Behavioral responses to water current of age-0 Arctic grayling from the Madison River, and their use of stream habitat
by Eric Donald Jeanes

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
Behavioral trials and field observations were conducted on age-0 Arctic grayling (Thvmallus arcticns) from the Madison River/Ennis Reservoir in 1993 and 1994 (ME) population to determine their riverine associated characteristics and residence. When tested in a natural stream, age-0 ME Arctic grayling displayed significantly greater downstream movement (P<0.005) than those from the fluvial population of the Big Hole River. In contrast, behavioral responses of age-0 F1 fluvial grayling originating from parents reared in non-fluvial environments strongly support the hypothesis that positive rheotaxis is a genetic trait in grayling from the Big Hole River. In both years, 805 of 824 (97.7%) age-0 grayling collected at the weir were recovered after the first 8-h period of daylight after release, consistent with the downstream grayling movement reported in other similar studies. In-stream acclimation more consistently reduced downstream movement of fluvial grayling than of either the ME grayling or a lacustrine grayling population from upper Red Rock Lake (RR). Field observations indicated that downstream movement of age-0 grayling to Ennis Reservoir occurred about 3.5-38-d after swimup. Age-0 ME grayling inhabited backwater habitats in the Madison River and resided in shallow water among macrophyte beds after moving downstream to Ennis Reservoir. Both behavioral trials and field observations indicate that, at least during the first four months after swimup, ME grayling behavior and distribution of ME grayling are more characteristic of adfluvial lacustrine grayling, than of fluvial grayling.

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Eric Donald Jeanes

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ABSTRACT

Behavioral trials and field observations were conducted on age-0 Arctic grayling (Thymallus arcticus) from the Madison River/Ennis Reservoir in 1993 and 1994 (ME) population to determine their riverine associated characteristics and residence. When tested in a natural stream, age-0 ME Arctic grayling displayed significantly greater downstream movement ($P<0.005$) than those from the fluvial population of the Big Hole River. In contrast, behavioral responses of age-0 F_1 fluvial grayling originating from parents reared in non-fluvial environments strongly support the hypothesis that positive rheotaxis is a genetic trait in grayling from the Big Hole River. In both years, 805 of 824 (97.7%) age-0 grayling collected at the weir were recovered after the first 8-h period of daylight after release, consistent with the downstream grayling movement reported in other similar studies. In-stream acclimation more consistently reduced downstream movement of fluvial grayling than of either the ME grayling or a lacustrine grayling population from upper Red Rock Lake (RR). Field observations indicated that downstream movement of age-0 grayling to Ennis Reservoir occurred about 35-38-d after swimup. Age-0 ME grayling inhabited backwater habitats in the Madison River and resided in shallow water among macrophyte beds after moving downstream to Ennis Reservoir. Both behavioral trials and field observations indicate that, at least during the first four months after swimup, ME grayling behavior and distribution of ME grayling are more characteristic of adfluvial lacustrine grayling, than of fluvial grayling.

INTRODUCTION

Two distinct life-history forms of Arctic grayling (Thymallus arcticus) are indigenous to the state of Montana. Lacustrine grayling (residing within lentic systems) are native to only the Upper and Lower Red Rock lakes and possibly nearby Elk Lake of the upper Beaverhead River drainage (Kaya 1992). Fluvial grayling (spending their entire life in lotic systems) are native to the upper Missouri River system above the Great Falls including the Madison, Gallatin, Jefferson, Sun, and Smith rivers (Tyron 1947; Vincent 1962). Both the lacustrine and fluvial populations of grayling in Montana are genetically distinct and divergent from populations in Alaska and Canada (Lynch and Vyse 1979; Everett and Allendorf 1985). In addition, fluvial grayling from the Big Hole River possess innate behavioral tendencies that enable them to reside in lotic environments (Kaya 1991).

Since the end of the 19th century, the distribution of fluvial grayling in Montana has declined substantially, and, at present, the only known self-sustaining fluvial population is confined to the upper Big Hole River, above the Divide Dam (Shepard and Oswald 1989). These Big Hole River grayling are also the last known fluvial population in the lower 48 states. This population appears concentrated within about 100 km of the Big Hole River, at estimated densities of about 18.6 yearling and older per km (30 per mile) since 1989 (Byorth 1993).

In contrast, the distribution of lacustrine grayling has been expanded through introductions to many western lakes, on both sides of the Continental Divide in Montana (Kaya 1992). Most of these populations appear to have originated from grayling captured in Meadow Creek, a tributary of Ennis Reservoir on the Madison River (Kaya 1992) or from Red Rocks lakes (Leary 1990).

In response to the diminished and uncertain future status of fluvial grayling in Montana, the Fluvial Arctic Grayling Workgroup (FGW) was formed in 1987. The FGW is made up of representatives from state, federal, and private agencies and from the two state universities. The FGW (1993) has derived a conservation goal of "the presence of at least five stable, viable populations distributed among at least three of the major river drainages within the historic range by the year 2020". Grayling used in restoration efforts must be capable of residing permanently in lotic environments to accomplish this goal.

Laboratory behavioral tests on age-0 grayling originating in Montana indicate that fluvial grayling from the Big Hole River are more positively rheotaxic (maintain position in water current) than lacustrine stocks (Kaya 1989). Other populations of grayling have been suspected of exhibiting fluvial characteristics. One of these, the Madison River/Ennis Reservoir grayling population (ME), may represent a remnant population originating from grayling residing in the Madison River prior to the construction of the impoundment in 1906. The ME population presently appears to be adfluvial, residing in the reservoir and spawning in the Madison River channels, upstream of Ennis Reservoir (Byorth and Shepard 1990), and has fluctuated in abundance since 1906. In 1983, the population was reduced to very low numbers, apparently due to an early spring drawdown of the reservoir to control macrophyte growth (Byorth and Shepard 1990; Jourdonnais et al. 1992a).

Although ME grayling appear to be adfluvial, other observations suggest the possibility of fluvial characteristics in this population. Sporadic reports have been received by Montana Department of Fish, Wildlife & Parks (MDFWP) personnel of grayling being captured during non-spawning periods as far upstream as the West Fork of the Madison River, approximately 85 km upstream from Ennis Reservoir (Pat Clancey, MDFWP, pers. comm.). Also, electrophoretic analysis indicates that ME grayling resemble fluvial grayling from the Big Hole River more closely than any other population within Montana (Leary 1990).

The extent to which ME grayling in the upper Madison River system exhibit fluvial characteristics is of obvious importance to FGW conservation goals. To address the uncertainty of the fluvial nature of ME grayling, this study examined the early life history of this population, testing the hypotheses:

(1) H_O: in streams, behavior and early life history of age-0 ME grayling are characteristic of those from fluvial populations.

H_A: in streams, behavior and early life history of age-0 ME grayling are not characteristic of those from fluvial populations.

(2) H_O: in streams, behavior and early life history of age-0 ME grayling are characteristic of those from adfluvial lacustrine populations.

H_A: in streams, behavior and early life history of age-0 ME grayling are not characteristic of those from adfluvial lacustrine populations.

To test these hypotheses, the objectives of this study were: (1) experimentally compare the rheotactic behavior of age-0 ME grayling with those from known fluvial (Big Hole River) and adfluvial lacustrine (Red Rock Lake) populations in a natural stream; (2) determine the distribution and residence time in the Madison River of age-0 ME grayling; and, (3) determine whether age-0 ME grayling have a lacustrine residence phase.

STUDY SITE

Deep Creek

Field trials on rheotactic behavior were conducted in Deep Creek, a tributary of the Missouri River. Behavioral tests in a natural stream setting provide a novel approach to testing rheotactic behavior, in that responses can be compared over an extended length of natural stream, instead of an artificial stream or channel. Deep Creek originates on Grassy Mountain of the Big Belt Range in the Helena National Forest, and flows through Broadwater County in central Montana (Figure 1). It is formed by 19 tributaries within the U.S. Forest Service boundary. Deep Creek flows westward for approximately 41 km to its confluence with the upper Missouri River, 4 km south of the town of Townsend. The elevation at the confluence of Deep Creek with the Missouri River is 1,180 m.

The Deep Creek watershed drains 22,000 ha, of which approximately two-thirds is U.S. Forest Service land, with the remainder being comprised of 37 tracts of private land. Major land uses in the watershed include woodlands, livestock grazing, small grains, and irrigated haylands (Ostreich 1992). In this area, average annual precipitation is 27 cm. Monthly mean temperatures range from lows of 4 C to a high of 14 C ("Montana" 1988).

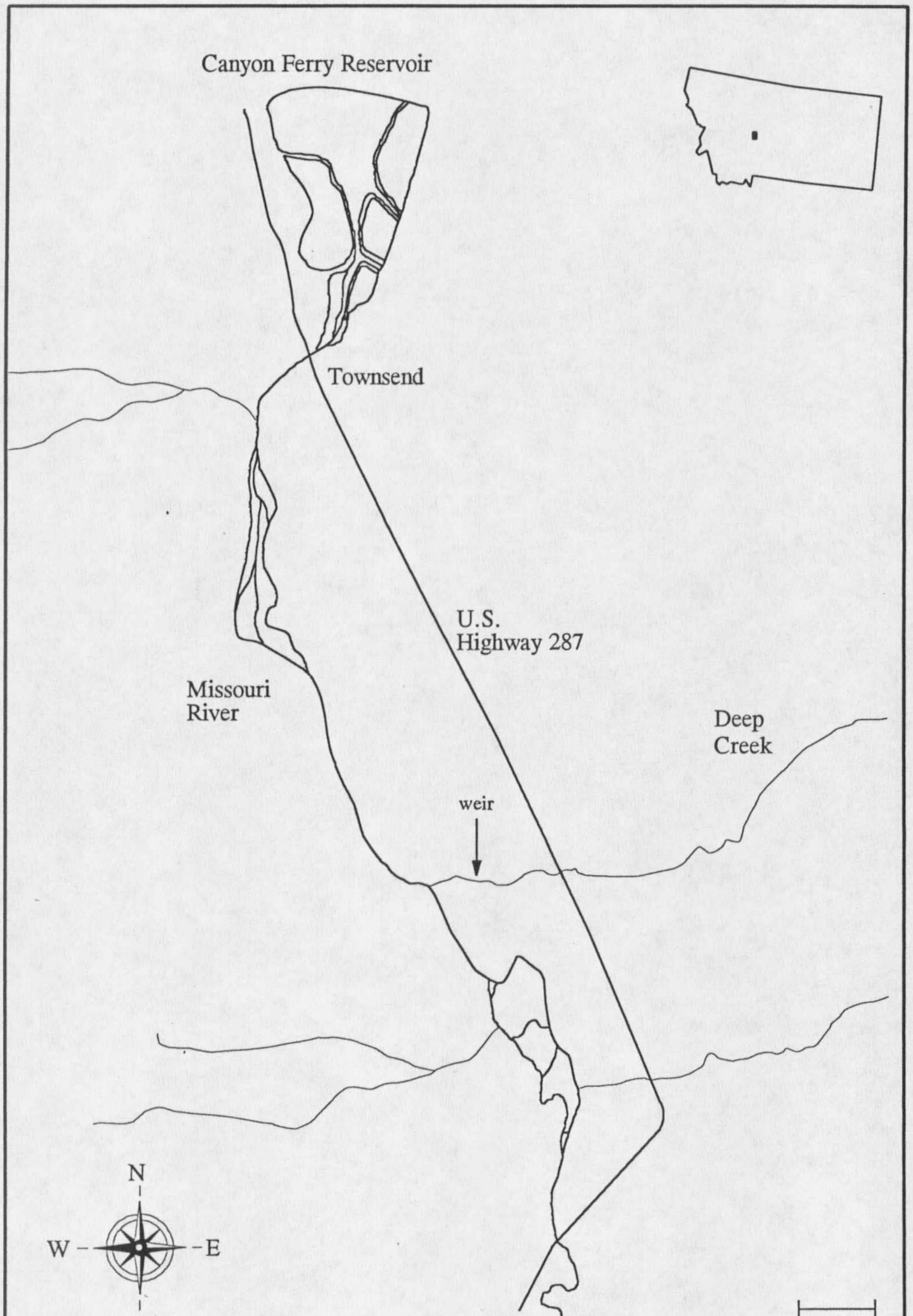

Figure 1. Location of the Deep Creek study site.

