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# POPULATION GENETICS OF ARCTIC GRAYLING:
# GREBE LAKE, YELLOWSTONE NATIONAL PARK

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# INTRODUCTION

Arctic grayling (Thymallus arcticus) live in freshwater drainages in northern Asia and North America. A disjunct population exists in Montana, and another survived in Michigan until it went extinct in 1936. These two populations are thought to be remnants of a post-glacial distribution that have been separated from northern populations since the Wisconsin glaciations. It has been postulated that the encroachment of man with the accompanying habitat alteration, pollution, introduction of exotic fishes, exploitation, and an overall lack of genetic diversity caused the extinction of the Michigan grayling and the decline of the Montana grayling (Vincent 1962). Though they may be well-suited to the harsh environment where they evolved, grayling may not have enough genetic variability to persist where rapid environmental changes occur.

Arctic grayling are considered a "Fishes species of special ~~interest or~~ concern" in Montana by the U.S. Fish and Wildlife Service (USFWS) and by the Montana Department of Fish, Wildlife, and Parks (MDFWP) (Holton 1980). The original range included the tributaries of the Missouri river above Great Falls (Henshall 1906). With the influx of man and the consequent environmental changes, populations of grayling declined, and efforts to conserve them began. They were raised in hatcheries, transplanted into isolated barren lakes, and grayling were, at least once, introduced from the ? Arctic into Montana waters. These early conservation efforts resulted in many stocks of mixed origin in Montana and Wyoming. Varley (in Peterson 1981) estimated that grayling populations in Montana, as of 1975, have been reduced to four percent of their original river range in spite of all the programs to preserve them.

The stream-dwelling Arctic grayling is listed as a "species of special concern" by the American Fisheries Society (Deacon et al. 1979). While there are still grayling in some rivers and streams and in several lakes in Montana and Wyoming, it is not known if the remaining populations in streams or the stream-derived stocks planted in lakes were unchanged genetically or how they are currently related to each other. Transplanting bottlenecks, adaptation to lake habitats, or introgression of Arctic fish, as well as mixing of subpopulations from different areas, may have altered the gene pools. It is also not known if the sources of the lake populations (primarily Madison River tributaries) were historically different genetically from the other river populations or if current differences between lake and stream populations have resulted from divergence subsequent to their isolation from each other.

Many biologists believe that the southern fluvial grayling are genetically distinct from the Arctic populations. Differences in length of life, age at maturity, and growth rate have been documented (Tryon 1947). Electrophoretic differences have also been reported (Lynch and Vyse 1979). McPhail and Lindsey (1970) report introductions of grayling from the Arctic to Montana. Though planting records show one plant into certain lakes in Montana in 1952, it has been unclear whether or not these Arctic fish were mixed in with Montana populations. It was also not known whether or not such introductions would have altered the genetic character of the southern stock.

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## Grebe Lake grayling

Grayling were native in the Gibbon and Firehole Rivers and in Grayling Creek in Yellowstone National Park. In 1921, as grayling populations declined in the rivers, fry from eggs taken at Georgetown Lake, Montana were transplanted into Grebe Lake in the Park. The sources of the Georgetown stock were two tributaries of the Madison River near Ennis Lake. The Grebe Lake population originated, therefore, from a fluvial Madison River population (Varley 1979). I have seen no other references to plants of grayling into Grebe Lake.

Since that time Grebe Lake has been used extensively as an egg source for the transplant of millions of grayling in Montana and thirteen other states (Varley 1979). Recently, Grebe Lake stock was used in an unsuccessful effort to restore grayling into a rehabilitated stream, Canyon Creek, in Yellowstone National Park. It has been suggested that adaptation to a lacustine environment has resulted in a loss of the tendency to hold stream position that could indicate divergence between the lake and original stream "ecotypes" (Jones et al. 1977). Grayling from other sources have been introduced into Canyon Creek in order to establish them there. These attempts have also been unsuccessful (USFWS Annual Project Technical Reports, YNP, 1976 - 1980). Questions have been raised, then, regarding the most useful source of grayling for successful transplantation into streams in the native range of the species.

center Heading

## Objectives

Information on the population genetic structure of grayling in Montana and Wyoming should be valuable to the management of the species. Genetic variation is the basis of the adaptability of populations. Differences between populations could provide data to suggest which populations might be more successfully used in restoration programs. If stream-dwelling grayling are indeed different from the present "lake" stocks, it could be that they would be better suited in some way to repopulate a stream. If Arctic fish have been mixed in with southern populations the resulting stocks would not be appropriate for a native fish restoration program.

