Review of the Decline and Status of Fluvial Arctic Grayling, *Thymallus arcticus*, in Montana

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Abstract

Fluvial (permanently stream-dwelling) Arctic grayling were once widely ited in the upper Missouri River and tributaries in Montana, but are now to a small remnant population in the upper Big Hole River. In contrast, the tion of lacustrine populations has been greatly expanded through introduc- to lakes in Montana and other states. Arctic grayling in Montana are lly diverged from more northern populations in Alaska and Canada, and the fluvial population of the Big Hole River drainage is a reproductively isolated Montana grayling that is genetically identifiable and behaviorally adapted to existence. Reasons for the decline of fluvial grayling in Montana are not but may involve a combination of interactions with introduced non-native abitat degradation, and fishing overharvest. Fish stocking programs have not red self-sustaining populations to any streams. Fluvial Montana grayling are ed a fish of "special concern" and the U.S. Fish and Wildlife Service has been d to list these fish as threatened or endangered.

INTRODUCTION

The status of fluvial (permanently stream-dwelling) Arctic grayling, *us arcticus*, in Montana has been of increasing concern in recent years. h grayling in Montana (hereafter referred to as Montana grayling) are still as adfluvial lacustrine populations (living in lakes and spawning in streams), Montana grayling have declined severely and appear reduced to a small, population in the Big Hole River drainage of the upper Missouri River This remanant fluvial population appears in decline. Because of the uncertain fluvial Montana grayling, it has been designated a fish of "special concern" ndangered Species Committee of the American Fisheries Society, the Chapter of the American Fisheries Society, the Montana Department of dlife and Parks (MDFWP), and the Montana Natural Heritage Program of re Conservancy (Deacon et al. 1979; Holton 1980; Johnson 1987; Williams et al. 1989; Clark et al. 1989). The U.S. Fish and Wildlife Service classifies fluvial Montana grayling in Category 1, the final category before listing as threatened or endangered, and has recently been petitioned, in October 1991, to list these fish as threatened or endangered. The purpose of this report is to review the history and present status of fluvial their decline. Information for this review was obtained from published articles, unpublished reports, personal communications with individuals, and MDFWP computer databases.

IDENTITY AND ADAPTATION OF FLUVIAL GRAYLING IN MONTANA

Taxonomy and Biogeography

Arctic grayling are classified in the Subfamily Thymallinae, of the Family Salmonidae (salmon, trout, whitefish and grayling),. Order Salmoniformes. The Subfamily Thymallinae contains only the genus *Thymallus*, with four species of *Thymallus* generally recognized (Norden 1961; McAllister and Harington 1969). Two species have very limited distributions in Asia and two species are widely distributed, one across Europe and the other across northern Asia and North America. *Thymallus nigrescens* [Dorogostaisky] is known only from Lake Kosogol in Mongolia and *T. brevirostris* [Kessler] has a distribution limited to northwest Mongolia. The European grayling, *T. thymallus* [Linnaeus], is distributed across northern and central Europe and the British Isles. The Arctic grayling, *T. arcticus* [Pallas], is distributed from the Ural Mountains in central U.S.S.R., across Siberia, on Saint Lawrence Island in the Bering Strait, and across Alaska and Canada to Hudson Bay. Two geographically isolated populations of *T. arcticus* formerly existed south of Alaska and Canada, one in Michigan and the other in the upper Missouri River drainage in Montana. Grayling disappeared from Michigan about 1936 (McAllister and Harington 1969).

The Arctic grayling has been variously classified into several separate species, into several subspecies, and more recently, as a single species without subspecies. Arctic grayling from the Ob River in Siberia were first described and named *Thymallus arcticus* by Pallas in 1776. European-American discovery of Arctic grayling in North America is attributed to members of the Lewis and Clark Expedition, who caught fish that Meriwether Lewis described as a new, "whte speceis of trout" in the Beaverhead River of the upper Missouri drainage in 1805 (Moulton 1986). Milner provided the first formal description of Montana grayling in 1872, from specimens caught in a tributary of the Missouri River near Camp Baker, and designated them *T. montanus*. This had been preceded by descriptions of Arctic grayling in Canada as *T. signifer*, and in Michigan as *T. tricolor*. Thus, North American grayling were formerly considered three separate species, *T. signifer* [Richardson 1823] in Alaska and Canada, *T. tricolor* [Cope 1865] in Michigan, and *T. montanus* [Milner 1872] in Montana (Hensall 1907; Jordan and Evermann 1934). The monospecific designation of all Arctic grayling has been widely accepted since

Walters (1955) described *T. signifer* as conspecific with *T. arcticus*. Present subspecific designations, including that of Montana grayling as *T. a. montanus* (e.g., Williams et al. 1989), are of uncertain validity (Norden 1961; Scott and Crossman 1973) and not widely accepted.

The lack of presently accepted subspecific designations is based on morphological similarity among the disjunct populations which has persisted despite their long period of physical separation. Montana and Michigan populations of grayling were isolated from more northern populations by the most recent continental glaciation, the Wisconsinan, which began about 80,000 years ago, reached a maximum about 18,000 years ago, and terminated about 10,000 years ago (Lindsey and McPhail 1986). No morphological characteristic has yet proven reliable in separating Montana or Michigan grayling from other Arctic grayling (Hubbs and Lagler 1958).

Despite the lack of distinct morphological differentiation, however, more recent comparisons using biochemical genetic techniques have demonstrated divergence of Montana grayling from Alaskan and Canadian grayling (Lynch and Vyse 1979; Everett and Allendorf 1985). Everett and Allendorf (1985) concluded that (1) Montana grayling differ in genetic variation from Alaskan or Canadian grayling, and (2) there is no evidence of genetic mixing of northern grayling into Montana populations despite one attempt to introduce Alaskan grayling into Montana (into Fuse Lake in the Rock Creek drainage of the Clark Fork River system). Thus, Montana grayling are a recognizable biological entity, both geographically isolated and genetically identifiable from those further north in Canada and Alaska.

Further, grayling in the Big Hole River represent a separate stock of Montana grayling, in accordance with the concept of a stock as a geographically or temporally isolated spawning group (Ricker 1972; MacLean and Evans 1981), and are genetically identifiable. After electrophoretic comparisons of grayling from the Big Hole River and seven other populations from Wyoming, Montana, Alaska, and Canada, Everett and Allendorf (1985) concluded that:

> 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.

After further biochemical genetic comparisons, R. Leary (1990) more recently concluded that Montana grayling can be separated into two genetic groups, a Big Hole-Madison group and a second group consisting of fish from Red Rock Lake and from lacustrine populations established through anthropogenic introductions.

Fluvial Adaptation of Big Hole River Grayling

Two recent studies have provided evidence for adaptation of Big Hole River grayling to a stream environment. Shepard and Oswald (1989) reported extensive annual migrations of adults in the river. They concluded, from recaptures of tagged fish, that at least some adults spend the winter in deep pools as far downstream as the Divide Dam, and move upstream in spring to spawn in sections of the river from the mouth of the North Fork to immediately above Wisdom (Figure 1). During years of average or greater stream flow adult grayling remain upstream through the summer and move back downstream in the fall. During years of low flow many move back downstream shortly after spawning. The longest movement recorded was about 80 km downstream. Some adults may overwinter in upstream reaches near Wisdom, in deep pools or areas of groundwater recharge or in tributaries.

Similar patterns of upstream migrations in spring and downstream in fall have been described for Alaskan fluvial grayling populations and appear adaptations for utilizing conditions in different parts of river systems and tributaries for spawning, feeding, and overwintering (Craig and Poulin 1975; Tack 1980, cited by Armstrong 1986; Hubert et al. 1985). Smaller, upstream segments or tributaries may provide more favorable conditions for spawning and for survival and growth of young, and large, deep, downstream pools may provide the best conditions for overwintering.

