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Competitive Interactions between Arctic Grayling and Brook Trout in the Big Hole River Drainage, Montana

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Abstract.—We investigated mechanisms through which nonnative brook trout *Salvelinus fontinalis* could negatively influence native Arctic grayling *Thymallus arcticus*. We assessed occupied microhabitats, growth, and condition of Arctic grayling and brook trout in sympatric and allopatric groups in stream enclosures. Microhabitat use by both species was also measured in a natural assemblage. In stream enclosures and the natural assemblage, Arctic grayling and brook trout exhibited similar preferences for pools and runs, but they spatially segregated in microhabitats. Arctic grayling occupied faster focal point and mean column velocities closer to the surface than brook trout. Brook trout occupied slower focal point velocities in proximity to structural cover. Specific growth rates indicated that intraspecific competition operated more strongly than interspecific competition in regulating growth of both species in stream enclosures. In sympatry, Arctic grayling grew faster at a low density with a high density of brook trout. In contrast, Arctic grayling at high densities in the control and a sympatric treatment exhibited slow or negative growth. Similarly, brook trout grew faster in a low-density enclosure in sympatry with a high density of Arctic grayling. We found little evidence that nonnative brook trout negatively affected microhabitat use or growth of native Arctic grayling.

Introduction

Historically in Montana, fluvial Arctic grayling *Thymallus arcticus* occurred in discrete areas throughout the Missouri River drainage above the Great Falls. Currently, the only exclusively fluvial, self-sustaining population of Arctic grayling in Montana exists in the Big Hole River drainage. The reduction in the native range of Arctic grayling has been attributed to climatic change, habitat alteration, overexploitation, and competition with introduced species (Vincent 1962; Kaya 1992).

Competition is interference between organisms or inhibition of one by another through common use of limited resources (Pianka 1976). Crowder (1990) suggested that for competition to occur, two organisms must share a limited resource and "there must be some evidence of mutual negative effects on resource use, growth, or some other measure correlated with fitness." Species evolving sympatrically develop mechanisms that result in resource partitioning, allowing them to coexist (Nilsson 1967). However, introduced species often compete with native species for limited resources, especially species with similar life histories (Moyle et al. 1986; Fausch and White 1986; Fausch 1988). Nonnative species may displace natives from preferred habitats or exploit limited resources more efficiently than natives (Moyle et al. 1986; Hearn 1987).

Arctic grayling densities in the Big Hole River are lowest below its confluence with the Wise River, where rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* numerically predominate (Figure 1). Highest densities of Arctic grayling occur in the upper Big Hole basin near the town of Wisdom, where brook trout *Salvelinus fontinalis* are the predominant species. Brook trout were introduced into the North Fork of the Big Hole River between 1910 and 1930 (Liknes and Gould 1987; Kaya 1992). Thus, potentials for competitive interactions exist in these habitats. Previous studies indicated that adult brook trout prefer low-velocity water close to cover in pools (Butler and Hawthorne 1968; Griffith 1972; Cunjak and Green 1983). Similarly, adult Arctic grayling prefer pools and runs (Vascotto and Morrow 1973; Hughes and Dill 1990). However, the mechanisms and outcomes of interactions between Arctic grayling and brook trout in the Big Hole River have never been studied.

In this study, we assessed potential mechanisms through which brook trout could negatively impact Arctic grayling. We tested the hypothesis that microhabitat use, growth, and condition indices of Arctic grayling would change in the presence of brook trout. Our objectives were to compare microhabitat use and growth of Arctic grayling in allopatry versus sympatry with brook trout at two densities in stream enclosures. To assess bias due to controlled conditions and the use of hatchery-