The study area began at the intersection of U.S. Highway 287 with Deep Creek and continued 1 km downstream to a weir. Until 1992, an irrigation canal, the Montana Ditch, intersected Deep Creek. In January of 1992, the Montana Ditch was routed under Deep Creek through a 2 m cement siphon, and the weir was constructed to monitor salmonid movements to a previously dewatered spawning tributary.

Riparian vegetation at the study area consisted of willows (Salix sp.), woods rose (Rosa woodsii), and common snowberry (Symphoricarpos albus). Resident fish fauna of Deep Creek include rainbow trout (Oncorhynchus mykiss), brown trout (Salmo trutta), mountain whitefish (Prosopium williamsoni), longnose dace (Rhinichthys cataractae) and mottled sculpin (Cottus bairdi). In addition, migrating rainbow trout and brown trout from the Missouri River and Canyon Ferry Reservoir utilize Deep Creek during their respective spawning periods. Deep Creek is located within the historic range of fluvial grayling in Montana, but there have been no documented accounts of grayling residing within this stream (Ron Spoon, MDFWP; Cal Kaya, Montana State University, pers. comm.).

Madison River/Ennis Reservoir

The Madison River is formed by the confluence of the Gibbon and Firehole rivers in Yellowstone National Park, Wyoming. The Madison River leaves Yellowstone National Park and flows northeast through Madison and then Gallatin counties in southwestern Montana. It is impounded at river km 61 (Hebgen Lake), river km 70 (Quake Lake), and finally at river km 170 (Ennis Reservoir). The

Madison River combines with the Jefferson and Gallatin Rivers to form the Missouri River, at approximately river km 220.

The Madison River watershed drains approximately 650,000 ha, about two-thirds of which is national forest lands, and about one-third is private lands. Principal land uses within the drainage include woodlands, livestock grazing, recreation, and irrigated haylands (Pat Clancey, MDFWP, pers. comm.).

Hebgen and Madison dams are owned by Montana Power Company and are managed as run of the river facilities, specifically "to minimize spill and provide year-round minimum flow of 31 m^3/s in the Madison River below the Madison Powerhouse" (Jourdonnais et al. 1992b). Hebgen Dam has no hydroelectric facilities and is managed as a storage reservoir, while Madison Dam is managed as an electrical generation facility. Current practice is to draft the reservoir 0.3 m prior to 1 December and an additional 0.3 m prior to ice-out in March or April in an effort to combat shoreline erosion by ice.

The inlet of the Madison River into Ennis Reservoir is at 1,475 m elevation, approximately 8 km north of the town of Ennis. This area averages 30 cm in total precipitation and mean temperatures range from lows of -5 C to highs of 14 C ("Montana" 1988).

The study area began at the Valley Garden Fishing Access Site (VGFAS) at river km 143.5, extended downstream 6.5 km to the mouth of the Madison River, and included all of Ennis Reservoir. Emphasis was placed on the area of the Madison River known as the "Channels" (Figure 2). In this area, the Madison River forms

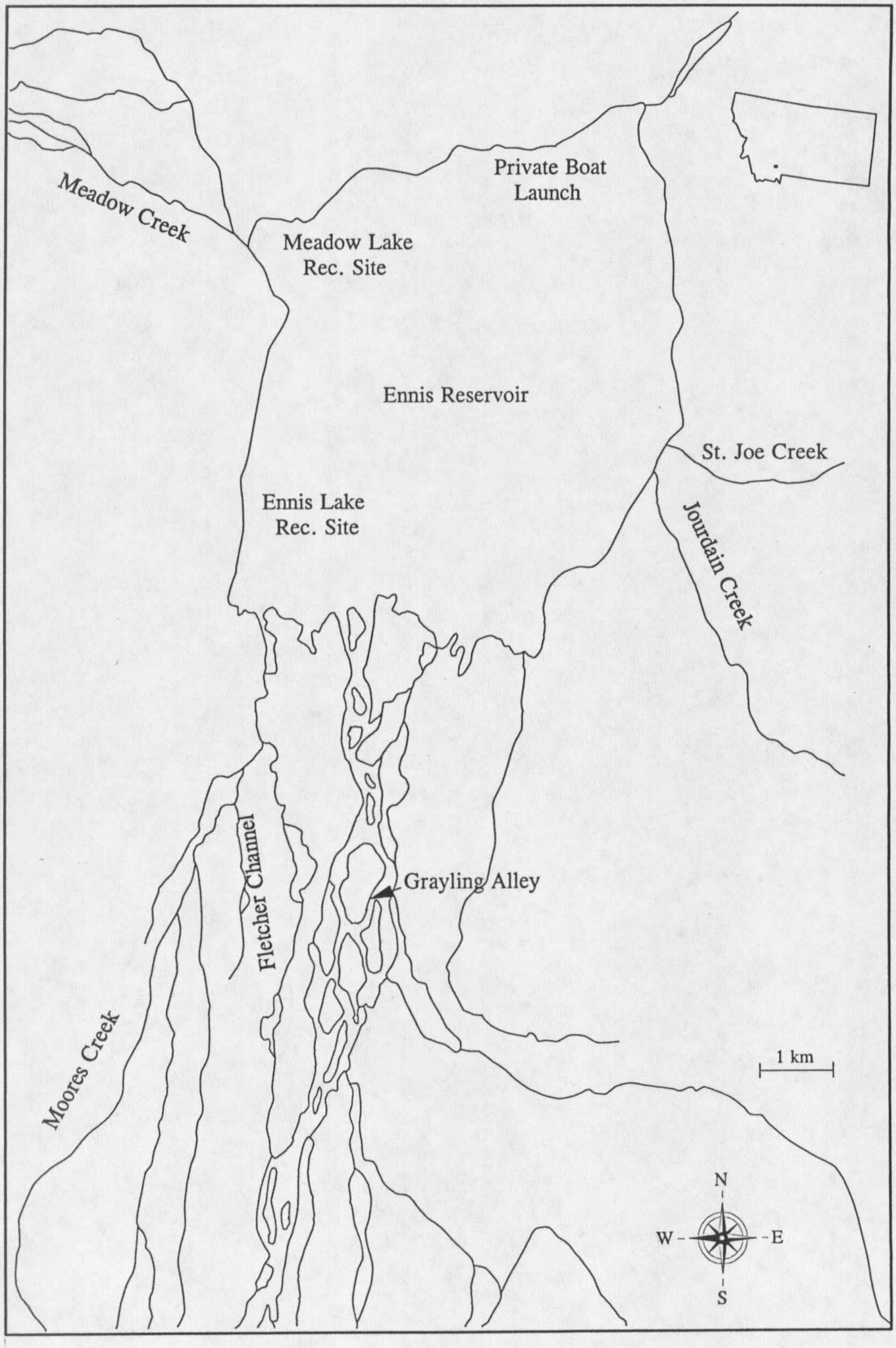

Figure 2. Location of Ennis Reservoir and Madison River study site.

braided channels resulting from deposition of suspended matter as river velocities decrease above Ennis Reservoir.

Ennis Reservoir was formed in 1906 by the impoundment of the Madison River. It is approximately 8 km long by 5 km wide, encompasses 1500 ha and impounds 5.7 X 10^7 m^3 of useable storage at full pool (Jourdonnais et al. 1992b). This reservoir is relatively shallow, with maximum depth of 10 m, and with 50% of the reservoir less than 3 m deep (Byorth and Shepard 1990). Due to its location in a shallow basin and exposure to strong winds, the reservoir rarely stratifies and has been identified as a potential source of thermal stress to the lower Madison River fish assemblage (Vincent 1981). In addition to the Madison River, four tributaries join Ennis Reservoir: Meadow Creek in the northwest corner, St. Joe and Jourdain Creeks in the southeast corner, and Moores Creek Canal which enters the southwest corner of the reservoir (Figure 2).

The north, west, and southern shorelines of Ennis Reservoir are characterized by dense mats of macrophytic vegetation. Jourdonnais et al. (1992a) found that sago pondweed (Potamogeton pectinatus), whitestem pondweed (P. praelongus), curly pondweed (P. crispus), coontail (Ceratophyllum demersum), water millfoil (Myriophyllum sibiricum), and waterweed (Elodea nuttallii) were present at various depths from 0-3 m at various times of the year. Waterweed has been the source of the problems with dam operations, and the drawdown in 1983 was intended to reduce this aquatic macrophyte.

Cottonweed (Populus sp.), willow, woods rose, and alder (Alnus sp.) are the predominant woody vegetation located along the Madison River and Ennis Reservoir riparian zones. The fish assemblage includes Utah chub (Gila atria), brown trout, rainbow trout, Arctic grayling, white sucker (Catostomus commersoni), longnose sucker (C. catostomus), and longnose dace.

METHODS

Deep Creek

Age-0 grayling from the Madison River, Big Hole River, and Upper Red Rock Lake were tested in 1993, while only grayling from the Madison and Big Hole Rivers were tested in 1994 trials. All age-0 grayling used in trials were incubated, hatched, and reared at the U.S. Fish and Wildlife Service, Bozeman Fish Technology Center (FTC), except for the ME grayling in 1993, which were incubated and hatched at the State of Montana Fish Hatchery in Big Timber and reared at the State of Montana Fish Hatchery in Great Falls. When possible, gametes were collected by stripping several ripe males and pooling the sperm to fertilize eggs stripped from a given female. Behavioral tests in Deep Creek were conducted from 21 July to 9 September 1993 and from 20 July to 24 September 1994.

Adults were captured in the Madison River above Ennis Reservoir using a Mark XXII-M Electro-shocker (Coffelt Manufacturing, Inc.) in 1993 and 1994. Age-0 grayling from the Madison River were produced from embryos collected from twelve females, each fertilized by three males (48 total grayling) from 12 April to 30 April in 1993. In 1994, four females, each fertilized by three males (16 total grayling) were utilized to produce ME embryos.

In 1993, fluvial age-0 grayling were produced on 24 May from 40 females, each fertilized by three males (160 total grayling) captured in over-night Fyke net sets in Axolotl Lake. These adult grayling in Axolotl Lake originated as embryos produced in 1988 from six females and nine males captured in the Big Hole River. The young fish were stocked into the lake at 14 weeks of age after having their rheotaxis tested in an artificial stream channel (Kaya 1991). The young from this source are hereafter referred to as F_1AL, indicating they are F_1 Big Hole River grayling from parents reared in Axolotl Lake.