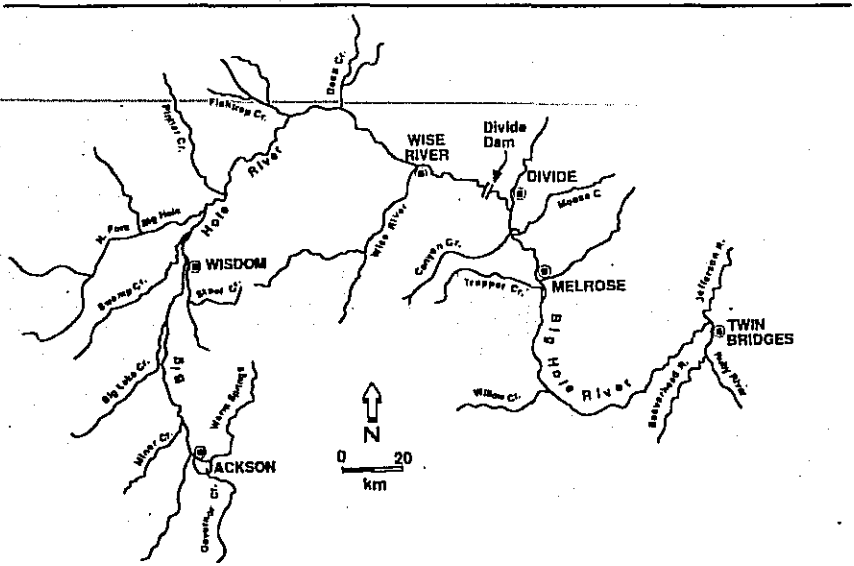

Figure 1. The Big Hole River and its major tributaries, from headwaters above the town of Jackson to its confluence with the Beaverhead River to form the Jefferson River, of the upper Missouri drainage in southwest Montana.

Young grayling from the Big Hole River have behavioral responses to water current that are advantageous for living permanently in a stream and that appear genetically controlled (Kaya 1991). They have significantly greater tendency to hold position in water current and lesser tendency to swim downstream than young grayling from inlet-spawning populations of Red Rock Lake and Lake Agnes, and these differences become increasingly greater with age from day of initial swimming to about 9-10 weeks later. Since fish from the different populations had been incubated and reared under identical conditions, the different responses appear genetically determined. A genetic basis for such behavior also was indicated by comparison of young grayling from inlet- and outlet-spawning populations (Kaya 1989). Young from the two populations have significantly different tendencies to swim upstream and hybrids between the two populations have intermediate responses. The responses of the young Big Hole River grayling would tend to keep them within a stream, while those of the inlet- and outlet-spawning populations would take the young upstream or downstream to the rearing lakes.

The importance of preserving this last indigenous population of fluvial Montana grayling is emphasized by these findings that they differ from all other populations analyzed, both genetically and in being adapted for riverine existence. Others have repeatedly stated the importance of managing and preserving individual stocks of salmonids in order to retain the ability of the species to occupy the varying habitats within its original distribution (Larkin 1972, 1979; Behnke 1972; Loftus 1976). The ability of Montana grayling to continue inhabiting streams may depend on preserving the remnant fluvial population of the Big Hole River.

DISTRIBUTION AND POPULATION STATUS OF FLUVIAL MONTANA GRAYLING

Historical Decline

Montana grayling originally were mostly stream-dwellers, occupying waters of the upper Missouri River drainage (Figure 2A) upstream from the Great Falls of the Missouri River near the present city of Great Falls, Montana (Hensall 1907; Vincent 1962). They were not found above waterfalls, with the exception of the Great Falls itself, and the only lakes accessible to and inhabited by grayling were Upper and Lower Red Rock lakes and possibly Elk Lake, near the headwaters of the Red Rock-Beaverhead drainage. The journals of Lewis and Clark (Moulton 1986) suggest that grayling were less abundant than trout in the main stem of the Missouri River and the Jefferson and Beaverhead rivers in 1805. The journals mention six occasions when trout (later identified as westslope cutthroat trout, *Oncorhynchus clarki lewisi*) were collected by angling or seining as the expedition progressed upstream from Great Falls along the Missouri, Jefferson, and Beaverhead rivers. In contrast, grayling were collected only once, on August 22, 1805, from waters around the former confluence of the Beaverhead and Red Rock rivers (presently submerged

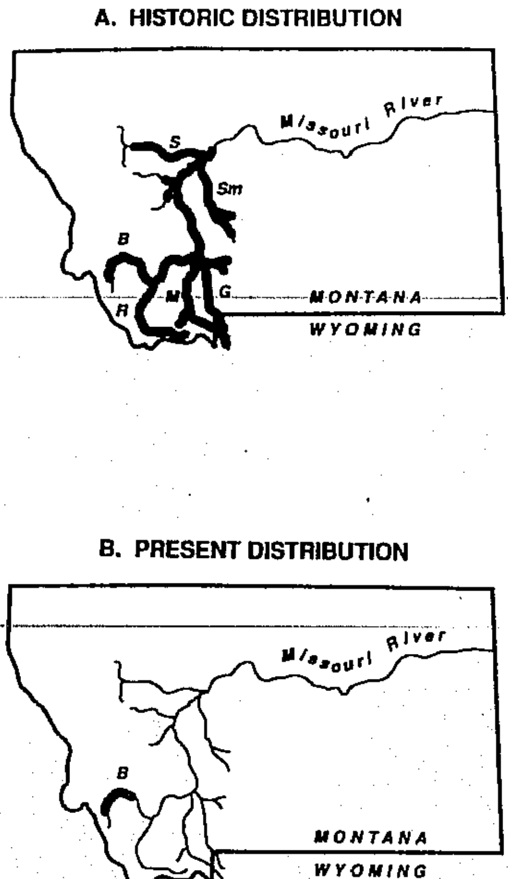

Figure 2. Approximate historic and present distributions of fluvial Arctic grayling in Montana (shaded sections of rivers). **A.** Historic distribution, until late 1800's to early 1900's: (B) Big Hole, (R) Red Rock-Beaverhead-Jefferson, (M) Madison, (G) Gallatin, (Sm) Smith, and (S) Sun rivers. **B.** Additionally, two populations with partially fluvial characteristics presently exist in the upper Madison River and in a canal diverted from the Sun River.

beneath Clark Canyon Reservoir). There were only 10 to 12 grayling among the 528 fish, mostly trout, collected.

The few other observations recorded during the 19th century also suggest that grayling were irregularly distributed in the upper Missouri River and its tributaries above Great Falls, and may have been most common in the Sun and Smith rivers and the drainages which make up the three branches of the Missouri, the Jefferson, Madison, and Gallatin drainages. According to Vincent (1962):

> The Sun and Smith Rivers were the only tributaries that had grayling below Three Forks. Reports of grayling in the Missouri River have come only from the vicinity of Craig. Evermann (1893) found none in tributaries below Three Forks or in the Blacktail, Ruby, or Boulder rivers of the Beaverhead-Jefferson drainage.

Grayling were also said to be abundant in the Canyon Ferry area of the Missouri River in the late 1870's and 1880's (Holton undated; Peterson 1981). Field surveys by Jordan (1891) and Evermann (1893) indicated that they were common and locally abundant in the upper Madison River and both its branches, the Gibbon and Firehole rivers, up to the first waterfalls above their confluence at Madison Junction. They also both reported that grayling were abundant in Horsethief Springs, a spring creek now submerged by Hebgen Reservoir on the upper Madison River. Evermann (1893) also visited Bozeman in August 1891 and reported that Bridger Creek and Bozeman Creek, "are said to be well filled with trout and grayling." Vincent (1962) reported that grayling were abundant in the Sun River until about 1908 and in the Smith River drainage until about 1910.