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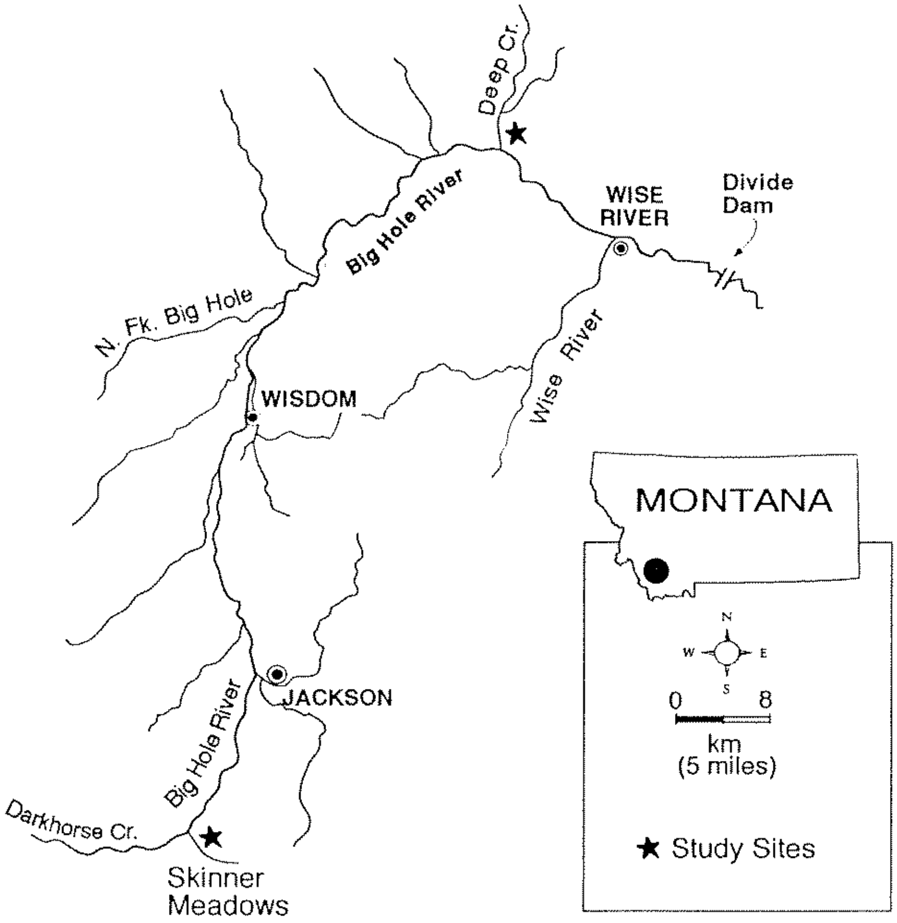

FIGURE 1.—Map of upper Big Hole River basin, Montana, showing sites of competition studies, 1993–1994.

reared fish, we compared microhabitat use of Arctic grayling and brook trout in stream enclosures with those in a wild species assemblage.

Study Areas

We selected two study sites in southwest Montana based on suitable stream size, water clarity, and access (Figure 1). We conducted stream enclosure experiments in Skinner Meadows (Beaverhead County, Montana) during August and September 1993. Skinner Meadows is an alpine meadow (mean elevation, 2,243 m) where Darkhorse and Skinner creeks join to form the Big Hole River. Wetted stream width averages 4.0 m, and the channel gradient is less than 1%. Mean midsummer flow was approximately 0.17 m^3/s, and water temperatures ranged from 3.3°C to 13.3°C during the study period. Riparian vegetation is dominated by sedges *Carex* spp. and sparsely distributed willows *Salix* spp. The fish community included mottled sculpin *Cottus bairdi* and brook trout.

The headwater reach of the Big Hole River at Skinner Meadows was also chosen to prevent any potential contamination of the native wild population of Arctic grayling with hatchery-reared juveniles. The study reach is isolated from occupied reaches by a series of beaver ponds and more than 35 km of river.

We observed microhabitat use of wild fish in Deep Creek during July and August 1994. Deep Creek arises in the Anaconda–Pintlar mountain range in Deer Lodge County, Montana, and flows south 15 km to its confluence with the Big Hole River. The study site was a 2.4-km reach at a mean elevation of 1,768 m. Wetted stream width averages 9.1 m. Mean channel gradient is less than 1%, and midsummer discharge averages 0.28 m^3/s. Water temperatures ranged from 15°C to 22°C dur-

TABLE 1.—Habitat variables for three treatments in a controlled competition study in Skinner Meadows, Montana, 1993. Treatment C is the control, with Arctic grayling in allopatry. Parenthetical values are SDs for mean depth and width.

Treatment	Total volume (m^3)	Pool volume (m^3)	Riffle volume (m^3)	Mean pool quality rating	Area undercut bank (m^2)	Total length (m)	Mean depth (m)	Mean width (m)
A	132.25	119.79	12.45	2	31.96	64.62	0.49 (0.11)	4.02 (0.86)
B	134.17	129.81	4.36	2	22.02	55.47	0.43 (0.18)	4.15 (0.75)
C	130.72	118.69	12.03	1	28.71	64.92	0.46 (0.19)	3.66 (0.31)

ing the study. Riparian vegetation in the study section is dominated by willows and sedges. Brook trout (601 fish/ha) and rainbow trout (470 fish/ha) predominate in Deep Creek. Arctic grayling density was approximately 44 fish/ha. Other resident fishes in Deep Creek are mountain whitefish *Prosopium williamsoni,* white sucker *Catostomus commersoni,* longnose sucker *C. catostomus,* longnose dace *Rhinichthys cataractae,* mottled sculpin, and burbot *Lota lota.* Brown trout were not observed during the study period but have been previously documented in other seasons. Cattle grazing is the major land use in both study areas.