The objectives of this project are (1) to determine the population genetic structure of Arctic grayling in Montana and Wyoming, (2) to determine if stream-dwelling grayling are genetically distinct from lake populations, and (3) to find out if grayling brought down from the Arctic are detectably different from southern stocks. The objective of this report is to compare the grayling from Grebe Lake, Yellowstone National Park to grayling from other populations from Montana and the Arctic.

# METHODS AND MATERIALS

I used horizontal starch-gel electrophoresis to identify protein products of gene loci. The methods used were those of Utter et al. (1974). Buffers and staining procedures were after Allendorf et al. (1977). Nomenclature used was that of Allendorf et al. (1983). The mobilities of enzymes were measured relative to the common homologous loci in rainbow trout.

I examined forty enzyme loci in three tissues (Table 1) from ten populations. We sampled seven populations of grayling from Montana and one (Grebe Lake) from Wyoming. Five of these populations (Grebe Lake, Rogers Lake, Lake Agnes, Elizabeth Lake, and Sunnyslope Canal) were started mainly from transplants of eggs from Madison River tributaries fish. Grayling were native in Red Rocks Lake and Elk Lake in the Red Rocks River drainage, but the lakes and their tributaries were planted repeatedly with Madison River stock (Randall 1978). The Big Hole River was also planted with Madison-derived grayling (MDFWP records). One of the samples of grayling came from a population (Fuse Lake, Montana) that was transplanted from the Arctic. I also acquired a sample from a natural population in the interior of Alaska. See Table 2 for names, location, sample sizes, and the year of sampling for the populations studied. Most samples were collected using hook-and-line, gill nets, or electrofishing equipment.

# RESULTS

Genotypic distributions at individual loci were tested for conformity to random mating (Hardy-Weinberg) proportions using multiple simultaneous chi-squared tests for goodness of fit. The genotypes of all populations studied were in random mating proportions.

Allele frequencies are reported in Table 3. The frequencies for duplicated pairs (i.e. Mdh-1,2 and Aat-3,4) were calculated as if they were single tetrasomic loci.

The amount of genetic variation was calculated by determining the percent of loci that were polymorphic (P), and the mean percent of heterozygous loci per individual (H). P is the proportion of loci examined that are variable, but gives no information about the frequency of that variation in the population. H is the percent of the time that you can look at a locus in an individual and expect to find that it is heterozygous. In the grayling populations studied, the percent of loci that were polymorphic ranged from 5 to 12.5. The average percent heterozygosity per individual varied from 0.88 to 3.24 (Table 4). Grebe Lake grayling had a P of 5.0% and an H of 2.05%. This is about average for these values among the populations founded from the Madison River tributary stock and Red Rocks Lake. The values of H for the lake populations are higher than the amount of variation in the Sunnyslope Canal or the Big Hole River population.

Allele frequency data for gene loci were compared between populations to test for genetic differences between the ten populations sampled. I used multiple simultaneous chi-squared tests for goodness of fit to make pairwise comparisons of polymorphic loci. The chi-squared values and the degrees of freedom for all variable loci in each pair of populations were summed. The significance levels used are specified in Table 5. The Alaska, Fuse Lake, Big Hole River, and Sunnyslope Canal populations were significantly different ($P<.001$) from all other populations. The Grebe Lake population was also significantly different from the Red Rocks Lake population ($P<.001$), and the Elizabeth Lake and Rogers Lake populations ($P<.05$). Most of the differences between populations were a result of differences in allele frequencies at one or two variable loci. The exception was Fuse Lake, with the Canada-derived population, that had more variable loci and significant differences at three to five loci when compared to other populations.