Although these early reports indicated that fluvial grayling were irregularly distributed but widespread and locally abundant in upper Missouri drainages until the end of the 19th century (Fig. 1), this situation changed substantially over the next 40 to 50 years. On the Madison River, Fuqua (1929) described grayling as abundant in the deep holes of the river between Ennis Reservoir and Hebgen Dam. Elrod (1931) claimed that grayling were still abundant and were "the principal fish in the South Fork of the Madison River" and also found elsewhere in the Madison River drainage including Grayling Creek and the lower Firehole and Gibbon rivers. By contrast, Vincent (1962) reported that grayling had become rare in the Madison River by 1940.

In the Yellowstone National Park section of the upper Madison River, grayling may have been common until at least 1926 (Russell 1925 and Philips 1926, cited by Vincent 1962), but were greatly reduced by 1933 (McCarty 1933, cited by Vincent 1962). More than 6 million grayling fry were planted in this part of the river and the Gibbon River between 1933 and 1943 (Varley 1981). Benson et al. (1958) reported that small numbers of grayling were still being caught by anglers on the Madison River and its two tributaries, the Firehole and Gibbon rivers, between 1953 and 1957. . In a 1957 electrofishing survey of sections of the Madison River between

Madison Junction and West Yellowstone, Benson et al. (1959) captured 1320 brown trout, 560 rainbow trout, and only 1 grayling.

In other drainages, Vincent (1962) concluded that grayling were nearly gone from the Sun River by 1913, had undergone marked decline in Sheep Creek of the Smith River by 1915, and had taken a sharp drop in the Gallatin Valley (Gallatin River and Bridger Creek) by 1890-1900. "Old-timer" accounts indicated that grayling were abundant in the Smith River upstream from Fort Logan near White Sulfur Springs, but such reports ceased by about 1950 or earlier (Holton undated). Brown (1943) reported that the distribution of fluvial grayling had been reduced to the Big Hole River drainage and the upper Gallatin River, with their presence in the latter due to plantings of fingerlings. Tyron (1947) confirmed the plantings of grayling fingerlings into the Gallatin River and also stated that "with few exceptions" (unspecified), grayling were only found in the upper Big Hole River and in lakes.

There have been contrasting reports, however, of grayling persisting in some streams until the 1950's or later. Data from creel census by game wardens indicate that grayling were present in the Sun River until 1954 (Hanzel 1959). Personal accounts mentioned by Peterson (1981) suggest that some grayling may have persisted in the Sun River until at least 1970 and in the Madison River and its South Fork (which flows into Hebgen Reservoir) until at least 1975.

Some of these later reports of grayling in streams may have been influenced by stockings of hatchery fish, which began on large scale in the 1920's. An example, planting of grayling into the upper Gallatin River, has been mentioned. MDFWP fish stocking records (tabulated by Kaya 1990) indicate that grayling were planted in small numbers into the Madison River between Hebgen Reservoir and Ennis Reservoir in 1946 and 1966 and in large numbers (2,400,000 total) into the South Fork of the Madison in 1928, 1929, and 1938. The Smith River was stocked with grayling in 1933 and 1937 (2,200,000 total). Other recent reports (since the 1950's) of grayling in streams outside the Big Hole River drainage appear to be of fish spending part of the time in streams, particularly during spring and early summer spawning periods, or drifting down out of lakes in the drainage (Kaya 1990).

Unlike the situation with other drainages like the Madison River, reports on past abundance of grayling in the Big Hole River appear lacking and this population is only briefly mentioned in Vincent's (1962) comprehensive treatise. Whatever their former abundance in the river may have been, grayling were low in numbers in the upper river when the first electrofishing surveys were conducted in the 1950's. A survey in 1959 of four 90-m sections of the main river between Skinner Meadows and Swamp Creek Road yielded 3 rainbow trout (*Oncorhyncus mykiss*), 280 brook trout (*Salvelinus fontinalis*) and only 3 grayling, while 90-m sections of 13 tributaries between Deep Creek and Wise River yielded 197 rainbow trout, 589 brook trout and no grayling (Heaton 1960).

In the lower river, below Divide Dam, grayling were absent or scarce by 1964; an electrofishing survey that year of a section near Melrose yielded 244 brown trout (*Salmo trutta*), 22 rainbow trout, 2 brook trout and no grayling (Wipperman 1965). More recent surveys have confirmed that the salmonid community of this lower part of the river below the Divide Dam is dominated by brown and rainbow trout and grayling are scarce (Oswald 1986).

Results of electrofishing surveys in the Big Hole River from 1978 to 1991 have indicated that grayling are most common in the stream sections and tributaries near the town of Wisdom, and that their distribution extends downstream for approximately 80-100 km to the Divide Dam (Liknes 1981; Liknes and Gould 1987; Shepard and Oswald 1989, 1990; Byorth 1991). Small numbers of grayling are found in tributaries of the upper Big Hole River, most commonly in lower reaches near the confluence with the river (Liknes 1981; Wells and Decker-Hess 1981). Tagged fish have been observed to move between these lower reaches and the river (Shepard and Oswald 1989, 1990; Byorth 1991). The upper Big Hole River and its tributaries thus appear to support a single population.

In stream sections near Wisdom, where grayling appear most numerous, estimated numbers of age-1+ (age 1 and older) grayling appeared to decline from 1983 to 1987 and have remained at low levels since (Table 1). Estimates have gone from already low numbers of about 69 per km in 1983, to about 21 or less per km from 1987 to 1991. These estimates indicate that this last, remnant, riverine population of Montana grayling has been reduced to dangerously low levels, especially in recent years. If the recent estimates of about 20 per km in sections near Wisdom are extrapolated to the approximately 80 to 100 km of stream inhabited by grayling, then this leads to an optimistic estimate of approximately 1,600 to 2,000 age-1+ grayling in the entire Big Hole River. Some streams in Montana contain as many or more trout per mile (1.6 km), including sections of the Madison and Beaverhead rivers, both within the original native range of Montana grayling.

The approximately 80 to 100 km of Big Hole River occupied by this remnant, self-sustaining fluvial population may represent about 4 to 5% of the historic range of the species in Montana. Montana grayling may have occupied about 2,000 km of streams in the upper Missouri River drainage until about the late 1800's. This estimate of historic range assumes that grayling were widely distributed within the main stem of the upper Missouri River above Great Falls, and the main stems of its major branches and tributaries: the Gallatin River and its tributary, the East Gallatin River; the Madison River and its tributaries, the Gibbon and Firehole Rivers up to the first cascades; the Jefferson River and its tributaries, the Red Rock, Beaverhead, and Big Hole rivers; the Smith River and its tributary, Sheep Creek; and the Sun River (Figure 2A). This estimate would be subject to modification by two opposing consideration: first, the possibility that some sections of these major streams were not actually occupied by grayling; and second, the likelihood that grayling also occupied smaller tributaries and spring creeks not included in the estimate.

In recent decades, therefore, fluvial Montana grayling in Montana have been reduced to a small remnant population in the upper Big Hole River and its

Table 1. Estimated densities (number per km) of age-1+ grayling and age-2+ brook trout in McDowell (8.0 km in length) and Wisdom (9.8 km in length) sections of the Big Hole River upstream and downstream from the town of Wisdom (Oswald 1990, unpublished data; Byorth 1991). Younger brook trout were recaptured in too low numbers to permit estimates, and rainbow trout were also present but in numbers too low to estimate. Brown trout are not present in these upper reaches of the river.