In 1994, age-0 fluvial grayling were produced on 17 April from gametes collected from the Big Hole River broodstock at the FTC from 38 females and 38 males (76 total grayling). Broodstock were progeny of 28 females and 48 males taken directly from the Big Hole River (Pat Dwyer, USFWS, pers. comm.). The young from this source are hereafter referred to as F_1BZ, indicating they are F_1 Big Hole River grayling from parents reared at the FTC in Bozeman.

In 1993, lacustrine age-0 grayling (hereafter referred to as RR) were produced from six females and six males from the upper Red Rock Lake population. On 19 May, adults were captured on their spawning grounds in Red Rock Creek, approximately 6 km from Upper Red Rock Lake with an Electro-shocker backpack unit (Coffelt Manufacturing, Inc.).

All fertilized eggs were placed in containers and transported in insulated coolers refrigerated with ice. Except for the 1993 ME, which were taken to the state hatchery at Big Timber, all fertilized eggs were transferred to the FTC. At the FTC, they were placed in screened incubation boxes and maintained in springwater at approximately 8 C. After hatching occurred, 13-19 d after fertilization, water temperature was increased 2-3 C by mixing springwater of different temperatures. The young grayling were then transferred to 90-L rearing tanks that received a constant flow (4-5 L/min) of springwater. Swimup (initiation of swimming) started on approximately day 22 after fertilization, and was completed on about day 29. All age-0 grayling used in trials will be referred to as post-swimup in age, with 0 being the day when peak swimup occurred. Age-0 grayling from the different sources were fed the same artificial trout food, increasing in particle size as the grayling grew. Grayling from the three sources were kept in different rearing tanks, but all tanks were adjacent to each other and provided with the same water.

Age-0 grayling were tested at ages ranging from 8-16 weeks. Test grayling were fin clipped to denote both their source (ME, F_1AL, F_1BZ, or RR) and the trial date, 1-7 d prior to transportation to Deep Creek. Fins clipped were single or in combinations of pelvic, anal, adipose, and upper and lower lobes of the caudal fin. Grayling to be tested in Deep Creek were anesthetized with MS-222 (tricane methanesulfonate), clipped, combined into one rearing tank, and allowed to recover for at least 1-d prior to transportation. Marked grayling were then transported approximately 100 km from the FTC to Deep Creek and placed into a 1.1 X 1.5 m holding pen which was anchored in the stream under the U.S. Highway 287 Bridge. A subsample of 50 grayling from each source was randomly measured at this time to the nearest mm total length (TL). Pre-release acclimation time within Deep Creek varied from 1-, 7-, or 14-d for all sources. Grayling acclimated for only 1-d were not fed, while grayling acclimated for 7-or 14-d were given the same artificial trout pellets they had received at FTC, twice daily. Few mortalities were observed, ranging from 0 to 15 grayling per source during both 1993 and 1994 acclimation periods. These were subtracted from initial numbers to provide numbers released. For each trial, grayling were released at 1200 hrs (Mountain Daylight Time) following acclimation to stream conditions.

With one exception, all trials were conducted with grayling from at least two sources (Tables 1 and 2). The one exception, on 21 June 1993, was a trial with only ME grayling. This single, unpaired trial also involved grayling reared at a different hatchery. For these reasons, this trial is not closely comparable to the other trials and is not included in results of the study. Additionally, two other trials were attempted in July 1994, but abandoned when water temperatures approached or exceeded lethal levels of 28 C (Feldmuth and Eriksen 1978).

In 1993, I intended to conduct initial trials with F_1Al and RR grayling acclimated and released separately, in consecutive weeks. However, we did not release the first group of F_1AL on the date intended, because of increased discharge. Instead, the first group of RR grayling were added to the holding pen with the F_1AL grayling and held until their release on 9 August after acclimations of 7-d (RR) and 14-d (F_1AL). Thereafter, age-0 grayling from lacustrine and fluvial origins were placed in the holding pen at the same time and acclimated and released together.

Table 1. Date of release, source, number released, mean total lengths (mm) (standard deviation in parenthesis) of age-0 Arctic grayling tested during the 1993 behavioral trials in Deep Creek. Statistical comparisons (ANOVA) were made between values within columns.

Release Date	9 Aug	14 Aug	28 Aug	9 Sep
Source	ME[1]	F_1AL	F_1AL	F_1AL
Number	648	542	490	318
Mean TL	54(4)+	63(5)	53(5)	55(7)
Source	F_1AL	RR	RR	RR
Number	550	594	500	317
Mean TL	46(4)	58(5)	49(5)	50(6)-
Source	RR			
Number	549			
Mean TL	51(5)+			

+ Significantly greater than F_1AL ($P<0.01$).

- Significantly less than F_1AL ($P<0.01$).

[1] 1993 ME grayling were incubated and reared at the state Big Timber and Great Falls hatcheries. All other grayling in 1993 and 1994 were reared at the federal, Fish Technology Center in Bozeman.

Temperature, discharge, and turbidity on release dates were recorded (Table 3). Temperature was recorded 10 m upstream from the weir with a Taylor recording thermograph, which was calibrated with a hand-held thermometer. Mean temperatures were calculated by averaging the minimum and maximum daily temperatures recorded at the thermograph. Discharge and turbidity were measured at a water quality site

Table 2. Date of release, source, number released, mean total lengths (mm) (standard deviation in parenthesis) of age-0 Arctic grayling tested during the 1994 behavioral trials in Deep Creek. Two other trials, on 20 July and 27 July, were abandoned when stream temperatures approached or exceeded lethal levels (28 C) during the acclimation period. Statistical comparisons (ANOVA) were made between values within columns.

Release Date	17 Sep	24 Sep
Source	ME	ME
Number	350	350
Mean TL	84(6)+	85(8)+
Source	F_1BZ	F_1BZ
Number	350	350
Mean TL	71(7)	75(7)

+ Significantly greater than F_1BZ ($P < 0.01$).

located about 100 m upstream from the weir. Turbidity was measured with a Hach Model 16800 meter and recorded in nephelometric turbidity units (NTU). Flows recorded at a nearby gauge station were calibrated against estimates of discharge at the water quality site. Discharge at the water quality site was estimated by dividing the stream transect into 18-20 sections and then following the methods of Nielsen and Johnson (1983). A Gurley AA pygmy current meter was used to measure water velocities for the discharge estimates.

Table 3. Temperature, discharge, and turbidity of Deep Creek on dates of release of age-0 Arctic grayling tested during the 1993 and 1994 behavioral trials in Deep Creek.

Release date	Temp (C)	Volume (m^3/s)	Turbidity (NTU)
9 Aug 1993	15.8	1.81	31
14 Aug 1993	12.2	1.25	21
28 Aug 1993	13.0	2.30	32
9 Sep 1993	14.8	2.30	20
17 Sep 1994	19.4	0.62	21
24 Sep 1994	12.2	0.62	10

Temperature, discharge, and turbidity on release dates were recorded (Table 3). The weir extended across the stream and the entire flow of Deep Creek passed through the four vertical slots in the weir. For each net, headboards were placed in a slot to reduce flow through that slot and to direct flow through a 53 cm-wide notch in the top headboard. Water then dropped approximately 50 cm before entering the mouth of the net. Each net was 2.4 m long with a 58 X 63 cm mouth. Each net tapered toward the rear, and was joined to a 30 cm long, 20 cm diameter PVC pipe which entered a 0.6 X 0.6 X 1.4 m screened box. All net mouths were suspended approximately 30 cm above the water surface below the weir to prevent grayling escapement. In 1993, nets were placed at two of the four slots for the initial two trials, and at three slots for the remaining trials. The remaining one or two slots had to be left unsampled due to high discharge. By measuring depth, width, and water velocity through the headboard notches and the unobstructed weir slots, it was estimated that 9% of total stream flow was passing through each net in 1993. In 1994, lower stream discharges enabled us to use two nets to capture all fry passing through the weir. The two remaining slots were screened to prevent the passage of fish. On the day the grayling were released, nets were examined at 2-h intervals until sunset, and again at sunrise the next morning. After that, nets were checked at sunrise and sunset each day for the next 2 d. The stream section was electrofished twice each year, 10-and 12-d after conclusion of the trials in 1993, and 18-and 25-d after trials in 1994. Except for the recapture run in 1994, the entire stream section from the weir up to a beaver (Castor canadensis) dam located approximately 50 m above the release site was electrofished with an Electro-shocker backpack unit (Coffelt Manufacturing, Inc.). On the second run in 1994, about 33% of this section was electrofished, but equipment failure prevented further effort.

Proportions of fluvial versus lacustrine recovered at the weir and proportions of fluvial versus lacustrine captured in electrofishing surveys were recorded and compared via chi-square analysis. Expected recoveries were calculated by multiplying the number recovered from all sources by the ratio between grayling released from a particular source (Tables 1 and 2) and the total number of grayling released from all sources, for each trial. Mean sizes of grayling (Tables 1 and 2) were compared by ANOVA. If results of ANOVA were significant ($P<0.01$), I used Tukey's Test to conduct multiple comparisons (Shaefer and Faber 1992).

Madison River/Ennis Reservoir

Observations during 1994 of age-0 grayling in the Madison River above the reservoir were conducted from 25 May to 12 July. The river channels were searched from the beginning of Fletcher Channel, approximately 5 km above the reservoir, to the mouth of the Madison River into Ennis Reservoir (Figure 2).

Visual observations were used to determine the distribution of ME grayling in the Madison River. When grayling were encountered, a 31 X 46 cm, 1 mm meshed dip net was used to capture grayling and verify their identities. Backwaters and stream margins were searched with a 1.3 X 10 m seine with 1 mm mesh. Two 5 m long stationary drift nets were secured in lower regions of Fletcher Channel and "Grayling Alley" to monitor recent swimup ME grayling (Figure 2). Each net had a 0.5 X 1 m mouth and tapered down to a 15 cm collection jar. A mobile electrofishing unit (Cofelt Manufacturing, Inc.) was used to search the main river channel, including "Grayling Alley" on 12 July. Total lengths, to the nearest millimeter, and capture locations were recorded for all salmonids during the observations in the Madison River.

River discharge and mean river temperatures were obtained from the Montana Power Company. Discharge was measured 2.8 km below Madison Dam at U.S. Geological Survey Hydrologic Unit 10020007, while river temperatures were collected at a location approximately 1 km upstream from the head of "Grayling Alley".

Temperatures were recorded by a two-channel Omni-data datapod.

Observations were conducted during 1994 in Ennis Reservoir from 16 June until 1 September. Grayling were collected with a 31 X 1.5 m seine with 6 mm mesh along and near shoreline areas, in depths up to 1.5 m. Waters further off-shore, in depths from 2 to 10 m, were searched with a 5 X 18 m purse-seine with 6 mm mesh. All salmonid capture locations were recorded and each fish was measured to the nearest millimeter TL.

Growth rates of age-0 grayling captured from the river and the reservoir were calculated and compared using multiple linear regression. All statistics were performed on MINITAB® Release 8 (Schaefer and Farber 1992).