Methods

To assess potential affects of brook trout on Arctic grayling, we measured microhabitat use, growth, and condition factor of Arctic grayling in allopatry versus sympatry with brook trout at two densities in stream enclosures. A habitat survey was conducted in the study reach at Skinner Meadows to delineate three enclosures with similar habitat conditions. At each consecutive habitat unit we identified habitat unit type (Bisson et al. 1982); measured its length, average wetted width, and depth; and recorded areas of undercut banks, large woody debris cover, and backwaters. Dominant and subdominant substrates were classified according to the Wentworth scale (Welch 1948). In pools, we measured maximum depth and rated pool quality according to Platts et al. (1983). We positioned enclosures to provide equal volumes of riffle and pool habitats, pool quality, and cover (Table 1).

Enclosures: biomass and growth.—Enclosures consisted of an upstream barrier constructed of 1.1-cm plastic mesh supported by steel rods driven into the substrate and anchored with gravel and sandbags from bank to bank. Use of a smaller mesh size was precluded by excessive debris accumulation. The downstream barrier contained an outmigrant trap with plastic mesh leads anchored into the banks. Additional mesh barriers were constructed above and below the enclosures to prevent fish from escaping into adjacent enclosures.

After constructing the enclosures in August 1993, we removed resident brook trout that were 10 cm total length and longer. We used a mobile anode bank shocker consisting of a 4,000-W AC generator and a Coffelt Mark XXII rectifying unit. We electrofished each section repeatedly until no fish larger than 10 cm were captured. Fish less than 10 cm were deemed capable of reinvading enclosures and were excluded from biomass calculations. Brook trout were anesthetized in an ethyl aminobenzoate bath and fin clipped, and their total lengths and weights were recorded. These brook trout were released outside of the enclosures.

We assumed that the biomass of brook trout removed from each section represented its carrying capacity. To observe interactions at or above carrying capacity, we introduced high densities of fish into each enclosure and allowed voluntary emigration (Morhardt and Mesick 1988; Lohr 1993). To ensure that carrying capacity was exceeded in each enclosure, Arctic grayling and brook trout were stocked at a combined biomass of approximately 1.5 times the estimated pretreatment brook trout biomass.

Two treatments and a control were chosen for the study. The control was stocked solely with Arctic grayling, treatment A was stocked with 75% brook trout and 25% Arctic grayling, and treatment B was stocked with 75% Arctic grayling and 25% brook trout. Assemblages were assigned to enclosures at random by coin toss.

Juvenile (age-1) Arctic grayling released into enclosures were hatchery-reared F_1 progeny of wild Arctic grayling acquired from the Big Hole River as fertilized eggs. The broodstock was spawned and eggs were reared at the Bozeman Fish

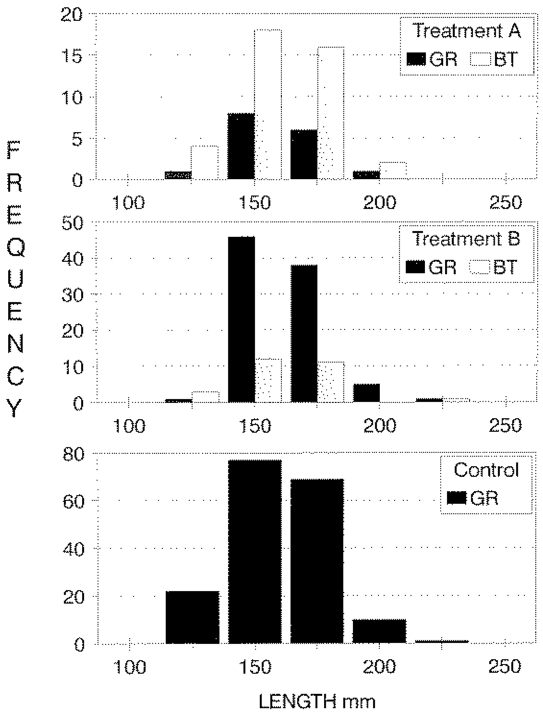

FIGURE 2.—Length-frequency histograms of Arctic grayling (GR) and brook trout (BT) by 25-mm length-groups in three treatments of competition studies at Skinner Meadows, Montana, 1993.