		Estimated Number per Km	
Section	Year	Grayling	Brook
McDowell	1978	43	68
Wisdom	1983	69	145
Wisdom	1984	46	171
McDowell	1985	24	130
Wisdom	1985	20	207
McDowell	1986	32	132
McDowell-Wisdom	1987	19	51
McDowell-Wisdom	1989	14	39
McDowell-Wisdom	1990	21	40
McDowell-Wisdom	1991	21	

tributaries (Fig. 2B). With the extirpation of grayling from Michigan, those of the Big Hole River drainage have also become the last known fluvial grayling south of Alaska and Canada. In contrast, populations of lacustrine Montana grayling have been greatly expanded in distribution, through their successful introduction into numerous lakes in Montana and other states (Kaya 1990).

Other Possible Fluvial Populations

While the population of the Big Hole River is the only one in Montana confirmed to be entirely fluvial, there are others that may have partially fluvial characteristics. One is the population that inhabits the Madison River and Ennis Reservoir. Most grayling in this system appear to be adfluvial, inhabiting the reservoir and ascending the river to during spring to spawn. However, some are found in the Madison River upstream from the reservoir throughout the summer and into at least early fall, well beyond the spawning season (Vincent, pers. comm.; Byorth and Shepard 1990). The Madison River is native habitat for fluvial grayling, and the reservoir fills an area originally occupied, in part, by a small, shallow lake. Studies are currently underway by biologists from MDFWP and the Montana Power Company to try and better define the life histories of grayling in the river and the reservoir.

The other population is found in an unusual habitat, Sunny Slope Canal below Pishkun Reservoir on the Teton River drainage. This population apparently originated from grayling moving downstream after being introduced into the reservoir. Observations by Hill (pers. comm.) suggest that these fish live in a fluvial environment during the irrigation season, generally from early May to September, when water flows in large volumes through the canal. Since grayling are now virtually absent from the reservoir, it is apparent that the young are produced and persist within a fluvial environment during the irrigation season. However, during the remaining seven months of the year, much of the canal goes dry and the grayling live in isolated pools. Since these isolated pools are non-flowing waters and thereby resemble lacustrine habitats, these grayling do not appear to permanently inhabit a fluvial environment.

Many other streams in Montana and other western states provide temporary habitats for grayling. Adults from lacustrine populations enter inlet or outlet streams to spawn, and some adults may remain in streams for varying amounts of time after spawning. Most young appear to move to lakes or reservoirs shortly after becoming free swimming, but those of at least one lacustrine population remain within the stream for over a year (Deleray and Kaya 1992). Individuals of varying sizes can move or be displaced downstream from lakes or reservoirs. Recent observations on tagged fish have confirmed that some grayling from Ennis Reservoir move over the dam and thus enter the Madison River downstream (Byorth, pers. comm.).

Such fish can establish self-sustaining populations, as has apparently happened within Sunny Slope Canal. However, a recent evaluation of other streams in Montana reported to contain grayling concluded that, with the possible exceptions of the Madison River and the Sunny Slope Canal, there is no present evidence for the existence of any other reproducing, self-sustaining, permanently fluvial population of Montana grayling (Kaya 1990).

FACTORS ASSOCIATED WITH DECLINES OF FLUVIAL GRAYLING

Explanations for the decline of fluvial grayling in Michigan and Montana have focused on three categories of human-related factors: fishing overharvest, introductions of non-native fish, and habitat degradation. The past contributions of any of these factors is difficult to determine, because field or laboratory studies of causative relations are lacking, and because the three factors tend to occur concurrently through increased human development and exploitation of a river and its drainage basin. Also, effects of different factors could be related. For example, a population being overharvested could be more susceptible to competition from introduced salmonids or to habitat degradation. Fluvial grayling underwent decline and elimination from most of their former range in Montana before their status could be evaluated through field surveys. The major part of Vincent's thesis (1962) dealt with possible factors contributing to decline (and in Michigan, eventual extirpation) of fluvial grayling in Michigan and Montana. Much of the following discussion on possible reasons for past declines of grayling is based on his comprehensive review and analysis. Vincent had to rely largely on circumstantial evidence for his evaluation, and this same lack of "hard" information continues to the present.

Angling Exploitation and Overharvest

Arctic grayling have a reputation for being easily caught by anglers, and several studies in Alaska (summarized by Armstrong 1986) have demonstrated that angling pressure can detrimentally affect both lacustrine and fluvial populations. Exploitation and overharvest by sports fishermen may have been an important factor contributing to past declines of fluvial grayling populations in Montana. On the Madison River decline of grayling occurred as fishing pressure increased, as indicated indirectly by license sales in Montana and numbers of visitors to Yellowstone National Park (Vincent 1962). Grayling were common in the river until about 1920 but were severely reduced by 1940, with the exception of those in Ennis Reservoir. However, rainbow and brown trout, first introduced into the Madison River drainage in 1889 (Jordan 1891), were well established in the Madison River by 1940 and could have contributed to this decline.

Before the adoption of more restrictive angling regulations, grayling may have been caught and harvested at disproportionately high ratios from the Big Hole River. Grayling accounted for a much higher proportion of anglers' catches than obtained through electrofishing surveys in 1959. Grayling made up 6% of 500 salmonids reported in MDFWP warden creel census of the Big Hole River above Pintlar (Wipperman 1965), in contrast to 1% in the electrofishing surveys that same year in a similar portion of the river (Heaton 1960). In the nine years from 1954 to 1962, the average percentage of grayling among salmonids caught in the Big Hole River was about 10% between Divide Dam and Pintlar Creek (annual range 2.6-22.4%) and about 13% from Pintlar Creek upstream (annual range 1.1-44.9%) (Wipperman 1965). Varley (1977) reported that grayling made up only about 0.5% of fish sampled by electrofishing in the upper river, but were the predominant fish in catches of fishermen interviewed in the same area.

These figures suggest that grayling were easier to catch than trout and were being removed from the fish community at a disproportionately high rate. Regulations on angler harvest of grayling from the Big Hole River have become increasingly more restrictive in recent years, with daily limits declining from five fish (trout and grayling combined) up to 1983, to one grayling (1983-84 to 1987-1988), and then to catch and release (since 1988-89). Thus far, the grayling population of the Big Hole River has not responded to the more restrictive regulations and has remained at low levels.

Interactions with Non-Native Salmonids

Interactions between grayling and non-native fishes, especially salmonids, could include competition or predation. Competition occurs through common use of limited resources including food, shelter, and spawning areas and can lead to decline or elimination of less successful competitors. Grayling may be highly susceptible to predation, especially in early stages of development. Eggs are broadcast over the substrate instead of being buried, and young grayling fry are smaller and are weaker swimmers than trout fry. Newly free-swimming grayling fry are about 9 to 11 mm in length (Kaya 1991), compared to 20 mm for newly free-swimming trout fry (Northcote 1962).

According to Vincent (1962), fluvial grayling of the upper Missouri River drainage originally coexisted with only ten other species of fish, including two native salmonids, westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and mountain whitefish (*Prosopium williamsoni*). Additionally, lake trout (*Salvelinus namaycush*) may have coexisted with lacustrine grayling in Elk Lake. Observations by Lee (1985) suggest that grayling can compete effectively with native, sympatric salmonids. In a study of young grayling and two other species in Alaska, chinook salmon (*Oncorhynchus tshawytscha*) and round whitefish (*Prosopium cylindraceum*), Lee found that the grayling was the most aggressive species and dominated equal-sized individuals of the other two species.

