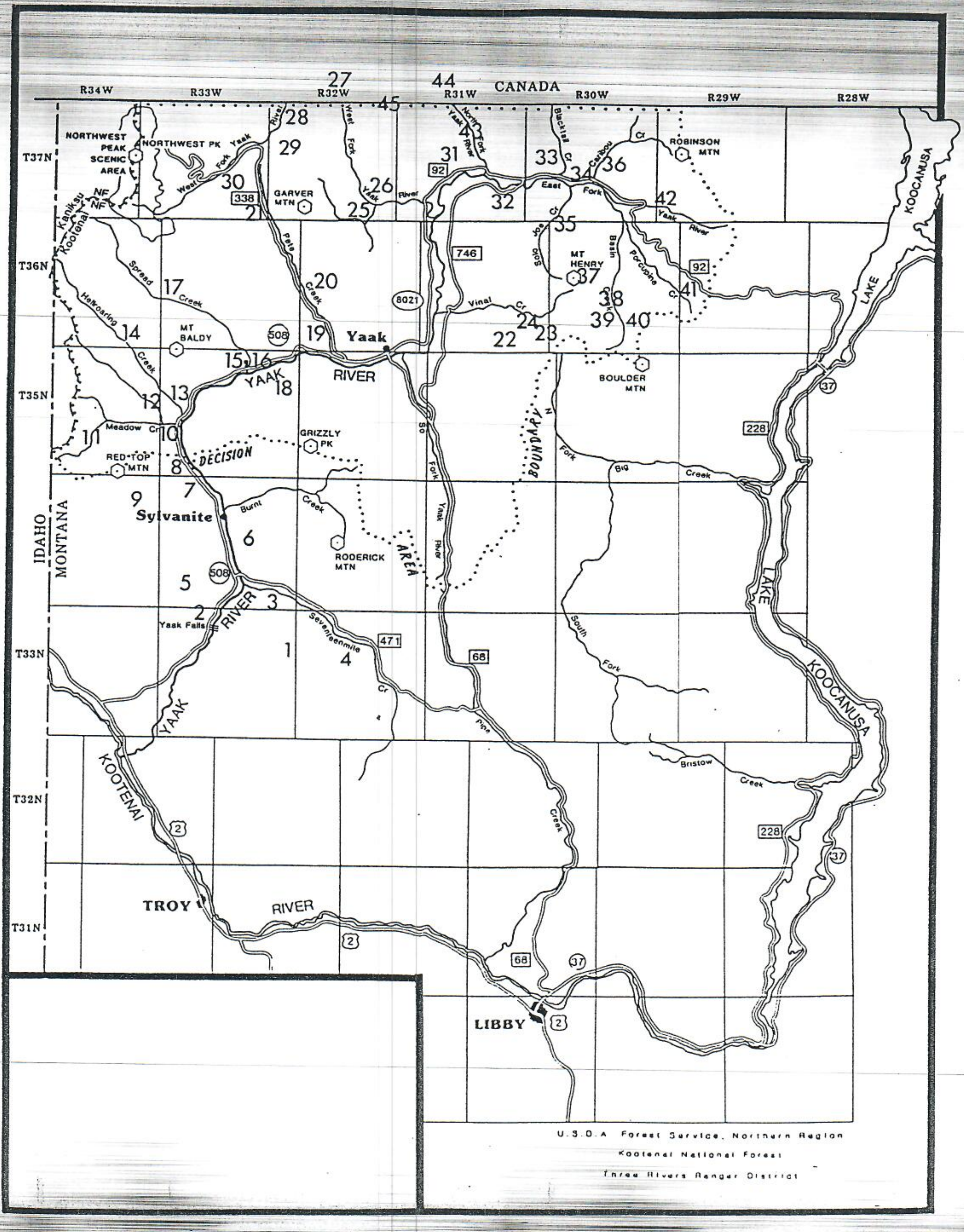
LDH-B2*24 is considered a westslope cutthroat trout allele because we have seldom observed it in a rainbow trout population but it is common in some westslope cutthroat trout populations in the Kootenai River drainage. In order to estimate the allele frequencies at these loci corrected for hybridization this allele is considered to be LDH-B2*100. The number listed below the sample corresponds to those in Table 1.

Table 8

Allele frequencies at the diagnostic loci between westslope cutthroat and Yellowstone cutthroat trout in the Yaak River drainage, Montana. The allele characteristic of westslope cutthroat trout is listed first.