Technology Center (U.S. Fish and Wildlife Service). Arctic grayling were measured, weighed, and tagged with individually numbered visible implant (VI) tags injected into the adipose tissue behind the left eye (Haw et al. 1990). Fish were transported to the study site in an aerated tank and held in a screened cage below the study section for approximately 24 h.

To reduce effects of prior residency, brook trout used in the study were obtained outside the study section (Lohr 1993). Of 67 brook trout, 29 were dip-netted and 38 were captured on hook and line. Brook trout were tagged with individually numbered VI tags, fin clipped to identify them by treatment, and measured for total length and weight.

To eliminate bias due to size advantage, we selected Arctic grayling and brook trout with equal length distributions for each enclosure (Figure 2). To calculate stocking levels, a length-frequency histogram was constructed for available Arctic grayling. We calculated the proportion constituting each 2.5-cm group. We also calculated mean mass of Arctic grayling per length-group. Stocking level was partitioned by species and length-groups according to the formula:

$$N_L = 1.5B(P_L)/W_L,$$

where N_L = number of fish within length-group L to be stocked; B = estimated pretreatment biomass; P_L = proportion of Arctic grayling available within length-group L; and W_L = mean mass of fish within length-group L.

Arctic grayling were measured, weighed, sorted, and released into the control enclosure for treatments A and B on 3 August 1993. On 3 and 4 August 1993, brook trout were released into enclosures for treatments A and B. Arctic grayling and brook trout were allowed to acclimate for 7 d. Out-migrant traps were monitored daily. During this period all fish captured in the out-migrant traps were noted and returned to respective enclosures. Beginning 11 August 1993, fish captured in the out-migrant traps were weighed, measured, identified by tag number, and released outside the enclosures.

At the conclusion of the study (1 September 1993), we removed fish from enclosures by electrofishing until no Arctic grayling or brook trout longer than 10 cm were captured. We conducted an additional electrofishing pass on 2 September. Upon removal, each fish was weighed, measured, and identified by tag number.

We calculated biomass of fish remaining in each enclosure. Individual initial and final Fulton's condition factor ($K = [W/L^3] \times 10{,}000$) and change in condition factors (final K − initial K) were calculated for each fish and averaged by species within treatments (Anderson and Gutreuter 1983). Because Cone (1989) considered K to be a biased measure of length–weight relationships, we also calculated specific growth rates by length (G_l) and weight (G_w) for each fish and averaged them by species and treatment as a second measure of change in condition (Busacker et al. 1990). Specific growth rates were calculated as:

$$G_y = (\log_e Y_2 - \log_e Y_1)/(t_2 - t_1),$$

where Y = length or weight, and t = time. Fish we could not account for at the end of the study, either by removal or emigration, were presumed to have died.

Enclosures: microhabitat use.—To test whether brook trout exclude Arctic grayling from preferred habitats, we compared microhabitats used by Arctic grayling between allopatric and sympatric treatments. Microhabitats were identified by snorkeling each enclosure five times between 13 August and 30 August 1993. Teams snorkeled between 1000 and 1630 hours when daylight ensured the best visibility. To account for potential individual bias, we randomly selected which of three divers snorkeled each enclosure.

Snorkelers entered the lower end of an enclosure and moved upstream. Upon locating a fish, the observer waited 1–2 min to ensure the fish was maintaining its position (i.e., focal point) undisturbed. Fish species and habitat unit type were identified, and fish location was marked with a numbered, colored stone. Focal point elevation (measured as distance of a fish's head above the substrate) was estimated with a half-meter stick, and fish activity was noted (i.e., feeding or resting). The diver relayed data to a recorder on the bank. Divers located 15–20 fish during each snorkeling survey.

Immediately after each snorkel survey, we measured microhabitat variables at each marked location. Measurements included water column (total) depth, mean water column velocity (0.6 depth), focal water velocity, and distance to nearest cover. Water velocities were measured with a Price type AA current meter. Cover, defined as any object that could conceal the fish from a human's overhead view, was differentiated into three categories: depth, turbulence, and structure. We considered depth as cover if water was greater than 0.6 m deep. We defined turbulence as sufficient agitation of the water surface to obscure fish from overhead view. Examples of structural cover included aquatic and overhead vegetation, woody debris, rocks, or undercut banks.