The introduction of non-native fishes, especially salmonids, appears to be an important, and perhaps the most critical, factor affecting the decline of fluvial Montana grayling. One or more species of non-native salmonids - brown, rainbow, or brook trout - appears to be present in every stream in Montana known to be formerly occupied by grayling. Rainbow, brown and brook trout were introduced into grayling streams of the upper Missouri River drainage by 1900. All three species had been introduced into tributaries of the upper Madison River within Yellowstone Park by 1890 (Jordan 1891), and brown and rainbow trout were common in the upper and middle (near Ennis) parts of the river by about 1915 (Vincent 1962). The Madison River became known for its rainbow and brown trout fisheries and by about 1940 the once- abundant grayling of the Madison River had become rare, except in Ennis Reservoir.

In the Big Hole River, the best evidence for detrimental effects of interactions with non-native fishes is provided by the lower river below Divide Dam. Grayling have become rare in these lower reaches, which are dominated by brown trout and in which rainbow trout are also abundant (Oswald 1984, 1986). Brown trout may have entered the lower river after a local sportmen's club introduced the species into the Beaverhead River near its confluence with the Big Hole River, sometime during the late 1920's to early 1930's (Seidensticker, pers. comm.).

Interactions with non-native salmonids may also be important in the upper Big Hole River. According to a personal account cited by Liknes (1981), brook trout have been in the river since about 1929. Since at least the 1950's and continuing to the present, brook trout have been the dominant salmonid in the upper river and small numbers of rainbow trout are also present (Heaton 1960; Wipperman 1965; Oswald 1984, 1986). A recent upstream expansion of brown trout distribution in the Big Hole River represents obvious additional concern. Brown trout were not seen above Divide Dam in electrofishing surveys in 1959 and 1964 (Heaton 1960; Wipperman 1964), but started being seen in small numbers in later surveys (Wells and Rehwinkel 1980; Liknes 1981).

If species interactions are contributing to the present low densities and apparent continuing decline of fluvial grayling in the upper Big Hole River, only the brook trout appears sufficiently numerous to be exerting such an effect (Table 1). However, data are lacking on mechanisms of possible interactions between grayling and brook trout, and the relations between the two species are not understood. Nelson (1954) found grayling fry in the stomachs of brook trout in Red Rock Creek, a spawning tributary of Upper Red Rock Lake in southwest Montana. McMichael (1990) and Streu (1990) found little or no evidence of predation on young grayling fry in the Big Hole River by brook trout or by other fishes. However, stomach samples for these studies were collected from potential predators during summer, and did not include the late spring period when the fry are newly swimming and potentially most vulnerable to predation. Skaar (1989) found differences in habitat occupied by brook trout and grayling in the upper Big Hole River. Age-1+ brook trout were most abundant in higher gradient sections and faster flowing water, while grayling were more typically found in slow runs or pools with depths of 0.6 m or greater. It is not known whether this difference in habitat use results from difference in preference between the two species or from competitive displacement of one by the other.

Habitat Degradation

According to Vincent (1962), logging activities were the most important contributors to degradation of stream habitat for grayling in Michigan, while agricultural activities have been most important in Montana. In Michigan, log drives may have disrupted grayling spawning and caused erosion of stream beds and banks. This erosion would produce increased silt deposition into streams, removal of instream debris used for shelter by grayling, and dislodging of eggs and fry from gravel beds. Other possible effects of logging included increased inputs of silt from removal of vegetation from watersheds and disturbance of ground surface, and increased water temperatures from removal of vegetative canopies.

In Montana, degradation of fluvial grayling habitat appears most frequently to have been related directly or indirectly to agricultural irrigation (Vincent 1962). The most important disturbances have been reduction in stream flows through withdrawals of water for irrigation, blockage of streams by dams for reservoirs and diversions, and flooding of streams by reservoirs. Partial dewatering of streams can result in reduction of habitat available for fish, stranding of incubating eggs or young fish, increased predation on young through their being concentrated in remnant waters with adults and other fishes, reduced food availability through habitat reduction for aquatic invertebrates, and increased maximum daily temperatures. Dams to impound or divert stream waters can block migrations of salmonids to spawning, wintering, or summer feeding areas and the importance of such migrations to fluvial grayling in Montana and Alaska has been previously mentioned.

Vincent (1962) presents a number of examples in which habitat alterations appear to have had major adverse effects on fluvial grayling in Montana. Filling of Hebgen Reservoir in 1915 inundated Horsethief Springs, a tributary of the upper Madison River in which grayling had been abundant. In the Gallatin River and its tributaries, decline of grayling by about 1900 was associated with greatly expanded diversions of water for irrigation. Introductions of brook, rainbow and brown trout into this drainage began in 1897-1899, toward the end of the period of apparent grayling decline. In the Sun River and in Sheep Creek, a tributary of the Smith River, grayling appeared abundant until the early 1900's but had seriously declined by about 1913-1915. By then both streams and their tributaries had been extensively dammed and diverted for irrigation, and Willow Creek Reservoir had been built (1911) on one major tributary of the Sun River. Non-native trout (rainbow and brook trout) were planted in the Smith River drainage in 1898 and the Sun River about 1913, and in both grayling had declined before these introduced species had become common. Stream dewatering, possibly accompanied by increases in water temperatures during summer, were probably important in the Gallatin, Smith, and Sun River drainages. Blockage of instream migrations by dams may have also been important in the Sun River and Sheep Creek.

Among the factors most commonly cited as being detrimental to Big Hole River grayling is the partial dewatering of the river and its tributaries during the summer by irrigation diversions (Heaton 1960; Liknes 1981; Shepard and Oswald 1989). The mechanisms through which reductions in stream discharge volume may influence Big Hole River grayling have not been investigated, but it appears that weak year classes are associated with lower flows and strong year classes with flows normal to slightly above average (Shepard and Oswald 1989).

In addition to stream dewatering, the diversions are also causing loss of grayling, especially young fish. Grayling fry and juveniles are found in the ditches and may be carried into irrigated fields or left stranded in the ditches when headgates are closed at the end of the irrigation season (Shepard and Oswald 1989). While the magnitude of this loss is not known, an earlier study of trout in irrigation diversions from Montana streams indicates that such loss can be substantial (Clothier 1953).

Another major alteration on the river is the presence of Divide Dam near the town of Divide. The dam was originally built in 1899 by the Butte Water Company to divert water into its municipal supply system (Patterson, pers. comm.). A second, hydroelectric dam built a short distance upstream a few years later by the Montana Power Company was destroyed by a flood in 1927. The migrations of grayling between upstream spawning and downstream wintering areas in the Big Hole River (Shepard and Oswald 1989) and in Alaskan rivers (Armstrong 1986) have been previously mentioned. It is possible that migrations up and down the Big Hole River were originally more extensive than at present and included movements between the lower and upper reaches that became separated by these dams. Although grayling may be able to swim over the present dam during periods of high water flow, it is a general barrier to upstream migration (Heaton 1960; Wippperman 1965). Brown and rainbow trout replaced grayling in the lower river sometime after construction of these dams, perhaps because grayling declined from having their access to upstream spawning areas restricted, or through interspecific interactions with non-native salmonids.

Information is not available to determine whether other habitat parameters such as stream temperatures or turbidities of the Big Hole River have been degraded through human activities and have contributed to the decline of grayling. Present midsummer water temperatures in the upper Big Hole River may at times become marginal for grayling, and stream dewatering may be contributing to elevated temperatures. Liknes (1981) suggested that higher numbers of grayling in the Wisdom area than in areas further downstream could be related to cooler temperatures. However, temperatures may also become marginal in the Wisdom section. For example, continuous recordings by the U.S. Geological Survey (1989) indicate that maximum daily water temperatures in the Wisdom area consistently exceeded 20 oC during July 1988 and reached a maximum of 24.5 oC. Although 24.5 oC is below levels that would produce a thermal kill of grayling (Feldmeth and Eriksen 1978), temperatures above 20 ^{o}C may be higher than optimum for the species (Hubert et al. 1986).