RESULTS

Deep Creek

Discharge (Figure 3), temperature (Figure 4), and turbidity (Figure 5) in Deep Creek were within relatively narrow ranges on the release dates in 1993 (Table 3). During acclimation and release dates in 1994, flows in Deep Creek were lower (Figure 3), temperatures were generally higher (Figure 4), and turbidities (Figure 5) were lower than in 1993 (Table 3).

All but 7 of 571 grayling (98.2%) recovered at the weir in the four trials in 1993 and 49 of 309 grayling (84.1%) recovered during the two trials in 1994 were netted between their release at 1200 hrs and the following sunrise (Tables 4 and 5). Thus, because most downstream movement of fish occurred by the first sunrise after their release, I based comparisons of downstream movement of grayling recovered at the weir on results from this 18-h interval.

Except in the initial 1-d trial conducted in 1993 on 14 August, significantly greater ($P<0.005$) numbers of age-0 lacustrine RR and/or ME grayling were recovered at the weir than fluvial F_1AL grayling in 1993 or F_1BZ grayling in 1994. Much higher numbers and percentages of both RR and F_1AL grayling were recovered in the first of the two 1-d acclimation trials (14 August) than the second 1-d acclimation trial

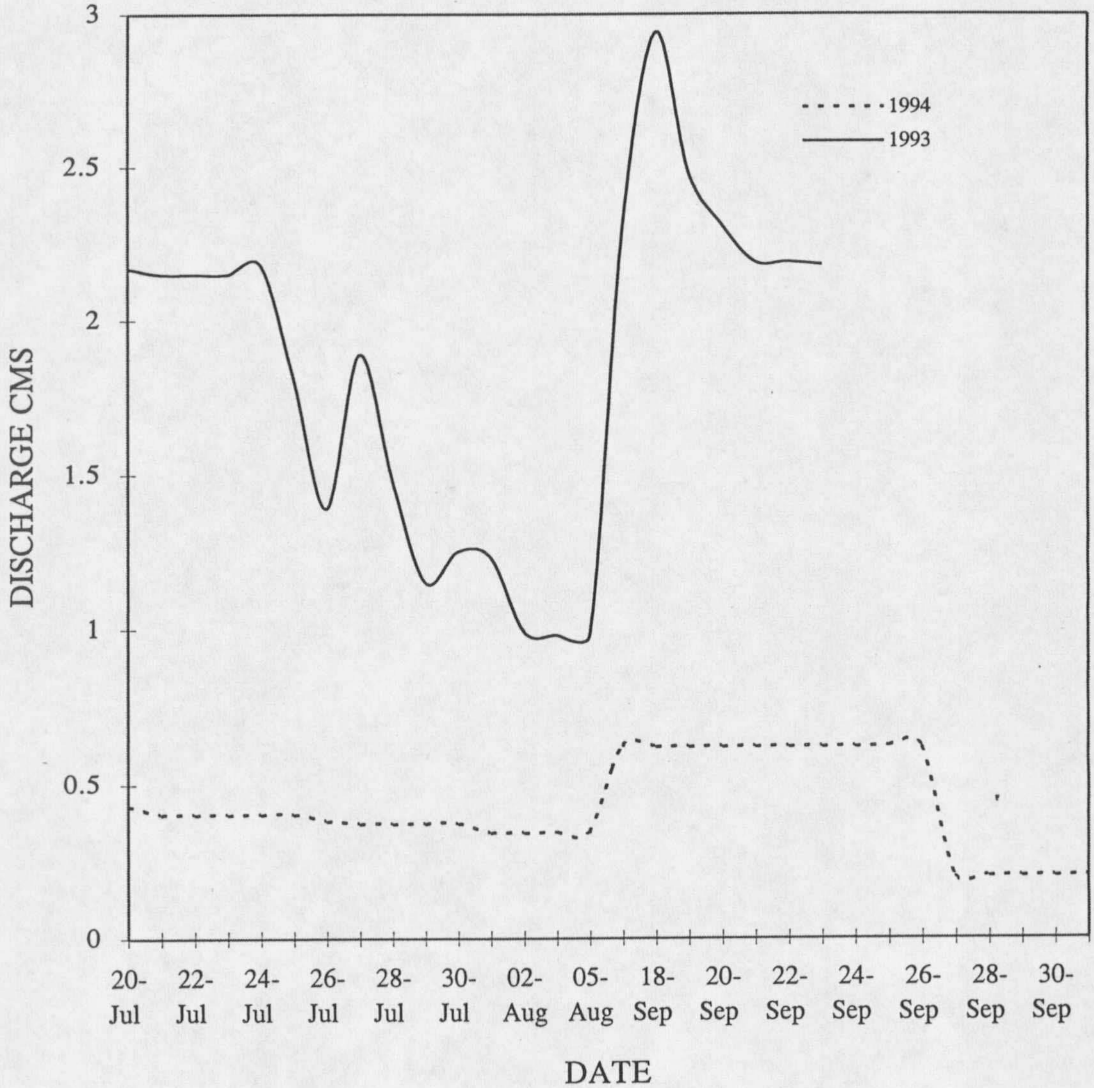

Figure 3. Discharge volume in Deep Creek during the 1993 and 1994 study periods.

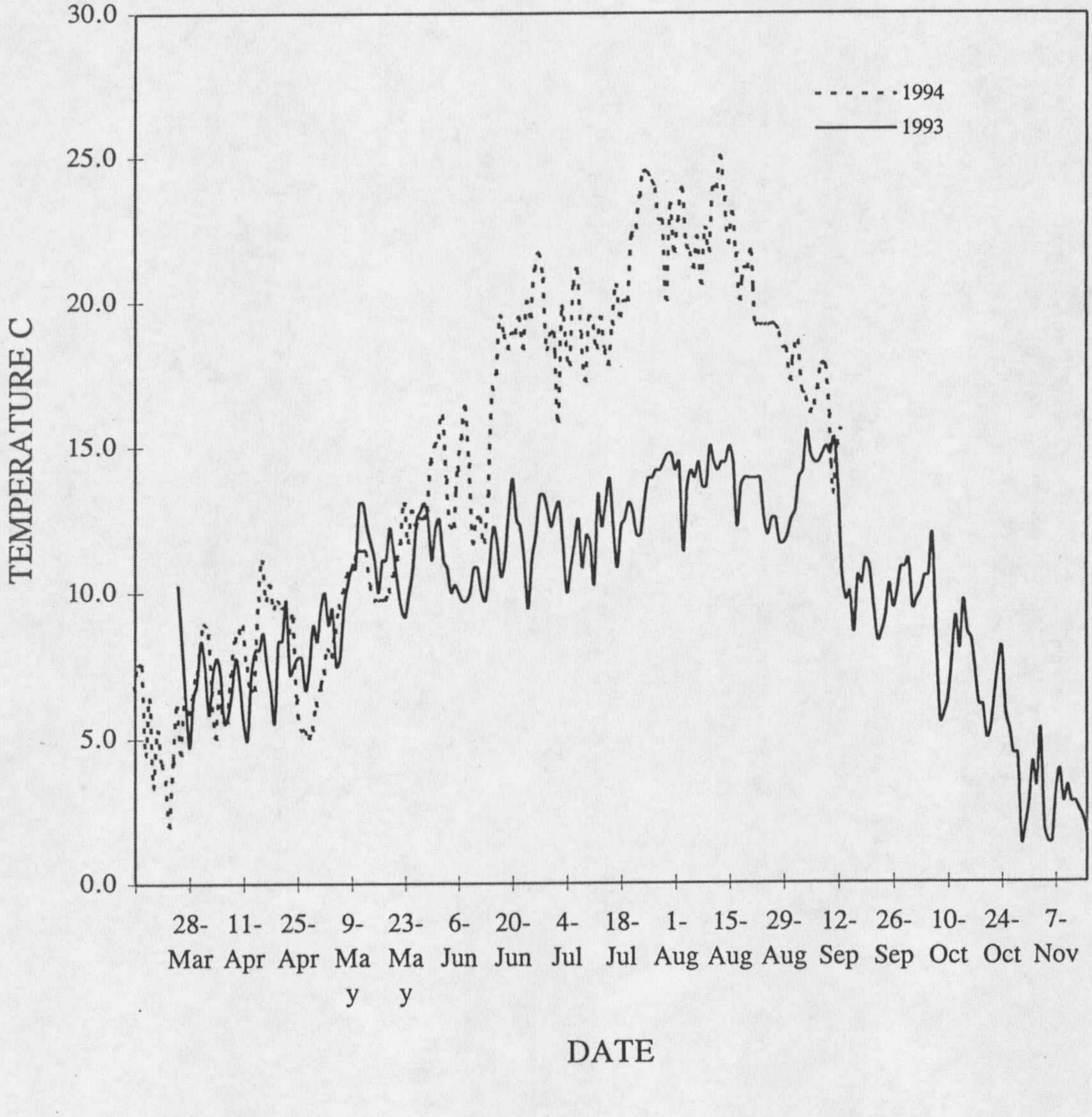

Figure 4. Mean temperatures in Deep Creek during the 1993 and 1994 study periods.

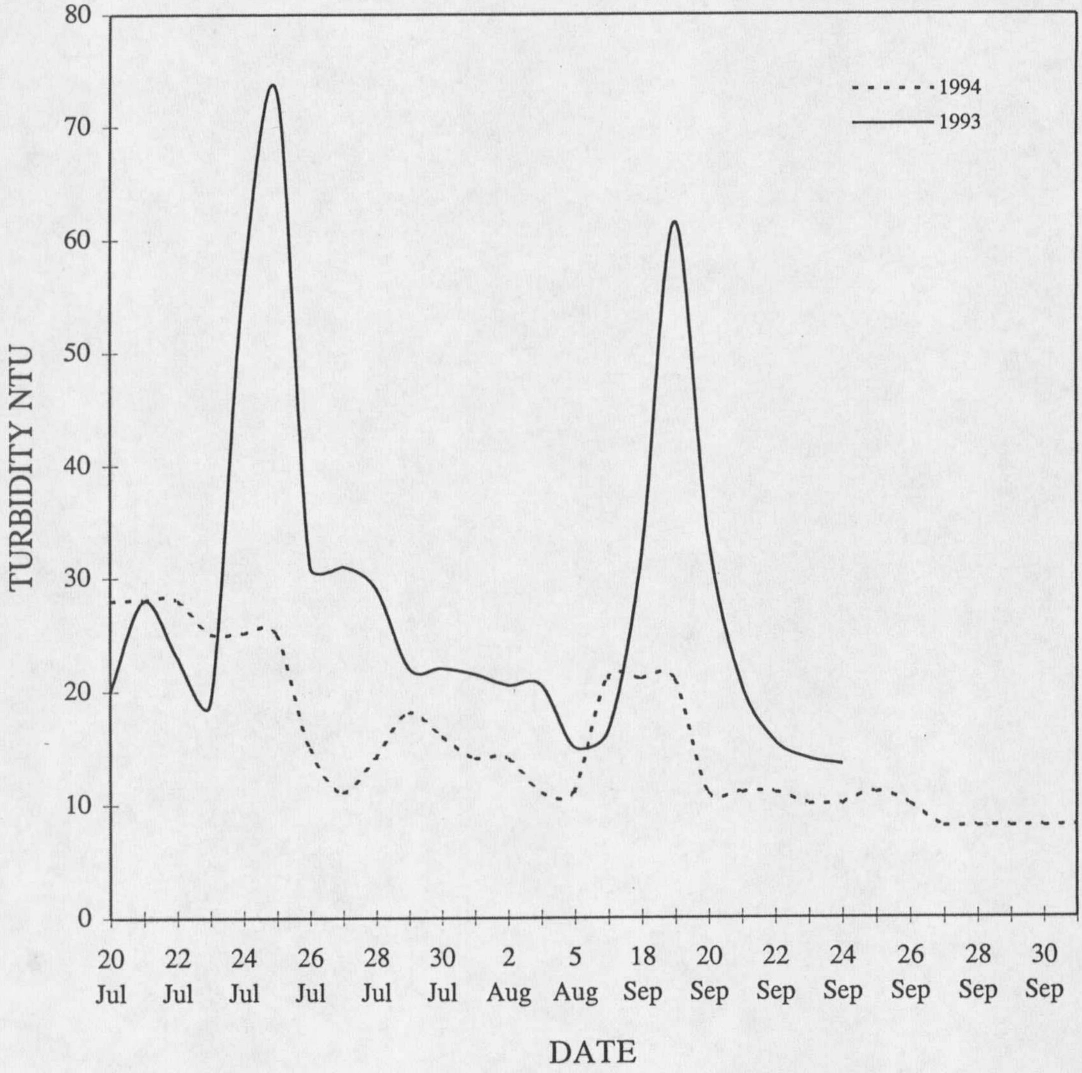

Figure 5. Turbidity levels in Deep Creek during the 1993 and 1994 study periods.