		Sample and Allele Frequencies
Locus	Alleles	(Upper) Hellroaring Creek
sAAT-1*	200	0.333
	165	0.667
CK-C1*	100	0.365
	38	0.635
GPI-A*	92	0.611
	100	0.389
IDDH*	40	0.463
	100	0.537
mIDHP-1*	100	0.574
	-75	0.426
mMEP-1*	88	0.444
	null	0.556
sMEP-1*	100	0.537
	90	0.463
sMEP-2*	100	0.556
	110	0.444
PEPA-1*	100	0.444
	101	0.556
PEPB*	100	0.481
	135	0.519
PGM-1*	100	0.537
	null	0.463
Average westslope		0.486
Average Yellowstone		0.514

Figure 1. Location of 45 trout samples collected from the Yaak River drainage, Montana. Numbers correspond to those in Table 1.



U.S.D.A Forest Service, Northern Region

Kootenai National Forest

Three Rivers Ranger District

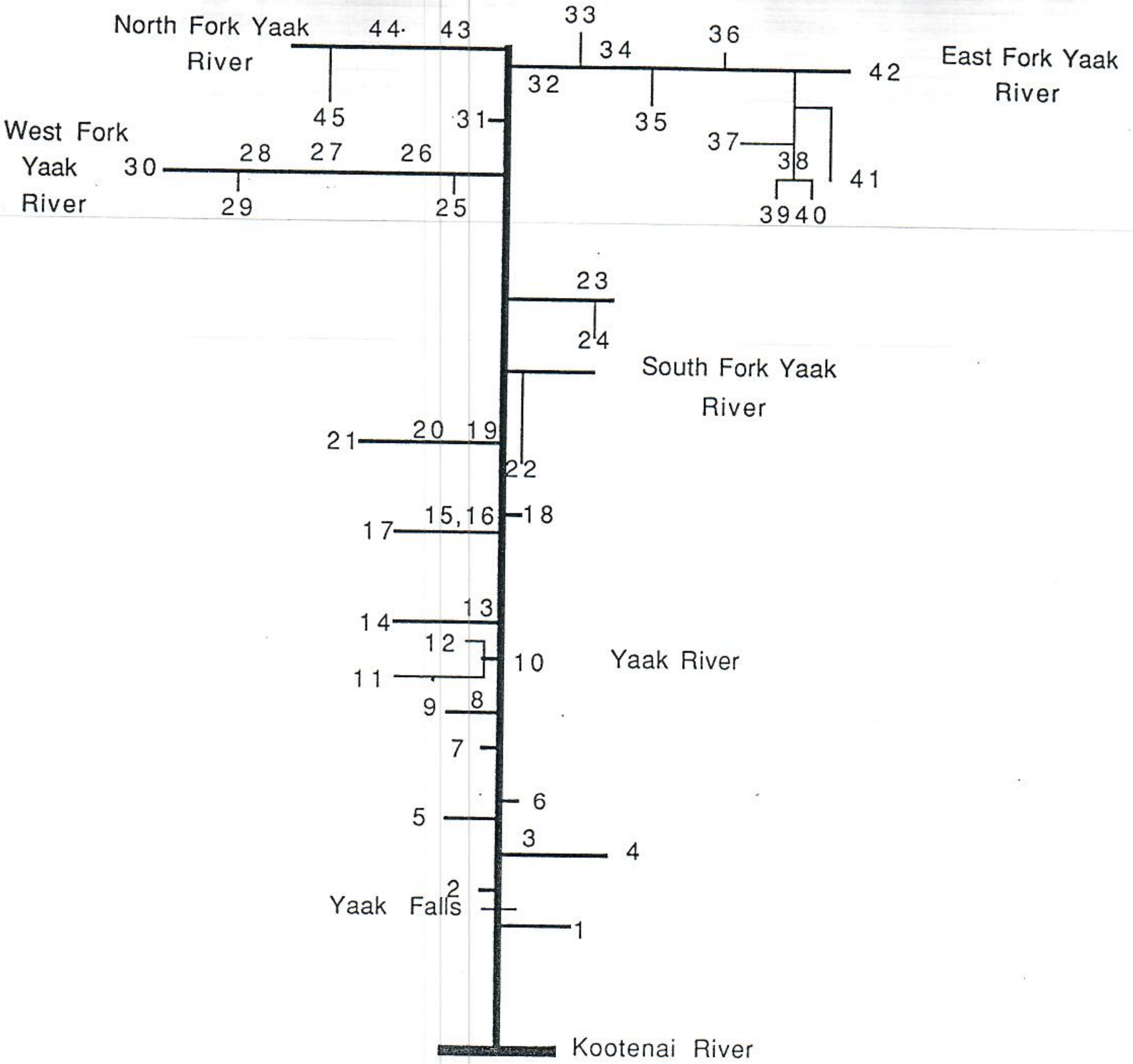


Figure 2. Schematic diagram of the locations of 45 populations sampled from the Yaak River drainage, Montana. The numbers correspond to those given in Table 1.