The amount of variation in populations that are pooled together can be compared to the amount of variation in the subpopulations which made up the pooled sample. Partitioning the genetic variation makes it possible to determine whether the total genetic variation in Arctic grayling is a result of differences between individuals within subpopulations or differences between subpopulations. Calculations were made to compare the amount of differentiation between populations to the amount of total variation in the following groups:

1) all ten populations, including those from Canada and Alaska,
2) all eight native Montana and Wyoming populations studied,
3) the six Madison- and Red Rocks-derived populations in lakes,
4) the six "lake" populations plus the Sunnyslope Canal population, and
5) the six "lake" populations plus the Big Hole River sample.

The results of these comparisons are given in Table 6. Only about three percent of the total variation in Montana/Wyoming lake grayling is due to variation between populations. If the total genetic variation in all native Montana/Wyoming populations is partitioned, the differences between populations account for about fifteen percent of the total. With the Canada-derived and Alaska populations, twenty-seven percent of the total variation in grayling is due to differences between populations as opposed to differences between individuals within populations.

I used the method of Rogers (1972) to measure the genetic similarity between populations. This similarity value is scaled from 0.0 to 1.0; 0.0 corresponds to complete allelic substitution at all loci, and 1.0 to populations that are electrophoretically identical. Genetic similarities between the ten populations sampled are reported in Table 5. Grebe Lake was similar to the other native Montana grayling stocks. I used a cluster analysis of the weighted averages of the genetic similarities to make a dendrogram (Figure 1) to show the relationships between populations.

## DISCUSSION

### Amount of genetic variation

Each sample of grayling analyzed was apparently composed of individuals from one random mating population. A deficit of heterozygotes in a sample would indicate that more than one population had been sampled from that one body of water. There are examples in the literature of reproductively isolated sympatric populations in several salmonid species (Allendorf et al. 1976, Behnke 1972) and specifically in grayling in Alaska (Haaken Hop, U. of Alaska, unpublished data). This was not the case with any population I examined.

The amount of genetic variation in grayling is low compared to other salmonids, other fish, and other taxa in general (Table 7). It has been suggested that grayling, especially in Montana and Michigan, were glacial relict populations. Populations with small effective numbers could have been isolated in headwater drainages. Low initial numbers would mean that, by chance, only a little of the variation typical of the species might have been included in the founding stocks. Genetic bottlenecks, caused by population crashes, have the same effect, i.e. loss of genetic variation. Another possibility is that low levels of genetic variability are typical of the species in general.

The grayling from the Northwest Territories of Canada, as represented by the Fuse Lake samples, have more genetic variation than do Alaska populations or native Montana/Wyoming populations. Fuse Lake grayling are variable at three loci that are monomorphic in native populations. Though the Fuse Lake population is more variable than the native Montana/Wyoming grayling, the amount of variability they have is still low compared to many other salmonids.

## Genetic divergence between populations

The amount of genetic variation in Arctic grayling is low compared to other taxa, but the variation present does provide valuable information about the relationships between populations. Grebe Lake fish have an average amount of genetic variation among native Montana/Wyoming lake grayling populations, and more variation than do the Sunnyslope Canal or the Big Hole River populations.

Differences between the Montana/Wyoming lake populations as a group and the Canal and River populations are evident when the amount of variation is partitioned among native populations. The lake populations in Montana and Wyoming, which were begun or mixed repeatedly with progeny from the Madison River and Red Rocks Drainage populations, are not greatly diverged from each other. They are considerably different from both the Sunnyslope Canal and the Big Hole River population. However, there is no indication that the Canal population and the River population are relatively similar to each other. Variation in the Canada-derived population and the Alaska population contribute to a large degree to the total variation and to the variation between populations

Fuse Lake´s Canada-derived population is significantly different ($P<.001$) in allele frequencies at variable loci from all other populations. This agrees with the work of Lynch and Vyse (1979), who suggested that grayling from the Arctic are probably a different subspecies. Unlike Lynch and Vyse, though, we found that Fuse Lake grayling are highly variable compared to other grayling. They are also readily identifiable because isocitrate dehydrogenase and malate dehydrogenase variants, present in high frequency, are unique to this population. The absense of these alleles in all grayling samples from Montana and Wyoming indicates that these populations do not contain genetic material from grayling derived from Fuse Lake or the Canadian Arctic.