Table 4. Total cumulative numbers, and percentages of released fish (in parenthesis), of age-0 Arctic grayling captured in nets at the weir in Deep Creek by the first sunset, the first sunrise (about 18-h), and by 48-h after release during 1993. Statistical comparisons (chi-square) were made between values within columns.

Release Date	9 Aug	14 Aug	28 Aug	9 Sep
Source	ME	F_1AL	F_1AL	F_1AL
Acclimation (d)	14	1	11	1
Total Netted by:				
Sunset	0	0	0	0
Sunrise	21*(3.2%)	176(32.5%)	9(1.8%)	15(4.7%)
48-h	21 (3.2%)	176(32.5%)	9(1.8%)	16(5.0%)
Source	F_1AL	RR	RR	RR
Acclimation (d)	14	1	11	1
Total Netted by:				
Sunset	0	0	7	1
Sunrise	5(0.9%)	175+(29.5%)	89*(17.8%)	43*(13.6%)
48-h	5(0.9%)	175 (29.5%)	89 (17.8%)	44 (13.9%)
Source	RR			
Acclimation (d)	7			
Total Netted by:				
Sunset	10			
Sunrise	52*(9.5%)			
48-h	52 (9.5%)			

* Significantly greater than F_1AL ($P<0.005$).

\+ Not significantly greater than F_1AL ($P>0.500$).

Table 5. Total cumulative numbers, and percentages of fish released (in parenthesis), of age-0 Arctic grayling captured in nets at the weir in Deep Creek by the first sunset, the first sunrise (about 18-h), and by 48-h after release during 1994. Statistical comparisons (chi-square) were made between values within columns.

Release Date	17 Sep	24 Sep
Source	ME	ME
Acclimation (d)	7	7
Total Captured by:		
Sunset	0	0
Sunrise	64*(18.3%)	127*(36.3%)
48-h	83 (23.7%)	148 (42.3%)
Source	F_1BZ	F_1BZ
Acclimation (d)	7	7
Total Captured by:		
Sunset	0	0
Sunrise	15(4.3%)	54(15.4%)
48-h	19(5.4%)	59(16.9%)

* Significantly greater than F_1BZ ($P<0.005$).

(9 September) or in both 7-14-d acclimation trials (Table 4). Numbers of RR and F_1AL recovered were almost identical ($P>0.500$) in the first 1-d acclimation trial. Recoveries of RR and F_1AL were significantly different ($P<0.01$) for the remaining three trials in 1993. Similarly, in trials with 7-d acclimation in 1994, significantly

greater numbers ($P < 0.005$) and percentages of ME than F_1BZ were recovered at the weir (Table 5).

Acclimation time had more consistent effects on responses of F_1AL than on RR grayling. Fewer and lower percentages of F_1AL grayling were recovered downstream in both 7-14 d acclimation trials when compared to the two 1-d acclimation trials (Table 4). With RR grayling, however, a greater percentage of released grayling was recovered downstream in one of the 7-14 d trials (28 August) than in one of the 1-d trials (9 September). No paired trials involving ME acclimated for 1-d were conducted during the study period.

Mean lengths of age-0 ME and/or RR grayling differed significantly ($P < 0.01$) from age-0 Big Hole River grayling in all trials. Mean lengths differed by only 5 mm or less in 1993 trials. In 1994, ME grayling averaged 13 mm and 10 mm longer in the two trials. Madison River/Ennis Reservoir and/or RR grayling moved downstream in significantly greater numbers in 1993 whether they were smaller (28 August and 9 September) or larger (9 August) than F_1AL.

In all trials, downstream movement of grayling took place predominately during the first night following their release (Tables 4 and 5). Only 19 of the 564 (3.4%) age-0 grayling in 1993 and none of the 260 grayling in 1994 recovered at the weir by the first sunrise were netted by the previous sunset (Tables 4 and 5). Of the 19 grayling netted during 8-h of daylight following release in 1993, all but one was of RR origin.

Results of electrofishing surveys in the 1 km stretch of stream between the release site and the weir (Table 6) complemented the recoveries of grayling at the weir.

Age-0 grayling from the Big Hole River were consistently captured in significantly

Table 6. Numbers of age-0 Arctic grayling captured (Cap) and recaptured (Recap) in electrofishing surveys conducted 9-and 11-d in 1993 and 18-and 25-d in 1994 after the final trial for each year. Statistical comparisons (chi-square) were made between values within columns.

Source	ME		Big Hole River		RR	
	Cap	Recap	Cap	Recap	Cap	Recap
Date						
19 Sep 1993	0	-	21	-	1	-
21 Sep 1993	0	0	20	8	1	0
Total	0	0	41*	8	2	0
12 Oct 1994	5	-	13	-		
19 Oct 1994	1	0	7	0		
Total	6	0	20*	0	4	0

* Significantly greater than ME and/or RR ($P<0.005$).

greater ($P<0.005$) numbers than either ME and RR in 1993 and ME in 1994. In 1993, 21 of 22 (95.5%) of the grayling collected on the marking survey and 28 of 29 (96.6%), including 8 recaptures, in the recapture survey were of Big Hole River origin. Likewise, in 1994 F_1BZ accounted for 13 of 18 (72.2%) grayling collected on the marking survey and 7 of 8 (87.5%) age-0 grayling collected in the recapture survey.

Electrofishing surveys conducted prior to the behavioral trials in 1994 (1 April, 7 July, and 17 July) revealed the presence of grayling remaining from the 1993 behavioral trials in Deep Creek (Table 7), and all were of Big Hole River origin.

Table 7. Mean and range of total lengths (mm) and source of Arctic grayling captured in Deep Creek prior to the 1994 behavioral trials, after having been released a year previously for the 1993 trials.

Date	Source	N	Mean (SD)	Range
1 Apr	F_1AL	1	127	127
7 Jul	F_1AL	1	165	165
17 Jul	F_1Al	2	159 (12)	147-170

<u>Observations in Madison River and Ennis Reservoir</u>

Age-0 grayling were seen on the first day of observations in the Madison River, on 25 May, in the "Grayling Alley" area (Figure 2). These grayling had a mean TL of 21 mm and, based on comparisons with ME grayling incubated and reared at the FTC, appeared to be about 7-10 d post swimup in age. Grayling at the FTC were those incubated and reared for use in the 1994 behavioral trials in Deep Creek. These embryos began to hatch on 5 May, and swimup of fry was observed on 16 May. Incubation and rearing temperatures at the FTC were about 10 C, similar to river temperatures during this period.

Observations on age-0 grayling in the Madison River continued from 25 May until they disappeared about 21 June, about 28-d later. Since they were estimated to be 7-10 d post swimup on 25 May, they remained in the river for about 35-38 d. Age-0 grayling were seen throughout the lower 3.5 km of the Madison River above the reservoir, up to about 1.25 km below the formation of Fletcher Channel (Figure 2). They were observed in all channels throughout the lower river, except "Bailey Channel" (Figure 2). They were most prevalent in the areas known as "Grayling Alley" where ripe adults were most frequently collected in April by electrofishing.

Rearing habitat in the Madison River consisted of backwaters along the margins of the braided channels or "slackwater" created by mid-channel bars of sediment deposition or by debris and vegetation along river banks. I could see no apparent preference for depth, temperature, or cover type. Age-0 grayling were consistently found in backwater areas throughout their residency in the Madison River, and less consistently in slackwater areas (Table 8).

In backwater areas, age-0 grayling were initially present in monospecific groups of 7-25. By 9 June, grayling had reached mean total length of 37 mm and were now found interspersed with age-0 mountain whitefish (Table 8). The age-0 grayling were frequently observed feeding on the surface throughout the period they were seen in the river, 25 May - 21 June.

The thalwegs of the river channels were not thoroughly surveyed, because visual observations and fry sampling techniques were not effective in the deeper, faster water typically found in these areas. No age-0 grayling were collected from such waters when the main channel was electrofished on 12 July (Table 9). Only two grayling, both age-0, were collected from stationary drift nets before the nets were removed on 17 June (Table 8).

Table 8. Mean and range of total lengths (mm) and habitat of age-0 Arctic grayling and mountain whitefish sampled in the Madison River, 25 May to 21 June 1994.

	Grayling			Whitefish			
Date	Mean (SD)	Range	N	Mean (SD)	Range	N	Hab
26 May	21 (3)	17-26	14	-	-	-	BW[1]
27 May	21 (4)	15-29	9	-	-	-	BW[2]
27 May	18	18	1	-	-	-	DN[3]
31 May	-	-	7-10[5]	-	-	-	BW[4]
2 Jun	-	-	20-25[5]	-	-	-	BW[2]
3 Jun	32 (3)	29-36	4	-	-	-	BW[2]
7 Jun	-	-	6[5]	-	-	-	MCB[6]
7 Jun	35	35	1	-	-	-	DN[7]
8 Jun	38 (2)	36-40	3	-	-	-	MCB[6]
9 Jun	37 (5)	29-45	15	42 (2)	40-46	7	BW[2]
13 Jun	42 (3)	39-46	4	-	-	-	BW[4]
16 Jun	51 (4)	48-55	3	54 (6)	47-59	3	BW[4]
21 Jun	57 (3)	54-60	4	50 (4)	38-58	24	BW[1]

[1] Collected with a macroinvertebrate kick net and a seine in backwaters of "Grayling Alley".

[2] Collected with a macroinvertebrate kick net and a seine in backwaters of Fletcher Channel.

[3] Collected with ichthyoplankton drift nets in thalweg of "Grayling Alley".

[4] Collected with a macroinvertebrate kick net and a seine in backwaters of the main channel of the Madison River.

[5] Visual observations in the Madison River.

[6] Grayling collected with a macroinvertebrate kick net and a seine behind mid-channel bars of the main channel of the Madison River.