Deep Creek: microhabitat.—To compare microhabitat use between brook trout and Arctic grayling in a natural assemblage, we measured microhabitats used by both species between 14 July and 15 August 1994 with the same methods described above. Snorkelers began at the lower end of the 2.4-km study section and moved upstream. Each of three divers snorkeled for approximately 1 h/survey in succession.

To account for differences in estimated focal point elevation measurements and fish length among divers, we tested each diver with dummy fish. A dummy was planted in the stream, the diver estimated microhabitat variables and length as a real fish, and measurement error was determined. Measurement error in the controlled study averaged 2.5 cm and ranged from 2.5 cm or less for focal point elevations less that 25.0 cm to 1.25–7.5 cm for focal elevations more than 25.0 cm. In Deep Creek, estimated focal point elevation measurements error averaged 3.28 cm and ranged from 0 to 20.3 cm. Measurements were within 1.27 cm of actual focal point elevations on test points below 25 cm and averaged 3.97 cm for elevations above 25 cm. In Deep Creek, where fish lengths were estimated, fish lengths were within 2.5 cm of actual length for 80% of estimates and were never more than 5.0 cm from actual measurements.

Statistical analysis.—A Wilks–Shapiro Rankit plot and Shapiro–Francia statistic were calculated for each variable to determine whether they conformed to a normal distribution (Shapiro and Francia 1972). Because each growth and condition variable was nonnormally distributed, we used nonparametric tests. A Mann–Whitney test was used to compare condition factors and specific growth rates between species in treatments A and B, and to compare variables between treatments A and B for brook trout (Conover and Iman 1981). A Kruskal–Wallis test was used to compare change in condition factors and growth rates among the three treatments for Arctic grayling, and a least-significance-difference test was conducted if significant differences were detected (Snedecor and Cochran 1980).

When microhabitat use between species was compared, some variables were nonnormally distributed, so we used a nonparametric Mann–Whitney test. To compare microhabitat use within species between treatments, we used Kruskal–Wallis test and a least-significant-difference test for focal point elevation comparisons (Snedecor and Cochrane 1980). Total depths, focal point velocities, and mean water column velocities were normally distributed and were analyzed with one-way analysis of variance and pairwise comparisons.

In Deep Creek, we used a chi-square analysis to test for independence between species and habitat unit type. We used Kruskal–Wallace and least significant difference tests to compare microhabitat variables. To compare distances to cover between species, a Kruskal–Wallace test with Tukey's method for pairwise comparisons was used. All statistical analysis was conducted with Statistix 4.0 (Analytical Software 1994). An alpha of 0.05 was used for all tests to determine significance.

Results

Enclosures: Biomass and Growth

By the end of the study period (20 d), total fish biomass returned to within 10% of pretreatment

TABLE 2.—Brook trout biomass removed (carrying capacity), Arctic grayling (GR) and brook trout (BT) planted, and final biomass by treatment in a controlled competition experiment in Skinner Meadows, Montana, 1993. Parenthetical values are the percent of carrying capacity; N is the number of BT or GR planted and recovered by treatment. Treatment C is the allopatric control.

		Planted					Final				
		BT		GR			BT		GR		
Treatment	Carrying capacity (g)	Biomass (g)	N	Biomass (g)	N	Total biomass (g)	Biomass (g)	N	Biomass (g)	N	Total biomass (g)
A	1,977	2,232	40	687	16	2,919 (148%)	2,336	39	697	13	3,033 (153%)
B	4,058	1,431	27	4,163	91	5,594 (138%)	1,506	24	2,932	59	4,438 (109%)
C	5,739			7,925	179	7,925 (138%)			5,473	112	5,473 (95%)

levels in the control and in treatment B (75% Arctic grayling, 25% brook trout; Table 2). Biomass in treatment A (25% Arctic grayling, 75% brook trout) remained near initial experimental levels. Arctic grayling biomass increased slightly in treatment A under lowest intraspecific densities, but decreased 31% in the control and 30% in treatment B. Brook trout biomass increased in both sympatric sections.

Reductions in biomass were assumed to be a result of predation by minks *Mustela vison,* belted kingfishers *Ceryle alcyon,* ospreys *Pandion haliaetus,* and great blue herons *Ardea herodias* that were frequently observed near the enclosures. At the end of the experiment, the fate of 102 (36%) of the Arctic grayling was unknown. Three Arctic grayling were lost from treatment A, 33 from treatment B, and 63 from the high-density control. In contrast, only 3 (4.5%) brook trout were unaccounted for. During the acclimation period, 52 Arctic grayling were caught in the emigration trap in the control treatment (96% on day 1), and 23 were trapped in treatment B (78% on day 1). We observed limited emigration (4 Arctic grayling from the control treatment, 3 brook trout from treatment A) after the acclimation period ended.