The sample of grayling from Alaska has low genetic variation and is significantly different in allele frequencies from southern grayling populations, but has no variants in high frequency not present in the Montana/Wyoming samples. The Alaska sample resembles Montana/Wyoming populations more than it resembles Fuse Lake or another Canada population (this report; Lynch and Vyse 1979). It is possible that after the glaciations the waters of interior Alaska were recolonized by southern grayling populations. The McKenzie River Drainage populations in Canada, from which the Fuse Lake population was derived, could have been repopulated by grayling from the northern (Bering) glacial refuge (McPhail and Lindsey 1970). This idea is supported by electrophoretic data from work with lake whitefish populations (Franzin and Clayton 1977) and studies of grayling lateral line counts (McCart and Pepper 1979).

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The Sunnyslope Canal population has diverged from the other Madison River-derived stocks. Current differences between the Canal and lake populations could be a result of random genetic drift, since the Canal population is known to fluctuate drastically in number. This possibility is supported by the low heterozygosity in the population, indicating loss of genetic variability.

The Big Hole River population is responsible for a large amount of the differentiation among the Montana/Wyoming grayling populations. My sample came from the upstream reach of the Big Hole River. Although this section of the river has been planted with Madison River-derived hatchery grayling at least once, the plants either did not take, or did not contribute overwhelmingly to the spawning population. There is no way of knowing if (1) Madison River and Big Hole River stocks have been diverged for a long time, (2) lake populations do not actually represent the Madison River stocks from which they were originally drawn, or (3) the surviving Big Hole population has changed significantly from its original genetic composition. Currently the allele frequencies at variable loci in the Big Hole River population are significantly different from those of the other Montana and Wyoming grayling populations sampled. This population also has a variant allele at Ck-1 in low frequency that has not been seen in other populations.

Grayling are also native in the Red Rocks River Drainage, but Red Rocks Lake and its tributaries have been planted repeatedly with grayling, including Grebe Lake grayling (Randall 1978). The Red Rocks population is significantly different (P<.001) in allele frequencies at variable loci from the Grebe Lake population. Elk Lake, and possibly other waters, have also been planted with both Grebe Lake and Red Rocks stock.

Despite mixing of stocks, the Red Rocks population, like the Big Hole River population, is still genetically distinct from the Grebe Lake stock. Other Montana/Wyoming lake populations are also significantly different from each other in allele frequencies of variable loci. The genetic similarities of the populations over all loci, though, are very high, and support their known recent common origin or genetic exchange. High similarity values between populations, however, do not mean that they are identical at all loci. Natural selection may cause changes at some loci that are not detected in electrophoretic surveys of isozymes.

# CONCLUSIONS

(1) Arctic grayling have a low level of genetic variation compared to other salmonids. Grayling populations from Canadian Arctic stock have more genetic variation than Montana/Wyoming populations. The southern populations are more variable than interior Alaska populations even though the Montana/Wyoming populations have a more reduced and restricted distribution.

(2) There is no evidence that grayling from the Canadian Arctic have been mixed in with southern populations. The Fuse Lake, Montana population that was derived from Arctic stock has variant alleles in high frequencey that are not present in native Montana/Wyoming populations. Any introgression between northern and southern stocks would have been detectable because of these alleles.

(3) The Big Hole River population is significantly different in allele frequencies at variable loci (P<.001) from all other populations studied. This population is the most diverged from the other Montana/Wyoming populations.

(4) Grayling are native in the Red Rocks River Drainage, but introductions of Grebe Lake stock have been made into these waters. In spite of the mixing of these two stocks, the Red Rocks population is genetically distinct. The Red Rocks Lake grayling have significantly different allele frequencies at variable loci from Grebe Lake grayling.