[7] Collected with ichthyoplankton drift nets in thalweg of Fletcher Channel.

Table 9. Mean and range of total lengths (mm) of fish collected during the electrofishing survey conducted on 12 July 1994, in the Madison River above Ennis Reservoir.

Species	N	Mean (SD)	Range
Mountain whitefish	6	74 (7)	65-84
Rainbow trout	10	134(68)	43-305
Brown trout	25	105(60)	50-279

Age-0 grayling and mountain whitefish disappeared from backwaters on or around 21 June, corresponding with substantial decrease in river discharge volume and increase in river temperature (Figure 6). Mean daily temperatures increased from about 10-14 C to about 16-17 C.

Total lengths of age-0 grayling collected in the river ranged from 17-26 mm on 26 May near the start of observations, and 54-60 mm on 21 June as they disappeared from the river (Table 7 and Figure 7). The relationship between total length and observation day during stream residence was:

$$TL = 19.75 + 1.27(OD); \ r = 0.896, df = 56.$$

Observation day 0 is defined as the day when age-0 were first seen, 25 May.

Age-0 grayling were collected in Ennis Reservoir on the first day of seining, 16 June, (Table 10) in a shallow bay located 0.5 km west of the inlet of the main channel of the Madison River (Figure 2). On this date, age-0 grayling were still present in the Madison River channels. During subsequent surveys, in July and August, age-0 grayling were commonly taken among macrophytes beds near the inlet of "Baileys Channel", the inlet of the main channel of the Madison River, the inlet of Fletcher Channel, along the entire west shoreline, and the inlet of Meadow Creek (Table 10). There was no indication of preference for particular types of macrophytes; most macrophyte beds consisted of mixtures of species and of broad- and narrow-leaf vegetation. Mountain whitefish were consistently captured in surveys together with grayling (Table 10).

Grayling were not captured from near-shore areas starting east of the "Bailey Channel" inlet, continuing around the east shore along the inlets of Jourdain and St. Joe Creeks north to the outlet of Ennis Reservoir, or along the north shore to the private boat launching area approximately 0.75 km of the bridge (Table 11 and Figure 2). These areas of the reservoir are typically deeper and without the extensive beds of macrophytes characteristic of the west and southwest shorelines.

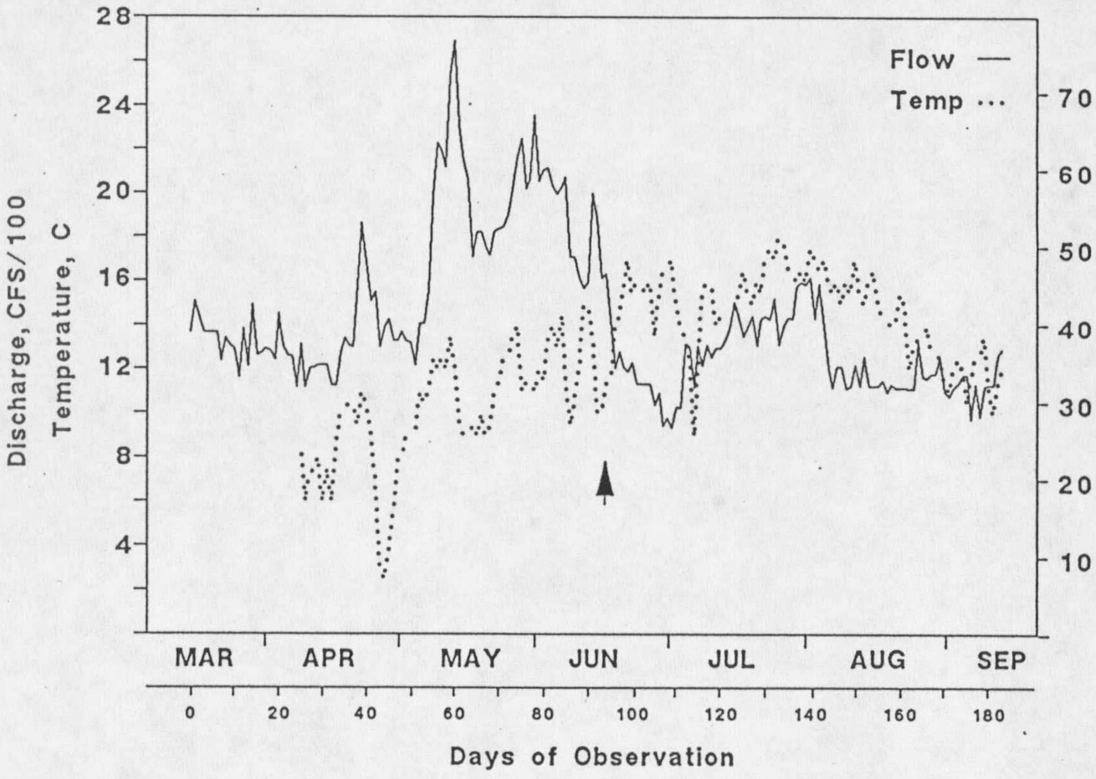

Figure 6. Mean daily temperature (°C) and discharge volumes (in ft^3/s, cfs; and m^3/s, cms) in the Madison River above Ennis Reservoir, 1994. The arrow indicates the approximate date (21 June) when age-0 grayling disappeared from the river, apparently moving downstream to the reservoir.

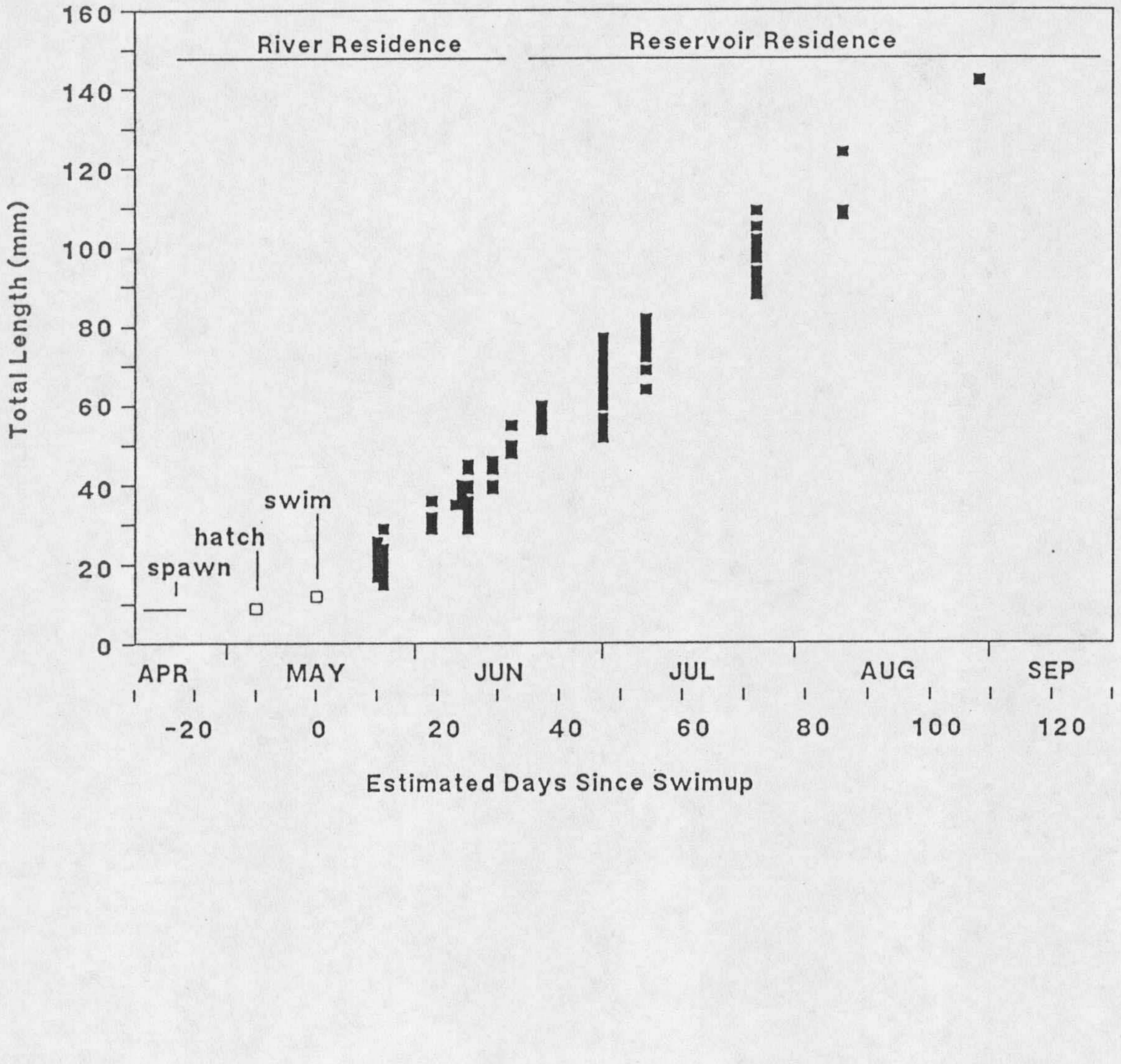

Figure 7. Distribution and sizes of age-0 Arctic grayling in the Madison River above Ennis Reservoir and in the reservoir, May through August 1994. Also depicted are the spawning, hatching, and swimup periods.

Table 10. Mean and range of total lengths (mm) and habitats of age-0 Arctic grayling and mountain whitefish sampled in Ennis Reservoir, 16 June to 1 September 1994.

	Grayling			Whitefish			
Date	Mean (SD)	Range	N	Mean (SD)	Range	N	Hab
16 Jun	58 (1)	57-59	2	60 (1)	59-60	2	SW[1]
1 Jul	66 (6)	52-77	35	63 (7)	45-81	36	SW[1]
8 Jul	69	69	1	65 (7)	57-70	3	SW[1]
8 Jul	77 (3)	72-79	4	74 (7)	63-80	5	SW[2]
8 Jul	70 (6)	64-74	3	73 (5)	63-80	5	SW[3]
8 Jul	77 (4)	69-82	9	69 (7)	60-85	37	SW[4]
8 Jul	56 (7)	69-82	3	79 (3)	77-81	2	SW[5]
8 Jul	-	-	-	73	73	1	SW[6]
26 Jul	-	-	-	74	74	1	SW[1]
26 Jul	99 (7)	90-109	7	82 (6)	74-92	19	SW[2]
26 Jul	94 (4)	91-97	2	83 (5)	76-87	6	SW[4]
26 Jul	88	88	1	80 (5)	76-83	2	SW[5]
10 Aug	114(9)	108-124	3	93 (6)	87-106	15	SW[2]
10 Aug	-	-	-	101	88-114	2	SW[7]
10 Aug	-	-	-	102(9)	93-110	3	SW[8]
10 Aug	-	-	-	93	90-95	3	SW[4]
11 Aug	-	-	-	97 (4)	92-102	6	SW[5]

31 Aug	142	142	1	103	103	1	SW[2]
1 Sep	-	-	-	109	101-115	6	SW[5]
1 Sep	-	-	-	103	92-121	27	SW[8]

[1] Collected in shallow water habitats with a beach seine near the mouth of Meadow Creek.

[2] Collected in shallow water habitats with a beach seine at Meadow Lake Recreation Site.

