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Competitive Interactions of Fluvial Arctic Grayling (*Thymallus arcticus*) and Brook Trout (*Salvelinus fontinalis*) In The Upper Big Hole River, Montana

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ABSTRACT

Fluvial Arctic grayling and eastern brook trout have existed sympatrically in the upper Big Hole River for 60-80 years. Little is known about their interactions or if they compete for limited resources. This study measured emigration, micro-habitat use, and growth rates in allopatry and sympatry in the upper Big Hole River. Limited emigration out of enclosures was greater for both species under high intraspecific densities. We documented evidence of spatial segregation at a micro-habitat level. In sympatry, grayling used positions with higher velocities, closer to the water surface in shallower depths; whereas brook trout positioned themselves in deeper, slower water and closer to substrate and cover. When compared to the allopatric control section, grayling in sympatry used very similar habitats. However, grayling in sympatry used slightly higher focal velocities than in allopatry. In allopatry high intraspecific densities may have forced utilization of less preferred habitats. Intraspecific competition appeared to affect growth and condition factor as both grayling and brook trout had higher specific growth rates (by weight) under low intraspecfic densities and lower specific growth rates under high intraspecific densities.

INTRODUCTION

Historically, fluvial Arctic grayling (Thymallus arcticus) in the lower 48 states were indigenous to northern Michigan and Montana. The Michigan stock became extinct by 1936 (Scott and Crossman 1973). The Montana form was intermittently distributed throughout the Missouri River drainage above Great Falls. Arctic grayling were native to the Big Hole, Red Rock, Beaverhead, Jefferson, Madison, Gallatin, Smith, and Sun rivers (Kaya 1992A). Currently, the only strictly fluvial, self-sustaining population exists in the Big Hole River drainage. The reduction in native range of grayling has been attributed to climatic change, habitat alternation, over-harvest, and competition with introduced species (Vincent 1962).

Competition is defined as interference between organisms or inhibition of one by another with regard to limited resources (Pianka 1976). Crowder (1990) suggested that for competition to exist, 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". Interspecific competition should be greater for those species with similar life histories that did not coevolve (Fausch and White 1986). Species evolving sympatrically develop mechanisms resulting in resource partitioning, allowing them to coexist (Nilsson 1967).

However, introducing exotic species often results in competition with native species for a limited resource (Moyle et al. 1986; Fausch 1988). Exotic species may displace native species from preferred habitats or exploit limited resources more efficiently than natives (Moyle et al. 1986; Hearn 1987).

The current distribution of grayling in the Big Hole River suggests that non-native rainbow trout (Oncorhynchus mykiss), brown trout (Salmo trutta), and brook trout (Salvelinus fontinalis) may displace grayling from key habitats. However, no direct evidence of competitive interactions between native and introduced species exists for the Big Hole River drainage. Grayling densities are lowest in reaches below Wise River which are dominated by rainbow and brown trout. Highest densities of grayling occur in the upper Big Hole basin near Wisdom, where brook trout are the predominant species (Liknes 1981, Shepard and Oswald 1989, Byorth 1993).

Brook trout were planted in the North Fork of the Big Hole River between 1910 and 1930 (reviewed by Kaya 1992A, D. Strodtman, Jackson, MT pers comm., D. Stanchfield, Wise River, pers comm.). Vincent (1962) predicted that 40 years were required for an exotic species to replace fluvial grayling. However, sympatric populations of grayling and brook trout have existed in the Big Hole River for 60-80 years. Grayling numbers have recently declined to low levels; however, causes of the decline are unknown. Drought conditions and severe dewatering of the upper Big Hole River were coincidental with the declines of both grayling and brook trout (Kaya 1992B, Byorth 1993). To date we have limited knowledge of the mechanisms and outcomes of interspecific interactions of grayling and brook trout in the Big Hole River.

It appears that both species prefer pool habitats; however, relative position and velocities within these habitats is not clear. Adult brook trout appear to prefer low velocity positions in pools close to cover (Butler and Hawthorn 1968; Griffith 1972; Cunjak and Greene 1983). Arctic grayling habitat in the Big Hole River is typically slow runs and pools often associated with backwater areas (Skaar 1989). Hughes and Dill (1990) found grayling in Alaska position themselves in the center of the current in the deepest part of pools.

Research indicates there may be differences in habitat usage and food selection between grayling and brook trout in the upper Big Hole River. Skaar (1989) documented spatial segregation between juvenile and adult grayling, and brook trout. Brook trout had a tendency to occupy faster water close to cover and were less abundant in typical grayling habitat. McMichael (1990) found that juvenile and adult grayling showed preference for surface-borne organisms while brook trout selected subsurface drift organisms during summer months in the Big Hole River. Streu (1990) and McMichael (1990) documented limited predation on age 0 grayling by brook trout. However, Nelson(1954) found predation on grayling fry by adult brook trout in Red Rock Creek, Montana.

This study was designed to investigate potential competitive interactions of grayling and brook trout at a micro-habitat level and test the hypothesis that brook trout interfere with resource exploitation by grayling. Specific objectives include:

1) Compare emigration rates between enclosures containing grayling in allopatry and in sympatry with brook trout,

2) Compare individual growth rates and condition factors of grayling and brook trout between allopatric and sympatric enclosures, and

3) Document and compare micro-habitat usage of grayling in allopatry and in sympatry with brook trout.