Speculations on Persistence of Grayling in the Big Hole River

It is not known why fluvial grayling remain in the upper Big Hole River despite their disappearance from all other streams in Montana and Michigan. The same factors suspected of contributing to declines of grayling in other streams - non-native fishes, habitat degradation, and overfishing - also appear applicable to the Big Hole River. One possibility is that effects of non- native salmonids have been delayed or ameliorated. The Divide Dam may have helped to preserve this population by inhibiting upstream colonization by brown trout. If this has been important, than the increasing numbers of brown trout being found above the dam in recent surveys could have ominous implications. Vincent (1962) concluded that it takes about 40 years for fluvial grayling to be replaced by introduced species. Grayling in the Big Hole River have persisted longer, since brook trout appear to have been present in the river for over 60 years. Thus, the complete replacement of grayling by non-native salmonids may have been slowed for unknown reasons, but may still be underway.

Another possibility is that the upper Big Hole River is marginal quality habitat for salmonids in general, and that fluvial grayling have persisted there because they are as able or better able to withstand certain unfavorable conditions, such as partial stream dewatering, than brown or rainbow trout. This speculation is indirectly supported by the situation previously described for the Sunny Slope Canal, where grayling persist despite severe seasonal dewatering and where rainbow trout are present in only small numbers. If this is speculation is correct, then marginal habitat conditions may have a dual effect on grayling in the upper river, serving both to depress the grayling population while preventing their replacement by non- native salmonids. As with other potential factors, however, evidence is lacking for the role or mechanisms of interactions between grayling and non-native salmonids in the upper Big Hole River.

EFFORTS TO RESTORE GRAYLING IN STREAMS

Numerous attempts to establish or restore grayling in streams in Montana, Michigan and other states through fish stockings have thus far been notably unsuccessful. Stockings of young (originating from Montana) into streams in Michigan were not successful (Kelly 1931) and the species continued its decline into extirpation in that state. Hatchery records, summarized by Kaya (1990), indicate that millions of young grayling have been stocked into the Big Hole River and its tributaries, and millions more into at least 32 other streams in 13 major drainages on both sides of the Continental Divide in Montana. These efforts did not result in the establishment of any self-sustaining fluvial population, and the failure of plants within the Big Hole River drainage is also indicated by the genetic distinction of this population (Everett and Allendorf 1985).

The reasons for the failure of these stocking programs to produce self-sustaining populations of grayling in streams are not known. In many cases, the streams may have been too small and turbulent to provide good grayling habitat. This may have been a contributing factor in many smaller, mountain streams. However, this would not account for failures in large, former grayling streams like the Madison River.

Another possibility is that, with the exception of recent plants into Canyon Creek in Yellowstone National Park (Jones et al. 1977; Jones 1979) and into a tributary of the Sun River (Hill, pers. comm.), all young grayling stocked into streams in Montana and other states have originated from inlet-spawning, lacustrine populations. Most grayling planted were progeny of fish spawning in inlets of Georgetown, Agnes, Rogers, Grebe, Upper Red Rock, and Ennis lakes and reservoirs. With the exception of Upper Red Rock Lake, all these lacustrine populations directly or indirectly originated from Ennis Reservoir. Georgetown Lake was a primary source of fertilized eggs for the Anaconda Hatchery, which provided young for many of the transplants into streams and also for establishing populations in Agnes and Rogers lakes, which in turn became important sources of grayling spawn for state hatcheries (MDFWP fish planting database). The Georgetown Lake population was started in 1908 with young originating from fish spawning in Meadow Creek, an inlet to Ennis Reservoir (also previously known as Meadow Lake) on the Madison River (Kelly 1931). The population of Grebe Lake in Yellowstone National Park was also started with plants of fish from Georgetown Lake (Varley and Schullery 1983). Grebe Lake became another important source of grayling eggs for stocking programs in other states.

Ennis Reservoir was built in 1900, and so the spawners in Meadow Creek from which eggs were taken in 1908 were almost certainly fish from Ennis Reservoir. Since most grayling in Montana first mature at age three, the spawners taken in 1908 probably represented fish that were at least two generations removed from a fluvial ancestry. The extent to which the population in Ennis Reservoir may have changed its behavioral characteristics because of selection for lacustrine rather than fluvial characteristics is not known. Further opportunity for loss of fluvial characteristics occurred through additional generations spent in Georgetown and other lakes before young were taken for stocking into streams.

Recent studies have supported the possibility that grayling derived from lacustrine populations may not be suitable for stocking into streams. Unlike young from the Big Hole River population, young grayling from inlet-spawning lacustrine populations do not have a behavioral tendency to maintain position in water current, but instead tend to move downstream (Kaya 1990). Jones et al. (1977) also saw evidence of the unsuitability of lacustrine grayling planted in Canyon Creek, Yellowstone National Park, and stated that:

> The apparent drift of Grebe Lake stock and maintenance of stream position by the Big Hole River grayling seems to lend credence to our hypothesis that important behavioral differences exist between fluvial and lacustrine ecotypes.

Another possible factor contributing to the failures may have been the earlier practice of planting very young fish, especially fry which had not yet absorbed their yolk sacs. Kelly (1931) described the prevailing practice in Montana up to that time as, "Because of the fact that no artificial feeding has proved successful with grayling, the fry are planted while in the 'yolk' stage." Survival in streams of such early fry was probably very low. After reviewing efforts in Alaska, Armstrong (1986) also concluded that stocking of grayling fry into streams has not proven successful. However, this cannot explain all failures since some later plantings were with larger juveniles up to 15 cm (Tyron 1947). The Canyon Creek effort also failed even though larger juveniles were stocked.

Interspecific interactions with non-native salmonids may also have prevented success of grayling plants into streams. It is not known whether grayling can be established in a stream which contains a population or community of non-native salmonids. Grayling were successfully introduced into Grebe Lake which already had an established population of non-native rainbow trout (Kruse 1959), but there are no examples of such success in a stream. If interspecific interactions were important contributors to the elimination of grayling from streams, then this same factor may have prevented establishment of grayling stocked into streams including their original habitats like the Madison, Gallatin, and Sun rivers.

Although not yet proven successful in establishing self- sustaining populations, stockings of grayling can provide temporary stream fisheries. Hatchery-reared grayling from 5.1- 15.2 cm (2-6 inches) in length were planted into the upper West Gallatin River from 1938-1941 and resulted in "good grayling fishing" for up to 12-14 inch (30.5-35.6 cm) fish by 1941-1942 (Tyron 1947). In 1945 and 1946, however, grayling were no longer being caught. Armstrong (1986) also mentions examples of grayling surviving and growing in Alaskan streams when planted as fingerlings rather than as fry. If some young grayling planted into Montana streams did survive, then such fish may have contributed to reports of the species persisting in some streams in the state until the 1950's or later.

Another aspect of past planting programs is the possible effect on the genetic integrity of Big Hole River grayling. Over 12 million grayling were planted into the Big Hole River and its tributaries between 1929 and 1957 (Kaya 1990), and most of the planted fish were descendents of Georgetown Lake stock. Big Hole River grayling are genetically similar to, although identifiable from, the current population in Ennis Reservoir and both populations are less similar to populations directly or indirectly derived from Georgetown Lake stock (Leary 1990). This suggests that the

Ennis Reservoir and Georgetown Lake populations diverged genetically after the latter was started through plants of progeny from the former, perhaps through genetic drift. The similarity between Big Hole River and current Ennis Reservoir populations may represent an original condition from which the Georgetown Lake population diverged, or may have resulted from change in the Ennis Reservoir population toward similarity with the Big Hole River population (Leary 1990). In either case, the difference between Big Hole River grayling and the lacustrine populations started through plants of hatchery fish suggests that past plants of grayling into the Big Hole River and its tributaries probably also failed and had little or no effect on the indigenous population. Past stockings of grayling into the Big Hole River drainage may have failed for the same reasons as discussed for other stream plantings of the species - use of lacustrine stock, plantings of very young fry (as indicated by the June to early July stocking dates of most of the plants), and for the tributaries, unsuitable stream habitat.