[3] Collected in shallow water habitats with a beach seine near Ennis Lake Recreation Site.

[4] Collected in shallow water habitats with a beach seine near the mouth of Fletcher Channel.

[5] Collected in shallow water habitats with a beach seine near the mouth of "Bailey Channel".

6 Collected in shallow water habitats with a beach seine near the mouth of Jourdain Creek.

7 Collected in shallow water habitats with a beach seine near Lake Shore Lodge on the north shore of Madison reservoir.

[8] Collected in shallow water habitats with a beach seine near the mouth of the main channel of the Madison River.

Later surveys (1 August to 31 August) again yielded age-0 grayling in shallow, near-shore areas from the inlets of the Madison River channels north to Meadow Lake Recreation Site (Table 10 and Figure 2). However, by this time, the macrophyte vegetation had grown so thick that the effectiveness of seining was substantially reduced.

Table 11. Summary of fish captured by beach seining conducted in Ennis Reservoir, 16 June to 1 September 1994.

			Catch							
Date	Location	Water Temp (C)	AG	MWF	RBT	BNT	WSU	UCH	LSU	Other
16-Jun	Fletcher Channel Inlet	9	2							
1-Jul	Meadow Cr Inlet	10	35	36	1					
8-Jul	Meadow Cr Inlet	11	1	1	1	1		1		
8-Jul	Meadow Cr Inlet	11								
8-Jul	Meadow Cr Inlet	11			5	13				
8-Jul	Meadow Cr Inlet	11		2						
8-Jul	Meadow L Rec Site	17	5	1			13	8	2	1
8-Jul	Meadow L Rec Site	17	2	2			4	18		
8-Jul	Meadow L Rec Site	17	1	4	2	4	24	84	4	4
8-Jul	Ennis L Rec Site	17	3	2	1			3		
8-Jul	Ennis L Rec Site	17	1				2	27	1	3
8-Jul	Ennis L Rec Site	19		3						
8-Jul	Fletcher Channel Inlet	19	9	38						
8-Jul	Baileys Channel	22	3	2						
8-Jul	Jourdain Cr Inlet	20			3					
8-Jul	N of Jourdain Cr	23		1		1	60	44	5	
26-Jul	Meadow L Rec Site	20	8	19		7	70	23		
26-Jul	Meadow Cr Inlet	19		1	2	8	1			
26-Jul	Ennis L Rec Site	20			3	1	60	6		
26-Jul	Fletcher Channel Inlet	18	2	6			118			
26-Jul	Baileys Channel	19	1	2			200	8		
10-Aug	Meadow Cr Inlet	19	3	15	1		3	7		
10-Aug	Meadow L Rec Site	20		10						
10-Aug	Meadow L Rec Site	21			1			2		
10-Aug	Timish Bays	22					2	6		
10-Aug	E of Timish Bays	26				1	2	84		
10-Aug	Lake Shore Lodge	24		1		1	8	26		
10-Aug	Lake Shore Lodge	26						2		
10-Aug	W of N Shore Beach	24		1			13	66		
10-Aug	W of N Shore Launch	24		3	1		1	1		
10-Aug	E of N Shore Launch	26			1		405	42		
11-Aug	Fletcher Channel Inlet	18		1			100			
11-Aug	Fletcher Channel Inlet	18		2			63			
11-Aug	Fletcher Channel Inlet	18				2				
31-Aug	Meadow L Rec Site	12	1	1			310	27		
31-Aug	Meadow Cr Inlet	14								
31-Aug	Baileys Channel	20								
1-Sep	Rainbow Point	15								
1-Sep	Fletcher Channel Inlet	17					58	7		
1-Sep	Fletcher Channel Inlet	17					33	8		
1-Sep	Channels	16		6						
1-Sep	Channels	16		27			5	3		
1-Sep	Channels	16		27			5	3		
Total Captured w/ Beach Seine			77	214	22	39	1560	506	12	8
Percent of Total Captured w/ Beach Seine			3.2	8.8	0.9	1.6	64.0	20.8	0.5	0.3

A purse-seine became available and was used from 10 August to 1 September to sample deeper, open waters of 2 to 10 m. No grayling were captured in this type of habitat (Table 11).

Total lengths of grayling captured in the reservoir ranged from 57-59 mm on 16 June, to 142 mm on 31 August (Table 10 and Figure 7). The relationship between total length and observation day for age-0 grayling in Ennis Reservoir was:

$$TL = 2.07 + 1.24(OD); \ r = 0.871, df = 68.$$

The TL-OD relationship was not significantly different in either slope ($T = -0.32$, $p = 0.727$) or intercept ($T = 0.20$, $p = 0.842$) between fluvial and lacustrine residence stages.

A total of 3,361 fish were captured by seining in Ennis Reservoir during 1994 (Tables 11 and 12). Grayling accounted for 2.3% of the total catch; 69 of 77 (89.6%) were age-0. Age-0 mountain whitefish were the most prevalent salmonid, comprising 6.5% of the total catch. Grayling, mountain whitefish, rainbow trout, and brown trout accounted for 21.5%, 61.5%, 10.9%, and 6.1%, respectively, of the total salmonid catch. White sucker and Utah chub were the most numerous species, comprising 58.6% and 29.2% of the total catch, respectively.

Table 12. Summary of purse-seining activities conducting in Ennis Reservoir, 11 August to 1 September 1994.

			Catch							
Date	Location	Water Temp (C)	AG	MWF	RBT	BNT	WSU	UCH	LSU	Other
11-Aug	Ennis L Rec Sit	19								
11-Aug	Ennis L Rec Sit	21		6			400			30
31-Aug	Rainbow Point	13								
31-Aug	Canyon Bridge	13								
31-Aug	Canyon Bridge	14					1	3		
31-Aug	Canyon	16					2	200		
31-Aug	Canyon	16					2	100		
31-Aug	Canyon	16					3	174		
31-Aug	N of St Joe Cr	16								
31-Aug	N of St Joe Cr	17								
1-Sep	Rainbow Point	15					2			
Total Captured w/ Purse Seine			0	6	0	0	410	477	0	30
Percent of Total Captured w/ Purse Seine			0.0	0.7	0.0	0.0	44.4	51.7	0.0	3.3

DISCUSSION

Results of behavioral trials in 1993 and 1994 and field observations in 1994 rejected the hypothesis that behavior and early life history in streams of age-0 Madison/Ennis Reservoir (ME) grayling are characteristic of those from fluvial populations. Instead, age-0 ME Arctic grayling possess the characteristics typical of an adfluvial lacustrine population. When tested in a fluvial environment, age-0 ME grayling displayed significantly greater downstream movement than those from a previously tested population of fluvial grayling, which appears to be adapted to a permanent stream existence (Kaya 1991). In their natural environment, age-0 ME grayling moved downstream to Ennis Reservoir about 35-38 d after swimup.

The creation of Ennis Reservoir in 1906 provided an opportunity for grayling to adopt a life history strategy allowing them to take advantage of a bountiful food source in a lentic environment. Armstrong (1986), in a review of migration patterns, indicates that grayling in Alaska are able to adapt to many different waters due, in part, to their rapid development in the egg and larval stages. O'Brien and Showalter (1993) conclude that Arctic grayling have very plastic feeding behaviors, allowing them to occupy many different systems.

Results from the behavioral trials provide further evidence that positive rheotaxis is a genetic trait in grayling of the Big Hole River. Responses of age-0, F_1

fluvial grayling originating from parents reared in non-fluvial environments strongly support this hypothesis. Other investigators provided evidence of innate rheotaxis by testing young originating directly from parents captured in native habitats (Raleigh and Chapman 1971; Bowler 1975; Kaya 1989). However, no other study that I am aware of has attempted to test F_1 fish originating from parents reared entirely, from fertilized eggs to adulthood, away from their native environments. These data provide evidence for the importance of conserving the gene pool represented by the Big Hole River grayling.

Studies on rheotactic behavior have been conducted on age-0 grayling (Kaya 1989; 1991), age-0 brook trout (Salvelinus fontinalis)(Van Offelen et al. 1993), age-0 cutthroat trout (O. clarki bouvieri)(Raleigh and Chapman 1971; Bowler 1975), age-0 rainbow trout (Northcote 1969; Kelso et al. 1981), yearling rainbow trout (Moring and Buchanan 1978), and age-0 sockeye salmon (O. nerka) (Raleigh 1971). Most of these experiments have concentrated on behavioral differences between inlet and outlet strains of fish. To my knowledge, testing a strain of fish originating from a fluvial environment but reared entirely in non-fluvial environments (hatchery and Axolotl Lake) has not been done before.

Various physical-chemical water parameters have been proposed as influencing the directionality and/or magnitude of rheotaxis in salmonids (Northcote 1962; Raleigh and Chapman 1971; Bowler 1975; Ottaway and Clark 1981; Heggenes and Traaen 1988). Factors such as discharge, temperature, and turbidity should not have had differential effects on grayling tested in Deep Creek, as all grayling within a trial were subjected to the same abiotic factors for the same duration during acclimation and following their release. In addition, behavioral differences between fluvial and lacustrine fish were consistent in 1993 and 1994, even though physical conditions in the stream varied.

Heggenes and Traaen (1988) found that critical water velocity (that velocity which elicits a directional response in movement) producing downstream displacement increases with increasing size of age-0 brown trout, Atlantic salmon (Salmo salar), brook trout, and lake trout (Salvelinus namaycush). Size of age-0 grayling did not seem to affect the results of behavioral trials in Deep Creek. Except on the first trial with only 1-d acclimation period, RR and ME grayling consistently moved downstream in greater numbers and percentages than F_1 Big Hole grayling, regardless of size.

Only 19 of 824 (2.3%) of the age-0 grayling captured at the weir in both years combined were recovered during the first 8-h period of daylight. Most downstream migrants were captured during their first night after their release. All but 1 of these 19 were RR grayling, further indicating a greater tendency of lacustrine grayling to move downstream. This nocturnal pattern of downstream movement is consistent with observations on other grayling populations (Kruse 1959; Lund 1974; Wells 1976). Deleray (1991) recovered 68% of the age-0 grayling moving downstream in Deer Creek between the period of 2200 and 0600 hours. Ginetz and Larkin (1976) and Gustafson-Marjanen and Dowse (1983) proposed that nocturnal movement is an anti-predation adaptation. Bardonnet and Gaudin (1990) hypothesized that daylight emergence of newly swimming European grayling (Thymallus thymallus) provides them "visual reference" to seek out refugia from the current while subsequent downstream drift at sunset is an anti-predatory behavior.

The 7-14 d periods of in-stream acclimation had a more consistent effect on fluvial F_1AL and F_1BZ than it did on the RR and ME age-0 grayling. Fewer and lower percentages of fluvial grayling were recovered at the weir in both 7-14 d acclimation periods compared to the two 1-d acclimation periods during 1993. Recoveries of both fluvial F_1AL and lacustrine RR grayling were nearly identical ($P > 0.500$) on the first 1-d trial on 14 August 1993. Cresswell and Williams (1983) witnessed similar results when testing acclimation times of brown trout. They concluded that 1-d in-stream acclimation was "insufficient to confer a significant advantage" when trying to release trout into rivers, and proposed an acclimation period of 14-d.