Comparisons of specific growth during the experiment indicated that intraspecific density-related effects were greater than interspecific effects. Average change in condition factor of Arctic grayling was not significantly different among enclosures (Table 3). However, at low densities in treatment A, the specific growth rate of Arctic grayling was significantly greater by length and weight than in either treatment B or the control. Specific growth rate of Arctic grayling did not differ between treatment B and the control by length or weight. Specific growth rate by length did not differ between species, although Arctic grayling gained significantly more weight than brook trout in treatment A.

In contrast, in treatment B, in which Arctic grayling predominated, specific growth rate by weight of brook trout was significantly greater than that of Arctic grayling, although there was no significant difference between species in specific growth rate by length. Brook trout also gained significantly more weight, and their condition factor increased significantly more in low densities in treat-

TABLE 3.—Means (SDs) of initial (K_i), final (K_f), and change ($K_f - K_i$) in Fulton's condition factor (K = [weight/length^3] × 10^4) and specifc growth ($G_y = [\log_e Y_2 - \log_e Y_1]/[t_2 - t_1]$, where Y = length or weight and t = time) by length (G_l) and weight (G_w) for Arctic grayling (GR) and brook trout (BT) in a controlled competition experiment in Skinner Meadows, Montana, 1993. Treatment C is the control. Results are reported for significant difference between treatments.

Treatment or comparison	Species	Percent biomass	K_i	K_f	$K_f - K_i$	G_l	G_w
A	BT	75	1.01 (0.09)	0.99 (0.07)	−0.02	0.10 (0.07)	0.24 (0.30)
	GR	25	0.80 (0.05)	0.85 (0.03)	0.05	0.12 (0.08)	0.58 (0.26)
B	BT	25	0.95 (0.07)	1.01 (0.10)	0.05	0.08 (0.14)	0.42 (0.54)
	GR	75	0.78 (0.06)	0.80 (0.05)	0.02	0.06 (0.05)	0.26 (0.30)
C	GR	100	0.79 (0.06)	0.82 (0.06)	0.03	0.08 (0.08)	0.33 (0.26)
Comparison	BT		A > B	A = B	A < B	A = B	A < B
	GR		A = B = C	A = C > B	A = B = C	A > B = C	A > B = C

TABLE 4.—Mean (median in parentheses) values of microhabitat variables measured for brook trout (BT) and Arctic grayling (GR) at Skinner Meadows and Deep Creek study sites in the Big Hole basin, Montana.

Treatment or comparison	Species	N	Focal elevation (m)	Total depth (m)	Focal velocity (m/s)	Column velocity (m/s)	Distance to cover (m)
			Skinner Meadows				
Treatment							
A	BT	42	0.08 (0.08)	0.65 (0.71)	0.10 (0.11)	0.14 (0.12)	0.47 (0.47)
	GR	40	0.13 (0.10)	0.56 (0.55)	0.20 (0.21)	0.23 (0.22)	0.54 (0.53)
B	BT	39	0.10 (0.05)	0.73 (0.70)	0.10 (0.09)	0.12 (0.11)	0.52 (0.48)
	GR	57	0.16 (0.10)	0.54 (0.49)	0.18 (0.16)	0.20 (0.17)	0.62 (0.53)
C	GR	128	0.18 (0.13)	0.55 (0.50)	0.13 (0.16)	0.15 (0.17)	0.60 (0.50)
A + B	BT	81	0.09	0.71	0.11	0.13	0.50
A + B	GR	97	0.15	0.55	0.19	0.22	0.58
Comparison							
A + B	BT versus GR		GR > BT	BT > GR	GR > BT	GR > BT	GR = BT
A versus B versus C	GR		A = B = C	A = B = C	A = B > C	A = B > C	A = B = C
			Deep Creek				
Treatment	BT	93	0.70 (0.08)	0.61 (0.64)	0.18 (0.13)	0.28 (0.23)	0.17 (0.42)
	GR	77	0.11 (0.10)	0.63 (0.64)	0.26 (0.25)	0.37 (0.37)	0.07 (0.26)
Comparison	BT versus GR		GR > BT	GR = BT	GR > BT	GR > BT	GR = BT

ment B than in the higher-density treatment A (Table 3).