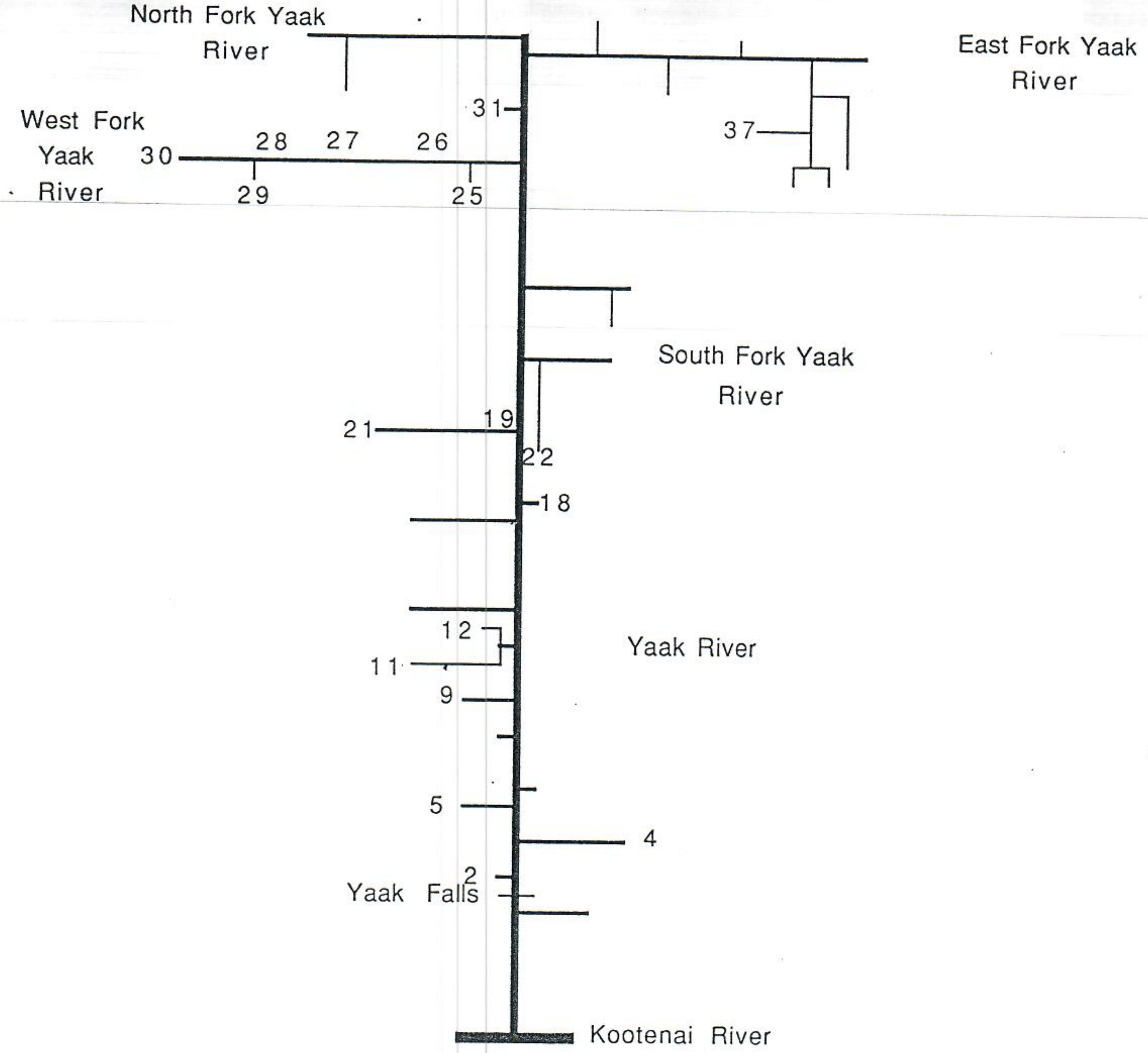


Figure 4. Schematic diagram of the locations of 18 putative westslope cutthroat trout populations sampled from the Yaak River drainage, Montana. The numbers correspond to those given in Table 1. Population 37 is derived from hatchery introductions of westslope cutthroat trout.