Results of longer in-stream acclimation were not consistent for lacustrine age-0 grayling. This suggests that those innately inclined to move downstream will do so regardless of pre-release acclimation duration. The 7-d period of acclimation on 9 August 1993 resulted in the lowest percentage of lacustrine grayling moving downstream to the weir, while 1-d of acclimation on 9 September 1993 resulted in the fewest number of grayling moving past the weir.

Behavioral responses of age-0 ME grayling in Deep Creek could be interpreted to be intermediate between the fluvial (Big Hole River) and lacustrine (Red Rock Lake) populations of grayling tested. This would seem consistent with the historic fluvial origin of the ME grayling population, and their resemblance, in electrophoretic analysis (Leary 1990), to grayling from the Big Hole River. However, experimental conditions do not permit such a conclusion. The 1993 ME grayling were incubated and reared at two hatcheries, both different from RR or F_1 Big Hole River grayling. Also, in 1994, ME and F_1 Big Hole grayling were compared under stream conditions and sampling methods which differed from 1993 comparisons between RR and F_1 Big Hole grayling.

Substantial differences in numbers of grayling released into Deep Creek and recovered either at the weir or through electrofishing existed. Although electrofishing effectiveness may have been limited by the small sizes of the age-0 fish, the small numbers recovered in the stream suggest that high mortalities occurred after the fish were released. Effects of predators or various other factors that could affect the survival of fish released in the stream were not addressed because the objective of the study was to compare downstream movement of age-0 grayling. However, the greater persistence of fluvial Arctic grayling, as indicated by electrofishing results, further suggests that they are better adapted to maintaining permanent residence in a stream than lacustrine fish.

Observations on age-0 ME grayling in the Madison River complement results of the field trials, and also indicate that their behavior is consistent with that of an adfluvial lacustrine population. The estimated stream residence of 35-38 d for the age-0 grayling in the Madison River may represent maximum, rather than average or typical, duration of stream residence in 1994. It is possible that many newly emergent young moved down to the reservoir before I first saw them in the river on 25 May, when they were already estimated to be 7-10 d postemergent. Others may have moved down during the 28-d when they were visible in the river. If so, however, they were not effectively surveyed by the drift nets. Age-0 grayling were captured on the first seining attempt in the reservoir on 16 June, when others were still present in the river.

The estimated 35-38 d of stream residence in the Madison River is within the ranges reported for certain other lacustrine populations of age-0 grayling from Montana (Table 13). Postemergent residence times of age-0 grayling differ among adfluvial populations. Wells (1976) found that age-0 grayling in the West Fork of Hyalite Creek moved downstream shortly after their emergence from the gravels. However, some age-0 young of other populations have been reported to remain in the spawning stream for more than 30-d (Kruse 1959; Lund 1974). Also, while investigating an allacustrine (outlet spawning) population of grayling, Deleray (1991) first found age-0 grayling in Deer Lake 40-d after swimup. In the Big Hole River, age-0 grayling have been found in fluvial habitats throughout their first summer of life. At least four juvenile grayling released into Deep Creek in 1993 did overwinter in the creek, all were of Big Hole River origin.

Fluvial macrohabitat preferences of age-0 grayling have been described for other populations. Hubert et al. (1985) and Armstrong (1986), in their reviews of Alaskan data, conclude that postemergent grayling are found in "backwaters, side channels, or in grassy areas of adjacent pools." Nelson (1954) found that age-0 grayling in Red Rock Creek inhabit backwaters and protected areas along the creek 2 to 3 weeks after they had hatched. Reynolds (1989) states that optimum rearing areas have at least 30% of the total area comprised of backwaters. Skaar (1989) and McMichael (1991) found age-0 grayling occupying areas in close proximity to abundant cover in the form of aquatic vegetation in the Big Hole River. Deleray (1991) indicated that age-0 grayling were most frequently observed within 20 cm of overhead cover, however, this figure was proportionally lower than expected and may have resulted from their "avoidance behavior."

Table 13. Stream residence period (ending with the date of appearance at a lake or reservoir) and mean total lengths (mm) at this time of some age-0 Arctic grayling populations.

Population	Residence (d)	Mean	Reference
Deer Lake	40	52	Deleray (1991)
Grebe Lake	36	43	Kruse (1959)
ME	33	60	This study
Elk Lake	26-32	42	Lund (1974)
U Red Rock L.	5	13	Nelson (1954)
Hyalite Res	1-3	-	Wells (1976)

Skaar (1989) and McMichael (1991) found age-0 grayling in total water column depths ranging from 6 to 91 cm with mean water column velocities ranging from 0 to 66 cm/s. McClure and Gould (1991) reported that age-0 grayling in an artificial stream spent most of their time (97%) at depths less than 31 cm. On his observations of age-0 grayling in Deer Creek, Deleray (1991) found that 90% were positioned at focal point depths ranging from 0 to 10 cm above the substrate. Reynolds (1989) used 15 cm/s as the optimal mean column water velocity in his evaluation of the Habitat Suitability Model for fluvial grayling in Alaska, while McClure and Gould (1991) found that age-0 Big Hole River grayling chose mean column water velocities ranging from 0 to 10 cm/s 85% of the time. Deleray (1991) found age-0 grayling using the slowest focal point velocities available, usually less than 10 cm/s.

Although I did not measure specific habitat parameters, it appeared that postemergent grayling in the Madison River used slackwater areas as temporary shelter, similar to those described by the above authors. An interesting similarity between the ME and Deer Lake age-0 grayling populations existed in what Deleray (1991) termed an "avoidance behavior." Like grayling in Deer Creek, when age-0 grayling were disturbed in the backwaters of the Madison River, they would swim away to another area of the backwater instead of seeking overhead refugia. This behavior is contrary to Red Rock Creek age-0 grayling, which Nelson (1954) described as "helpless and made very little effort to hide when disturbed" in similar habitat. Age-0 grayling in the Madison River were consistently found in backwater habitats, many of which appeared to have near zero velocity water, and with the only current source existing in the form of small springs. Grayling were encountered behind numerous mid-channel bar formations and current breaks along the river banks, but were never as numerous as in the backwaters. They were no longer present in such locations starting around the first week in June, while still present in backwater areas. This leads me to believe that such areas are used as temporary habitat while in transit to backwater environments.

Scott (1985) reported that postemergent European grayling fed in waters close to the river bank. These grayling fed at or near the water surface until they reached lengths of 25-28 mm fork length, and then fed on benthic organisms. I also witnessed similar surface feeding by age-0 grayling in backwater habitats in the Madison River. I did not observe a shift to benthic feeding before they disappeared from the river. Scott (1985) noted that the onset of migration to the benthos took place at the age corresponding to that when Kratt and Smith (1979) found agonistic behavior developing in Arctic grayling. The time period discussed in both of these studies ranges from 21-36 d post swimup, which coincides with the first appearance of age-0 grayling in Ennis Reservoir.

Much less is known about habitat requirements when age-0 grayling enter lentic systems. Armstrong (1986) states that "little is known about the habitats selected by young-of-the-year grayling associated with lakes." I did not record quantitative habitat data during reservoir sampling for ME age-0 grayling. It was evident, however, that age-0 ME grayling use shallow water habitats among macrophyte beds in Ennis Reservoir. Age-0 grayling were consistently captured by seining in such habitats until sampling became difficult as macrophytes became dense in late summer. Age-0 grayling were not found in deeper waters without macrophyte growth. The decline of the ME grayling population in 1983, after reservoir drawdown for macrophyte control, coupled with what was learned from the seining activities in Ennis Reservoir, implies that these shallow water habitats are very important rearing areas for age-0 grayling.

I expected to find a significant difference in growth rates between age-0 grayling during their Madison River residence and their Ennis Reservoir residence stages. However, multiple regression did not indicate such a difference, suggesting that growth rates were similar in both environments. It is possible that grayling were already growing at or near their physical maxima in both habitats. In fact, when compared to other age-0 grayling populations in Montana, the age-0 ME grayling grew at a significantly greater ($P < 0.005$) rate (Table 14).

Sporadic reports of adult grayling residing in the Madison River far upstream of Ennis Reservoir during non-spawning seasons continue. These reports appear to fluctuate directly with the status of the Ennis Reservoir grayling population (Byorth and Shepard 1990). If grayling do reside permanently in these upper areas of the Madison River, they would not have been included among fish sampled for this study. However, with the high fishing pressure in the upper Madison, I would expect more consistent reports of grayling being caught, regardless of the status of the reservoir population, if such a fluvial population existed.

Data collected during this study, along with ongoing monitoring efforts of the ME grayling population, appear to indicate that this population is recovering from the effects of the drawdown of Ennis Reservoir that occurred in 1983 (Pat Clancey, MDFWP, pers. comm.). The capture of 35 age-0 grayling at the inlet of Meadow Creek suggests that mature grayling are again spawning in this tributary to Ennis Reservoir. Because this and other lacustrine populations of Arctic grayling have been known to undergo "boom or bust cycles" (Kaya 1990), it is important that the ME

Table 14. Slope and intercept comparisons between observation day-total length relationships from populations of age-0 Arctic grayling in Montana.

Population	Slope	Intercept	Reference
ME	1.24(OD)	20.0	This study
Big Hole River	0.83(OD)**	7.82*	Liknes 1981
Big Hole River	0.88(OD)**	63.1**	Skaar 1988
Big Hole River	0.85(OD)**	61.7**	McMichael 1990
Deer Lake	0.88(OD)**	28.6**	Deleray 1991
U Red Rock Lake	0.82(OD)**	16.1**	Nelson 1954

** Significantly different than ME ($P<0.005$).

* Significantly different than ME ($P<0.01$).

grayling population be monitored closely. Any reservoir activities that threaten the shallow water macrophyte beds could seriously affect at least one year class of grayling. Reduction in a year class would not become evident until at least 2 years later, as they begin to become sexually mature (Byorth and Shepard 1990).

CONCLUSIONS

1. When reared together and then acclimated and tested together in a fluvial environment, age-0 ME grayling displayed significantly greater downstream movement ($P < 0.005$) than those from a known fluvial population (Big Hole River).

2. Only 19 of 824 (2.3%) age-0 grayling collected at the weir in both years were recovered during the first 8-h period of daylight, consistent with the downstream movement exhibited by other grayling populations.

3. Fluvial grayling acclimated for 7-14 d had a consistently lower tendency to move downstream than those acclimated for 1 d, indicating that grayling used for restoration efforts should be acclimated more than 1-d and perhaps 7-d.

4. Age-0 young were observed within the Madison River up to 35-38 d after swimup. This period of stream residence is within the range reported for age-0 young of certain other lacustrine grayling populations in Montana.

5. Age-0 grayling inhabited backwaters while residing in the Madison River and were consistently found in shallow water among macrophyte beds in Ennis Reservoir.

6. Age-0 ME grayling grew at significantly greater rates ($P < 0.005$) than reported for other age-0 grayling in Montana and growth rate was not significantly different between their fluvial and lacustrine habitats.

7. Behavioral responses of age-0 F_1 fluvial grayling originating from parents reared in non-fluvial environments strongly support the hypothesis that positive rheotaxis is a genetic trait in grayling from the Big Hole River.

8. Both behavioral trials and field observations indicate that, at least during their initial 4 months after swimup, the behavior and distribution of ME grayling are more characteristic of adfluvial lacustrine grayling than of fluvial grayling.

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