(5) Grebe Lake appears to support a single, random mating population of Arctic grayling. Grebe Lake grayling are similar to the other Montana/Wyoming lake populations in the amount of genetic variation that

they have. When allele frequencies at variable loci are compared between populations, Grebe Lake grayling are most like other Madison River-derived stocks and were significantly different from Red Rocks Lake, Sunnyslope Canal, and Big Hole River populations $(P<.001)$. However, genetic similarities calculated using all forty enzyme loci are all 0.984 or greater, substantiating the close genetic relationship of all native Montana/Wyoming populations.

# LITERATURE CITED

Allendorf, F.W., K.L. Knudsen, and R.F. Leary. 1983. Adaptive significance of differences in the tissue-specific expression of a phosphoglucomutase gene in rainbow trout. Proc. Natl. Acad. Sci. USA. Vol. 80: 1397-1400.

Allendorf, F.W., N. Mitchell, N. Ryman, and G. Ståhl. 1977. Isozyme loci in brown trout (Salmo trutta): detection and interpretation from population data. Hereditas 86: 179-190.

Allendorf, F., N. Ryman, A. Stennek, and G. Ståhl. 1976. Genetic variation in Scandinavian brown trout (Salmon trutta L.): evidence of distinct sympatric populations. Hereditas 83: 73-82

Behnke, R.J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Bd. Can. 29: 639-671.

Deacon, J.E., G. Kobetich, J.D. Williams, S. Contreras and other members of the Endangered Species Committee of the American Fisheries Society. 1979. Fishes of North America endangered, threatened or of special concern: 1979. Fisheries 4(2): 29-44.

Franzin, W.G. and J.W. Clayton. 1977. A biochemical genetic study of zoogeography of lake whitefish (Coregonus clupeaformis) in western Canada. J. Fish. Res. Board Can. 34(5): 617-625.

Henshall, J.A. 1906. A list of the fishes of Montana. Bulletin of the University of Montana, Missoula. Vol. 34, Biological Series No.11: 1-12.

Holton, G.D. 1980. The riddle of existence: fishes of "special concern". Montana Outdoors 11(1): 2-6, 26.

Jones, R.D., J.D. Varley, R.E. Gresswell, D.E. Jennings, and S.M. Rubrecht. 1977. Annual Project Technical Report. Fishery and Aquatic Management Program, Yellowstone National Park. U.S. Fish and Wildlife Service publication.

Lynch, J.C. and E.R. Vyse. 1979. Genetic variability and divergence in grayling, *Thymallus arcticus*. Genetics 92: 263-278.

McCart, P. and V.A. Pepper. 1971. Geographic variation in the lateral line scale counts of the Arctic grayling, *Thymallus arcticus*. J. Fish. Res. Bd. Canada 28: 749-754.

McPhail, J.D. and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Bd. Can. Bulletin 173. 381 pp.

Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. 13: 121-177.

Peterson, N. 1981. Montana´s stream-dwelling grayling: worthy of "extra special concern". Montana Outdoors 12(4): 14-17.

Randall, L.C. 1978. Red Rock Lakes National Wildlife Refuge: an aquatic history, 1899 - 1977. U.S. Fish and Wildlife Service publication. 293 pp.

Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics, VII. U. of Texas. Publ. No. 7213: 145-153.

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

Tryon, C.A., Jr. 1947. The Montana grayling. Prog. Fish-Cult. 9(3): 136-142.

Utter, F.M., H.O. Hodgins, and F.W. Allendorf. 1974. Biochemical genetic studies of fishes: potentialities and limitations. In: Malins, D.C. and J.R. Sargent (eds.). Biochemical and Biophysical Perspectives in Marine Biology. Vol. 1: 213-238. Academic Press, N.Y.

Varley, J.D. 1979. Record of egg shipments from Yellowstone fishes, 1914 - 1955. Information Paper No. 36. USFWS publication.