Enclosures: Microhabitat Use

In allopatry, hatchery-reared age-1 Arctic grayling used positions with significantly lower focal point and mean column velocities than they did when in sympatry with brook trout in treatments A and B (Table 4). There were no significant differences in focal point or mean column velocities used by Arctic grayling in sympatric treatments A and B. Focal point elevation used by Arctic grayling in the control did not significantly differ from sympatric treatments. There were no significant differences in Arctic grayling usage of total depth or distance to cover between sympatric treatments and the allopatric control.

Arctic grayling generally occupied positions in faster velocities, higher focal point elevations, shallower depths, and greater distance from cover than brook trout in sympatry (Table 4). In both sympatric treatments, Arctic grayling used significantly faster focal and mean column velocities than brook trout. Arctic grayling also used shallower total depths and higher focal elevations than brook trout. In both sympatric treatments, brook trout maintained positions closer to cover than Arctic grayling, but differences were not significant.

Brook trout used similar microhabitats regardless of the density of Arctic grayling (Table 4). There was no significant difference in any measure of stream position, except total depth, between brook trout in treatments A and B. Brook trout were located in deeper areas in treatment B than in treatment A. However, brook trout focal point elevations did not significantly differ between enclosures.

Deep Creek: Microhabitat

We characterized 77 wild Arctic grayling and 93 brook trout microhabitat positions in Deep Creek during 1994 (Table 4). Mean lengths of Arctic grayling (225 mm; range, 152–330 mm) were significantly greater than brook trout (203 mm; range, 102–406 mm; $P = 0.006$; Figure 3). Contingency analysis indicated that Arctic grayling and brook trout were not using significantly different habitat unit types (chi-square = 3.35). Total depths used by Arctic grayling and brook trout did not differ significantly. However, other microhabitat variables differed between species (Table 4). Arctic grayling used higher focal elevations and faster mean column and focal point velocities than brook trout. Although 38% of brook trout positions were associated with structural cover, only 9% of Arctic grayling positions were near structural cover. Arctic grayling primarily relied on depth (55%) and turbulence (36%) for cover.

Discussion

Interspecific competition may result in the decline of a subordinate species by directly depleting a critical resource, interfering with its ability to exploit a resource, or through expenditure of energy in aggressive behavior (Schoener 1974). In

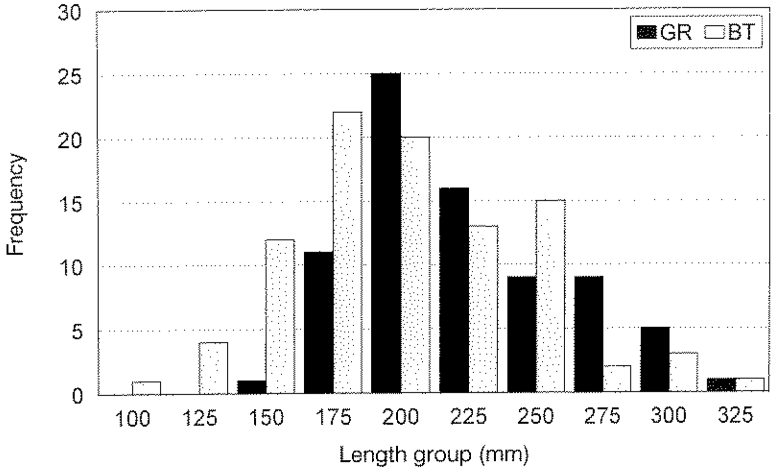

FIGURE 3.—Length-frequency histogram of Arctic grayling (GR) and brook trout (BT) by 25-mm length-groups observed in Deep Creek, Montana, 1994.

this study, we found little evidence to suggest that brook trout interfered with the ability of Arctic grayling to use microhabitats or negatively impacted their growth and condition.

Competition should result in negative effects on resource use, growth, or some other measure associated with fitness (Crowder 1990). If brook trout interfered with the ability of Arctic grayling to efficiently exploit resources, Arctic grayling growth or condition would have been expected to decline with increased brook trout density. In treatment A, where Arctic grayling density was lowest and brook trout density was highest, Arctic grayling had higher specific growth rates, by length and weight, than either the control or treatment B, which had higher Arctic grayling densities. We believe that intraspecific, density-dependent interactions rather than interactions with brook trout regulated growth and microhabitat use of Arctic grayling. Brook trout also grew fastest in low intraspecific densities in sympatry with high densities of Arctic grayling.