CONCLUSIONS

1. Montana grayling are genetically divergent from northern populations in Alaska and Canada, and the remnant fluvial population of the Big Hole River drainage is a genetically identifiable stock of Montana grayling that is behaviorally adapted for permanently inhabiting a stream environment.

2. The only confirmed, self-sustaining population of Montana grayling which lives continuously and permanently in a flowing-water environment is that of the upper Big Hole River and lower parts of its tributaries. This population appears to be in continuing decline. Estimated densities of age-1+ fish in the most heavily occupied section of the upper river, near Wisdom, have decreased progressively from an already low level of about 69 per km in 1983 to about 20 per km during 1987 to 1991.

3. Very little is known about the factors responsible for the disappearance of fluvial grayling from most streams in Montana, or which presently may be producing the low numbers, low densities, and apparent continuing decline of fluvial Montana grayling in their last refuge, the upper Big Hole River. Physical habitat alterations, interactions with non-native salmonids, and past fishing overharvest may all have contributed to this decline but the evidence in each of these categories is inconclusive and often speculative. It can even be hypothesized that marginal habitat conditions for salmonids in the upper Big Hole River may be contributing to the persistence of fluvial grayling by inhibiting the non- native salmonids.

4. Effects on Big Hole River grayling of the present and former Divide Dam are not known. It is possible that the dams have interrupted what were once

more extensive migrations between upper and lower reaches of the river and may have thereby contributed to decline of Big Hole River grayling. However, the dams may have contributed to the persistence of grayling in the upper river by inhibiting upstream colonization by brown trout.

5. Attempts to establish or restore self-sustaining populations in streams in Montana and other states through stocking programs have thus far proven unsuccessful. Major contributing reasons for these failures may have been the planting of fish derived from lacustrine populations, the planting of predominantly very young fry, and the presence of non-native salmonids in the streams planted.

6. In contrast to fluvial grayling, lacustrine populations of Montana grayling have been greatly expanded in distribution through introductions into lakes in Montana and other western states.

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LITERATURE CITED

Armstrong, R. H. 1986. A review of Arctic grayling studies in Alaska, 1952-1982. Biological Papers of the University of Alaska, 23:3-17.

Behnke, R. J. 1972. The rationale of preserving genetic diversity: examples of the utilization of intraspecific races of salmonid fishes in fisheries management. Proceedings of the 52nd Annual Conference of the Western Association of Fish and Wildlife Agencies.

Benson, N. G., O. B. Cope, and R. V. Bulkley. 1958. Fishery management studies on the Madison River system in Yellowstone National Park. U. S. Dept. Interior, Bureau of Sport Fisheries and Wildlife, Rocky Mountain Sport Fishery Investigations, Logan, Utah.

Benson, N. G., O. B. Cope, and R. V. Bulkley. 1959. Fishery management studies on the Madison River system in Yellowstone National Park. U.S. Department the of Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 307.

Brown, C. J. D. 1943. Age and growth of Montana grayling. Journal of Wildlife Management 7:353-364.

Byorth, P.A. 1991. Population surveys and analysis of fall and winter movements of Arctic grayling in the Big Hole River: 1991 Annual Report. Submitted to: Fluvial Arctic Grayling Workgroup; Beaverhead National Forest; Bureau of Land Management; Montana Council, Trout Unlimited; Montana Department of Fish, Wildlife and Parks; U.S. Fish and Wildlife Service.

Byorth, P. A. and B. B. Shepard. 1990. Ennis Reservoir/Madison River Fisheries investigation. Draft Final Report: 1990. Submitted to: Montana Power Company, Butte.

Byorth, P. A. Montana Department of Fish, Wildlife and Parks, pers. comm.

Clark, T. W., A. H. Harvey, R. D. Dorn, D. L. Genter, and C. Groves, eds. 1989. Rare, sensitive, and threatened speciesof the Greater Yellowstone Ecosystem. Northern Rocky Conservation Cooperative, Montana Natural Heritage Program, The Nature Conservancy, and Mountain West Environmental Studies.

Clothier, W. D. 1953. Fish loss and movement in irrigation diversions from the West Gallatin River, Montana. Journal of Wildlife Management 17:144-158.

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 4:29-44.

Deleray, M. A. and C. M. Kaya. 1992. Lakeward and downstream movements of age-0 Arctic grayling originating between a lake and a waterfall. (manuscript submitted for publication).

Elrod, M. J. 1931. History of the Montana grayling. Montana Wildlife 10:10-12.

Evermann, B. W. 1893. a reconnaissance of the streams and lakes of western Montana and northwestern Wyoming. Bulletin of the U.S. Fish Commission 11:3-60.

Everett, R. J. and F. W. Allendorf. 1985. Population genetics of Arctic grayling: Grebe Lake, Yellowstone National Park. Genetics Laboratory Report 85/1, Zoology Department, University of Montana, Missoula.

Feldmuth, C. R. and C. R. Eriksen. 1978. A hypothesis to explain the distribution of native trout in a drainage of Montana's Big Hole River. Internationale Vereinigung fur theoretische und angewandte LimnologieVerhandlungen 20:2040-2044.

Fuqua, C. L. 1929. Restocking the famous Madison. Montana Wildlife 1(9):10-11.

Hanzel, D. A. 1959. The distribution of cutthroat trout (Salmo clarki) in Montana. Proceedings of the Montana Academy of Science 19:32-71.

Heaton, J. R. 1960. Southwestern Montana fishery study. Federal Aid Project F-9-R-8, Job No. I. Montana Department ofFish, Wildlife and Parks, Helena.

Henshall, J. A. 1907. Culture of the Montana grayling. Report of the Commissioner of Fisheries, Bureau of Fisheries Document No. 628, 1-7.

Hill, W. J. Montana Department of Fish, Wildlife and Parks, pers. comm.

Holton, G. D. Undated. Notes to File. Montana Department of Fish, Wildlife and Parks, Helena.

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

Hubert, S. A., R. S. Helzner, L. A. Lee, and P. C. Nelson. 1985. Habitat suitability index models and instream suitability curves: Arctic grayling riverine populations. U.S. Fish and Wildlife Service Biological Report 82(10.110).

Hubbs, C. L. and K. F. Lagler. 1958. Fishes of the Great Lakes region. U. Michigan Press, Ann Arbor.

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

Jones, R. D., J. D. Varley, D. E. Jennings, S. M. Rubrecht, R. E. Gresswell. 1977. Annual project technical report - 1976. Fishery and Aquatic Management Program. Yellowstone National Park, Mammoth, Wyoming.

Jones, R. D. 1979. Annual project technical report for 1978. Fishery and Aquatic Management Program. Yellowstone National Park, Mammoth, Wyoming.

Jordan, D. S. 1891. A reconnaissance of the streams and lakes of the Yellowstone National Park, Wyoming, in the interest of the United States Fish Commission. Bulletin of the U.S. Fish Commission 9:41-63.

Jordan, D. S. and B. W. Evermann. 1934. American food and game fishes. Doubleday, Garden City.

Kaya, C. M. 1989. Rheotaxis of young Arctic grayling from populations that spawn in inlet or outlet streams of a lake. Transactions of the American Fisheries Society 118:474-481.