Vincent, R.E. 1962. Biogeographical and ecological factors contributing to the decline of Arctic grayling, *Thymallus arcticus* (Pallas), in Michigan and Montana. Ph.D. Thesis, U. of Mich. 169 pp.

TABLE 1

Enzymes and loci examined ( E = eye, L = liver, M = Muscle )

| Enzyme | Loci | Tissue |
|---|---|---|
| Aspartate aminotransferase (AAT) | Aat-1,-2<br>Aat-(3,4) | Liver<br>Muscle |
| Creatine kinase (CK) | Ck-1,-2<br>Ck-3 | Muscle<br>Eye |
| Glucosephosphate isomerase (GPI) | Gpi-1,-2,<br>-3,-4 | Muscle |
| Glyceraldehyde-3-phosphate dehydrogenase (GAP) | Gap-3,-4 | Eye |
| Glycerol-3-phosphate dehydrogenase (G3P) | G3p-1,-2 | Liver |
| Glycyl-leucine peptidase (GL) | Gl-1,-2 | Liver |
| Isocitrate dehydrogenase (IDH) | Idh-1,-2<br>Idh-(3,4) | Muscle<br>Liver |
| Lactate dehydrogenase (LDH) | Ldh-1,-2<br>Ldh-3,-4,-5 | Muscle<br>Eye |
| Lycyl-glycyl-glycine peptidase (LGG) | Lgg | Eye |
| Malate dehydrogenase (MDH) | Mdh-(1,2)<br>Mdh-(3,4) | Liver<br>Muscle |
| Malic enzyme (ME) | Me-(1,2)<br>Me-4 | Muscle<br>Liver |
| Phophoglucomutase | Pgm-1,-2 | Liver |
| 6-Phosphogluconate dehydrogenase (6PG) | 6Pg | Muscle |
| Superoxide dismutase (SOD) | Sod | Liver |
| Xanthine dehydrogenase (XDH) | Xdh | Liver |

The protein products of the pairs of loci in parentheses are electrophoretically indistinguishable. They are treated as single tetrasomic loci in all analyses.

TABLE 2

Population, location, number, and year sampled

| Populations | Location | Number sampled | Years sampled |
|---|---|---|---|
| Grebe Lake | Yellowstone NP, Wyoming | 41 | 1983 |
| Red Rocks Creek | Red Rocks NWR, Montana | 29 | 1983,1984 |
| Elizabeth Lake | Glacier NP, Montana | 13 | 1983,1984 |
| Elk Lake | Near Red Rocks NWR | 50 | 1983 |
| Rogers Lake | Kalispell, Montana | 43 | 1982,1984 |
| Lake Agnes | East Pioneer Mountains, Mt. | 36 | 1984 |
| Sunnyslope Canal | Pishkun Reservoir, Montana | 41 | 1983 |
| Big Hole River | Headwaters, Missouri River | 45 | 1983,1984 |
| Chena River | Interior Alaska | 38 | 1984 |
| Fuse Lake (Canada)<br>McKenzie River | Sapphire Mountains, Mt. | 92 | 1980,1983 |

## Table 3

Frequency of the common allele at the variable loci in ten populations of Arctic grayling

| | Locus | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Population | Aat-3 | Ck-1 | Gap-3 | Gap-4 | Idh-1 | Idh-3 | Ldh-2 | Mdh-2 | Sod-1 |
| Big Hole R. | 1.000 | 0.967 | 0.244 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.922 |
| Chena River | 0.987 | 1.000 | 0.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.203 |
| Elizabeth L. | 1.000 | 1.000 | 0.808 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.538 |
| Elk Lake | 1.000 | 1.000 | 0.714 | 1.000 | 1.000 | 1.000 | 0.990 | 1.000 | 0.650 |
| Fuse Lake | 1.000 | 1.000 | 0.837 | 0.972 | 0.647 | 0.972 | 1.000 | 0.654 | 1.000 |
| Grebe Lake | 1.000 | 1.000 | 0.634 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.768 |
| Lk. Agnes | 1.000 | 1.000 | 0.556 | 1.000 | 1.000 | 1.000 | 0.986 | 1.000 | 0.653 |
| Red Rocks L. | 1.000 | 1.000 | 0.857 | 1.000 | 1.000 | 1.000 | 0.983 | 1.000 | 0.534 |
| Rogers Lake | 1.000 | 1.000 | 0.616 | 1.000 | 1.000 | 0.988 | 0.954 | 1.000 | 0.570 |
| Sunnyslope C. | 1.000 | 1.000 | 0.634 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.122 |