We purposely exceeded pretreatment biomass to observe interactions at or above estimated carrying capacity. At high initial densities, Arctic grayling biomass returned to near pretreatment levels, suggesting that we indeed exceeded carrying capacity. Emigration rates were extremely low, but high mortality (presumed to be from predation) occurred in high-density treatments. By exceeding carrying capacity, an environment was created that would induce density-dependent factors. The fact that Arctic grayling biomass decreased most drastically in allopatry supports the contention that intraspecific factors predominated. In treatment A, the low-density treatment, Arctic grayling biomass increased slightly.

Although Arctic grayling (Vascotto and Morrow 1973; Hughes and Dill 1990) and brook trout (Butler and Hawthorne 1968; Griffith 1972; Cunjak and Green 1983) both use pools and runs, our studies suggest that Arctic grayling and brook trout segregate at the microhabitat level. In the controlled study at Skinner Meadows and in Deep Creek, Arctic grayling consistently used higher-velocity focal points, were higher in the water column, and seldom used structural cover (Table 4). In contrast, brook trout used lower velocities than Arctic grayling and were closer to the substrate and structural cover. Apparently, the preferred microhabitats of Arctic grayling and brook trout differ sufficiently to minimize potential competitive interactions.

Removal of the dominant species should induce a shift in resource usage by a subordinate species (Fausch 1984; Hearn 1987). In the allopatric control, Arctic grayling used significantly lower focal point and mean column velocities than they did in sympatry. This was the only indication that brook trout may create some competitive interference for lower-velocity positions. However, depth-related variables did not differ significantly among the allopatric control and sympatric treatments, and Arctic grayling use of depths and velocities did not differ between sympatric treatments with high and low brook trout densities. Moreover, Arctic grayling biomass did not change in sympatry with high densities of brook trout.

The lower focal point and mean column velocities used by Arctic grayling in allopatry may be a result of density-related displacement of subordinate fish into less suitable sites. Vascotto and Morrow (1973) described a strong social hierarchy in an Alaskan stream where behaviorally dominant Arctic grayling occupied and defended focal points in deep water near the thalweg. Subordinate Arctic grayling were distributed in peripheral areas. In our control treatment, with Arctic grayling planted at higher biomass than estimated pretreatment carrying capacity, many more subordinate Arctic grayling may have been excluded from suitable habitats. This could have biased observations of microhabitat use.

Our data did not indicate that extensive competition for microhabitats existed between brook trout and Arctic grayling, nor did measures of fitness indicate that brook trout negatively influenced the ability of Arctic grayling to efficiently exploit resources. However, competition for resources may occur under different conditions, seasons, and life stages.

In the controlled study at Skinner Meadows, we used hatchery-reared Arctic grayling. Hatchery-reared fish are known to exhibit poor poststocking survival and altered behavior (reviewed by White et al. 1995). We observed high mortality of Arctic grayling, presumably due to predation, in high-density treatments. Bachman (1984) and Mesa (1991) documented differences in habitat use and behavior between wild and hatchery-reared fish. Thus, microhabitat use by Arctic grayling in the controlled study may not be representative of preferred habitats of wild Arctic grayling. However, our observations of microhabitat use by wild fish in a natural assemblage at Deep Creek were similar to microhabitat use by hatchery-reared Arctic grayling and wild brook trout at Skinner Meadows (Table 4).

Observations of Arctic grayling behavior indicated that they rapidly acclimated to natural conditions. When hatchery-reared juvenile Arctic grayling (F_1 descendants of wild Big Hole River stock) were introduced into enclosures, they initially exhibited nonterritorial schooling behavior and limited predator avoidance, typical behaviors reported for hatchery-reared fish (White et al. 1995). Within the acclimation period, however, we observed progressively more territorial behavior and predator avoidance and uniform distribution throughout the enclosure. Nearly all (96%) Arctic grayling captured in emigration traps were captured during first days of the acclimation period. Agonistic behaviors, noted anecdotally and reflecting defense of focal points, were similar between Skinner Meadows and Deep Creek. These observations suggest that Arctic grayling used in the study rapidly acclimated to natural conditions and provided useful insights into interactions in the wild.

Competitive interactions between salmonids are known to be condition specific. Cunjak and Green (1986) and DeStaso and Rahel (1994) reported that intensity of competitive behavior in salmonids changed according to water temperatures. The ranges of water temperatures at which we observed microhabitat use (3.3–13°C and 15–22°C) was broad enough to represent typical spring through fall conditions in the Big Hole River basin. However, competitive interactions may occur during winter or under other environmental conditions that we did not study.

Further studies should investigate the role of intraspecific interactions among Arctic grayling, potential for competition with or predation by brook trout at other life stages and seasons, and interactions with rainbow trout and brown trout.

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