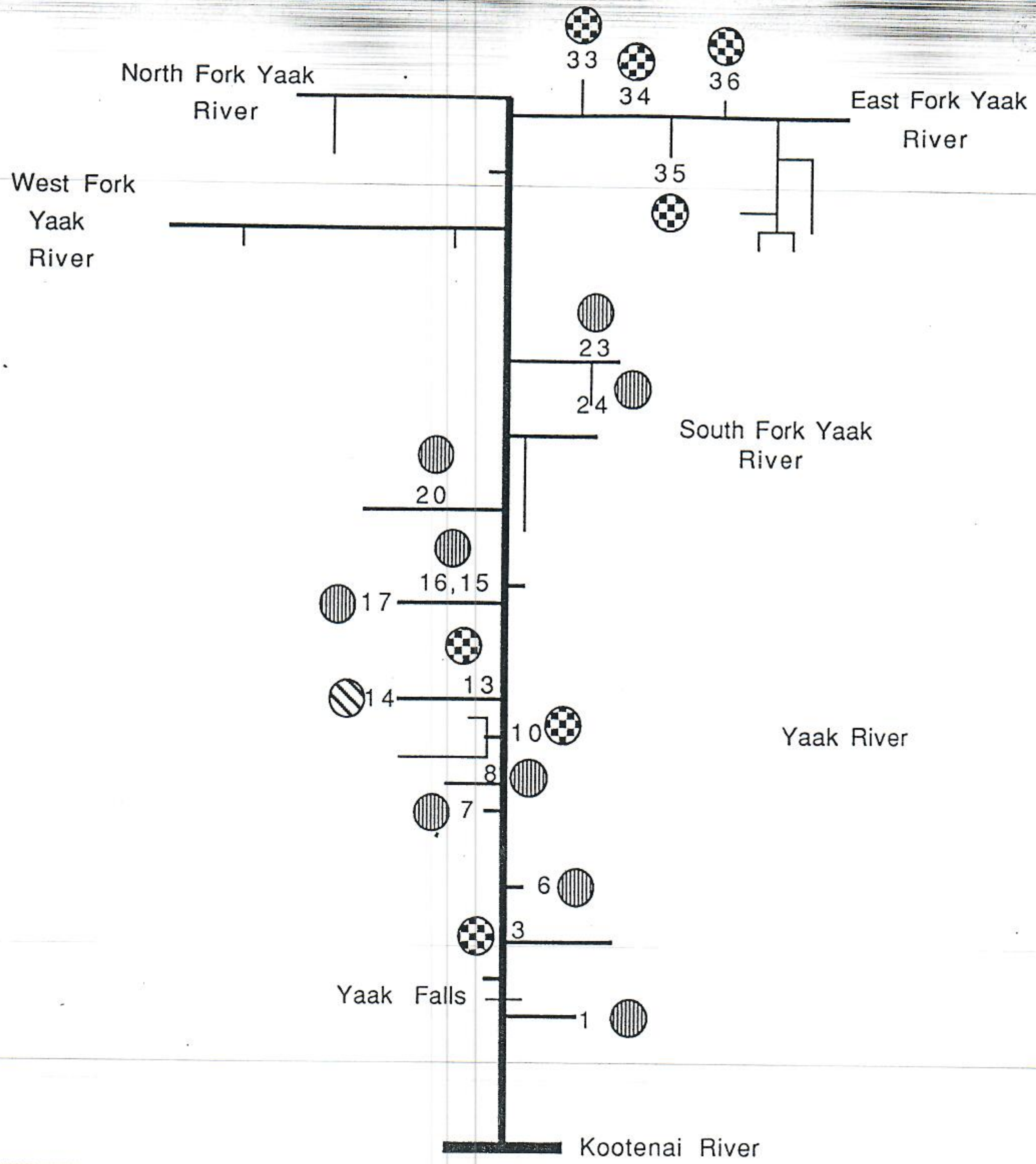


Figure 5. Schematic diagram of the locations of 18 hybrid populations sampled from the Yaak River drainage, Montana. The numbers correspond to those given in Table 1.

▦ Indicates a hybridized inland rainbow trout population.

▥ Indicates a westslope cutthroat by rainbow trout population.

⊘ Indicates a westslope cutthroat by Yellowstone cutthroat trout population.