## TABLE 4

Percent of loci polymorphic (P) and percent average heterozygosity per individual (H) in ten populations of Arctic grayling

| Population | P | H |
|---|---|---|
| Grebe Lake | 5.0 | 2.05 |
| Red Rocks Lake | 7.5 | 1.95 |
| Elizabeth Lake | 5.0 | 2.10 |
| Elk Lake | 7.5 | 2.22 |
| Rogers Lake | 10.0 | 2.72 |
| Lake Agnes | 7.5 | 2.47 |
| Sunnyslope Canal | 5.0 | 1.72 |
| Big Hole River | 7.5 | 1.46 |
| Chena River | 5.0 | .88 |
| Fuse Lake | 12.5 | 3.24 |
| Mean | 7.2 | 2.08 |

TABLE 5

Genetic similarities (Rogers 1972) between ten populations of Arctic grayling below the diagonal, and significance level of allele frequency differences above the diagonal.

| Populations | (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) |
|---|---|---|---|---|---|---|---|---|---|---|
| (1) Grebe Lake | - | *** | * | NS | NS | * | *** | *** | *** | *** |
| (2) Red Rocks | .988 | - | NS | NS | ** | * | *** | *** | *** | *** |
| (3) Elizabeth | .990 | .998 | - | NS | NS | * | *** | *** | *** | *** |
| (4) Elk Lake | .995 | .993 | .995 | - | NS | NS | *** | *** | *** | *** |
| (5) Lake Agnes | .995 | .989 | .990 | .996 | - | NS | *** | *** | *** | *** |
| (6) Rogers Lake | .993 | .992 | .993 | .994 | .995 | - | *** | *** | *** | *** |
| (7) Sunnyslope | .984 | .984 | .985 | .985 | .984 | .987 | - | *** | *** | *** |
| (8) Big Hole R. | .986 | .974 | .976 | .980 | .984 | .980 | .969 | - | *** | *** |
| (9) Chena River | .970 | .970 | .971 | .970 | .974 | .974 | .982 | .975 | - | *** |
| 10) Fuse Lake | .970 | .969 | .969 | .969 | .965 | .964 | .954 | .964 | .940 | - |