Kaya, C. M. 1990. Status report on fluvial Arctic grayling (Thymallus arcticus) in Montana. Prepared for: Montana Department of Fish, Wildlife and Parks, Helena.

Kaya, C. M. 1991. Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (Thymallus arcticus), and implications for the only remaining indigenous population of fluvial "Montana grayling". Canadian Journal of Fisheries and Aquatic Sciences 48:53-59.

~~Kelly, J. L. 1931. Nation watches Montana grayling. Montana Wildlife~~ 3:9-11.

Kruse, T. E. 1959. Grayling of Grebe Lake, Yellowstone National Park, Wyoming. Fishery Bulletin 149:307-351.

Larkin, P. 1972. The stock concept and management of Pacific salmon. p. 11-15 in The stock concept in fisheries management. H. R. Mcmillan lectures in fisheries. University of British Columbia Press, Vancouver.

Larkin, P. A. 1979. Maybe you can't get there from here: a foreshortened history of research in relation to management of Pacific salmon. Journal of the Fisheries Research Board of Canada 36:98-106.

Leary, R. 1990. Letter to Pat Byorth, Montana Department of Fish, Wildlife and Parks, September 27, 1990. MDFWP Files.

Lee, K. M. 1985. Resource partitioning and behavioral interactions among young-of-the-year salmonids, Chena River, Alaska. M.S. Thesis, University of Alaska, Fairbanks.

Liknes, G. A. 1981. The fluvial Arctic grayling (Thymallus arcticus) of the upper Big Hole River drainage, Montana. M.S. Thesis, Montana State University, Bozeman.

Liknes, G. A. and W. R. Gould. 1987. The distribution, habitat and population characteristics of fluvial Arctic grayling (Thymallus arcticus) in Montana. Northwest Science 61:122-129.

Lindsey, C. C. and J. D. McPhail. 1986. Zoogeography of fishes of the Yukon and Mackenzie Basins. In: C. H. Hocutt and E. O. Wiley (ed.), The Zoogeography of North American Freshwater Fishes. Wiley, NY.

Loftus, K. H. 1976. Science for Canada's fisheries rehabilitation needs. Journal of the Fisheries Research Board of Canada 33:1822-1857.

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

MacLean, J. R. and D. O. Evans. 1981. The stock concept, discreteness of fish stocks and fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 38:1889-1898.

McAllistor, D. E. and C. R. Harington. 1969. Pleistocene grayling, Thymallus, from Yukon, Canada. Canadian Journal of Earth Sciences 6:1185-1190.

McMichael, G. A. 1990. Distribution, relative abundance and habitat utilization of the Arctic grayling (Thymallus arcticus) in the upper Big Hole River drainage, Montana, June 24 to August 28, 1989. Report to: Montana Natural Heritage Program; Beaverhead National Forest; Montana Department of Fish, Wildlife and Parks; Montana Cooperative Fishery Research Unit.

Moulton, G. E. (editor). 1986. The journals of the Lewis and Clark expedition. Volume 5. University of Nebraska Press, Lincoln.

Nelson, P. H. 1954. Life history and management of the American grayling (Thymallus signifer tricolor) in Montana. Journal of Wildlife Management 18:324-342.

Northcote, T.G. 1962. Migratory behaviour of juvenile rainbow trout, Salmo gairdneri, in outlet and inlet streams of Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 19:201-270.

Norden, C. R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (Thymallus arcticus) and its phylogeny. Journal of the Fisheries Research Board of Canada 18:679-753.

Oswald, R. A. Montana Department of Fish, Wildlife and Parks, pers. comm.

Oswald, R. A. 1984. Southwest Montana Fisheries Study. Federal Aid Project F-9-R-31/F-9-R-32, Job no. I-b. Montana Department of Fish, Wildlife and Parks, Helena.

Oswald, R. A. 1986. Southwest Montana Fisheries Study. Federal Aid Project F-9-R-34, Job no. I-b. Montana Department of Fish, Wildlife and Parks, Helena.

Patterson, M. Butte Water Company, pers. comm.

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

Ricker, W. E. 1972. Heredity and environment: factors affecting certain salmonid populations. P. 27-60 in The stock concept in Pacific salmon, H. R. McMillan lectures in fisheries. University of British Columbia Press, Vancouver.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 1984. Ottowa, Canada.

Seidensticker, S. J. Twin Bridges, Montana, pers. comm.

Shepard, B. B. and R. A. Oswald. 1989. Timing, location andpopulation characteristics of spawning Montana Arctic grayling (Thymallus arcticus montanus [Milner]) in the Big Hole River drainage, 1988. Report to: Montana Department of Fish, Wildlife and Parks; Montana Natural Heritage Program - Nature Conservancy; and U.S. Forest Service, Northern Region.

Shepard, B. B. and R. A. Oswald. 1990. Timing, location andpopulation characteristics of spawning Montana Arctic grayling (Thymallus arcticus montanus [Milner] in the Big Hole River drainage, 1989. Report to: Montana Department of Fish, Wildlife and Parks; Montana Natural Heritage Program - Nature Conservancy; and U.S. Forest Service, Northern Region.

Skaar, D. 1989. Distribution, relative abundance and habitat utilization of the Arctic grayling (Thymallus arcticus) in the upper Big Hole River drainage, Montana, July 5 to September 8, 1988. Report to: Montana Natural Heritage Program - Nature Conservancy; Beaverhead National Forest; Montana Department of Fish, Wildlife and Parks; and Montana Cooperative Fishery Research Unit.

Streu, J. M. 1990. Select aspects of the life history and ecology of the Montana Arctic grayling (Thymallus arcticus montanus [Miler]) in the upper Big Hole River drainage, Montana, June 15 to August 31, 1990. Submitted to: Montana Natural Heritage Program - Nature Conservancy; Beaverhead National Forest; Montana Department of Fish, Wildlife and Parks; Montana Cooperative Fishery Research Unit; and U.S. Bureau of Land Management.

Tyron, C. A. 1947. The Montana grayling. Progressive Fish-Culturist 9:136-142.

U.S. Geological Survey. 1989. Water Resources Data, Montana, Water Year 1988. U.S.G.S., Federal Office Building, Helena, Montana.

Varley, J. D. 1976. Letter to George Holton, Montana Department of Fish, Wildlife, and Parks, November 11, 1976. MDFWP Files.

Varley, J. D. 1981. A history of fish stocking activities in Yellowstone National Park between 1881 and 1980. Information Paper No. 35, Yellowstone National Park, National Park Service, Mammoth, Wyoming.

Varley, J. F. and P. Schullery. 1983. Freshwater wilderness, Yellowstone fishes & their world. Yellowstone Library and Museum Association, Yellowstone National Park, Wyoming.

Vincent, Richard E. Montana Department of Fish, Wildlife and Parks, pers. comm.

Vincent, Robert E. 1962. Biogeographical and ecological factors contributing to the decline of Arctic grayling, Thymallus arcticus Pallas, in Michigan and Montana. Ph.D. Dissertation. University of Michigan, Ann Arbor.

Walters, V. 1955. Fishes of western Arctic America and eastern Arctic Siberia. Bulletin of the American Museum of Natural History 106:259-368.

Wells, J. D. and B. J. Rehwinkel. 1980. Southwest Montana fisheries study. Federal Aid Project F-9-R-27, Job No. I-b. Montana Department of Fish, Wildlife and Parks, Helena.

Wells, J. D. and J. Decker-Hess. 1981. Southwest Montana Fishery Study. Feder Aid Project F-9-R-28, Job No. I-b. Montana Department of Fish, Wildli and Parks, Helena.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras- Balderas, J. I Willliams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 198 Fishes of North America endangered, threatened, or of special concen 1989. Fisheries 14:2-21.