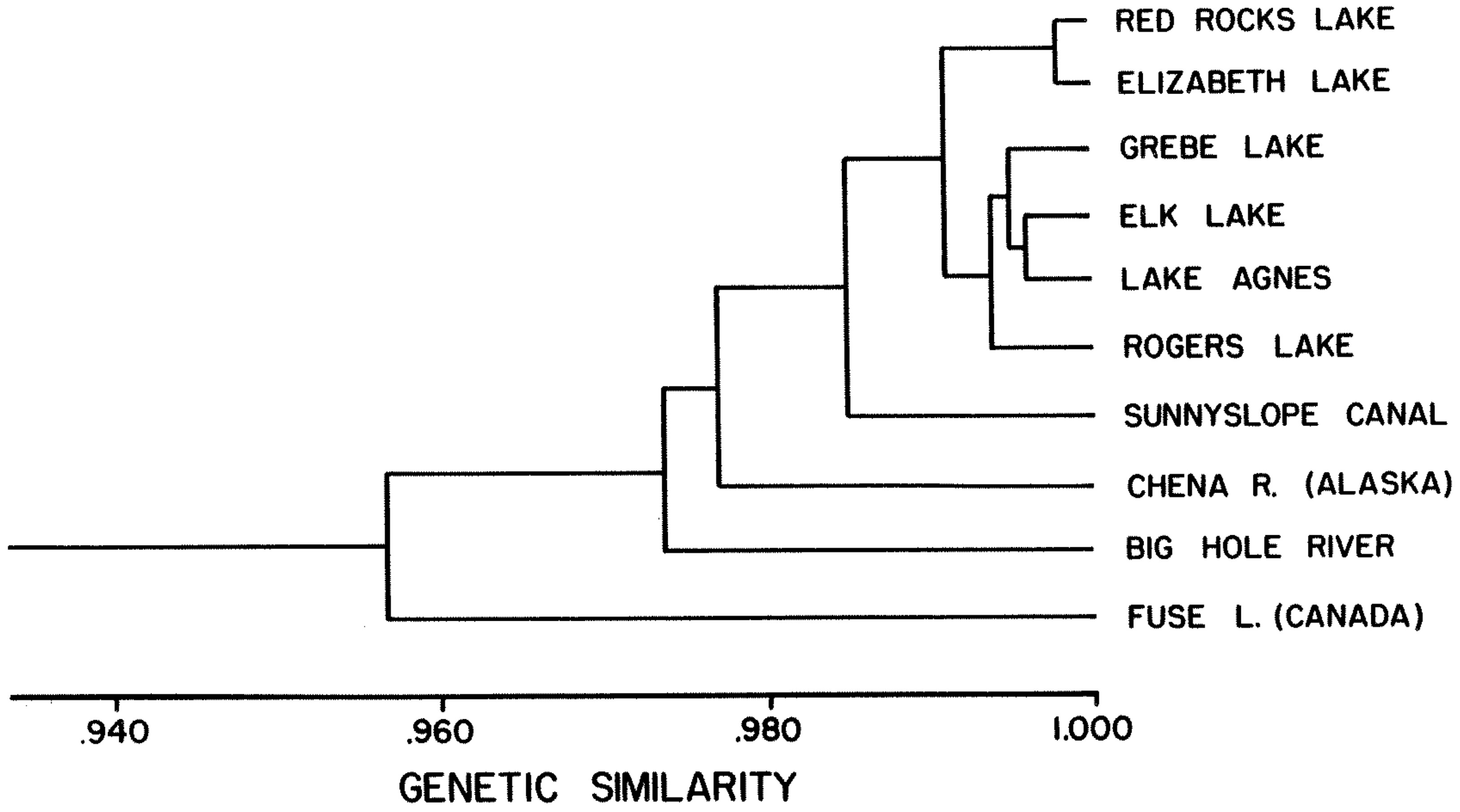
| | |
|---|---|
| NS | not significantly different |
| * | P <.05 |
| ** | P <.01 |
| *** | P <.001 |

## TABLE 6

Variation between populations as a percentage of the total variation in the groups identified

| Groups compared | Variation between (%) |
|---|---|
| All populations | 27.02 |
| All Montana/Wyoming populations | 15.02 |
| Montana/Wyoming "lake" populations | 2.78 |
| "Lake" populations with canal | 8.40 |
| "Lake" populations with Big Hole River | 10.08 |

Figure 1. Dendrogram of genetic similarities (Rogers 1972) for ten populations of Arctic grayling.


RED ROCKS LAKE
ELIZABETH LAKE
GREBE LAKE
ELK LAKE
LAKE AGNES
ROGERS LAKE
SUNNYSLOPE CANAL
CHENA R. (ALASKA)
BIG HOLE RIVER
FUSE L. (CANADA)
.940
.960
.980
1.000
GENETIC SIMILARITY

## TABLE 7

Average heterozygosity per individual in various taxa (Nevo 1978) and salmonids (Ryman 1983; this report).

| Taxa | H(%) |
|---|---|
| <u>Various taxa</u> | |
| Invertebrates | 13.4 |
| Vertebrates | 6.0 |
| Fishes | 8.2 |
| Mammals | 5.1 |
| Plants | 4.6 |
| <u>Salmonids</u> | |
| Rainbow trout | 6.9 |
| Sockeye salmon | 4.6 |
| Brown trout | 4.0 |
| Atlantic salmon | 3.4 |
| Arctic grayling | 2.1 |