STUDY AREA

The study site was located at the headwaters of the Big Hole River in Skinner Meadows (Figure 1). We chose the study site based on stream size, density of brook trout, relative isolation from the wild grayling population, and accessibility. Skinner Meadows is an alpine meadow located at approximately 2243 m at the confluence of Darkhorse Creek and Skinner Creek, a small stream draining Skinner Lake and a series of bogs. Riparian vegetation is dominated by sedges (*Carex* spp.) and few willows (*Salix* ssp). Aquatic vegetation is primarily composed of filamentous algae, pondweeds (*Potamogeton* spp.), and peat (*Sphagnum* spp). Primary land uses include cattle grazing and recreation. Resident fish species include mottled sculpins (*Cottus bairdi*), and brook trout. Potential predators observed in the vicinity of the study area include belted kingfishers (*Ceryle alcyon*), osprey (*Pandion halietus*), great blue heron (*Ardea herodias*), and mink (*Mustela vison*).

METHODS

Habitat

To test the hypothesis that brook trout negatively influence grayling, we measured micro-habitat utilization, growth, condition factor and emigration rates of grayling in allopatry and of grayling and brook trout at two levels of sympatry. A habitat survey was conducted in the study reach to ensure that each of the three enclosures contained similar habitat conditions. At each consecutive habitat unit we identified habitat unit type (Bisson et al. 1982), and measured its length, average wetted width, average depth, dominant and subdominant substrate, riparian vegetation type, bank stability, area of undercut bank, area of large woody debris cover within the unit, and percentage of vegetation covering the substrate. Dominant and subdominant substrate were classified using the Wentworth scale (Welch 1948, Appendix 1). Riparian type was classified as soil-rock, grasses, sedges, shrubs, or trees. Bank stability was classified stable if there was no evidence of recent erosion and unstable if there was evidence of erosion. In pools, maximum depth was measured and pool quality was rated according to Platts et al. (1983) (Appendix 2). Area of pocket pools and backwater were also measured.

We calculated the total volume of each habitat unit and combined habitat units for enclosures. We chose reaches for enclosures to provide equivalent riffle, pool, and total volumes, pool quality, and area of cover. Enclosures consisted of an upstream barrier constructed of 1.1 cm plastic mesh supported by rebar driven into the substrate and anchored with gravel and sandbags from bank to bank. To compare emigration rates between enclosures, the downstream barrier contained an out-migrant trap with plastic mesh leads anchored into the banks. Additional barriers were constructed above and below the enclosures to prevent escapement.

A Taylor Thermometer recorded daily maximum and minimum water temperatures. Discharge was monitored at a staff gage and flows were measured occasionally at a transect to develop a rating curve for the gage.

Fish Assemblages, Biomass and Condition

After constructing the enclosures, multiple pass electrofishing was used to remove resident brook trout. We used a mobile anode bank shocker consisting of a 4,000 watt AC generator and a Coffelt Mark XXII rectifying unit to convert output current to DC. Passes were repeated until no fish larger than 10 cm were captured. Fish under 10 cm were deemed able to reinvade enclosures and thus were excluded from biomass calculations. All brook trout removed were anesthetized in an Ethyl 4-aminobenzoate bath, fin clipped, and their total length to the nearest 0.1 inch and weight to the nearest 1.0 grams recorded. Lengths were converted to metric units. The total biomass removed (excluding fish < 10 cm) was calculated for each enclosure. Brook trout were then released outside the enclosures.

To observe interactions at potential short term carrying capacity, we introduced high fish densities into each enclosed stream section and allowed emigration (Morhardt and Mesick 1988; Lohr 1993). We assumed that the initial biomass of brook trout removed from each section represented its carrying capacity. To ensure that we exceded carrying capacity, grayling and brook trout were planted at approximately 1.5 times the resident biomass.

Three fish assemblages were chosen for the study: a control section was planted with only grayling, a section with 75% grayling and 25% brook trout (by biomass), and a third enclosure with 75% brook trout and 25% grayling (Figure 1). Assemblages were assigned to enclosures at random by coin toss. The upstream section (Section 3) was designated the control (100% grayling), Section 2 with 75% grayling/25% brook trout, and Section 1 - the furthest downstream - was designated 25% grayling/75% brook trout.

To eliminate bias due to size advantage, we attempted to select grayling and brook trout of equal length distributions for the enclosures (Appendix 3). A length frequency distribution was constructed for the lot of subject grayling. We calculated the proportion of the lot comprised by each 2.5 cm group (approximately 1.0 inch) and mean mass per 2.5 cm group. The biomass per section was multiplied by 1.5 and partitioned by species and 2.5 cm groups according to the length frequency distribution (i.e. fish 17.5 to 20.0 cm (7.0 - 7.9 inches) comprised 49% of available grayling: (removed biomass x 1.5 x 0.49)/mean mass of 2.5 cm group = number of fish in length group planted in section) (Appendix 3).

Juvenile age 1 grayling planted in the enclosures were acquired from the Big Hole brood stock raised at the U.S. Fish

Technology Center in Bozeman, Montana. The grayling were initially tagged on 15 July with individually numbered visible implant tags injected into the adipose tissue behind the left eye. Fish were transported in a hatchery truck on 2 August and placed in a live car in Skinner Meadows below the study section. On 3 August individual tagged grayling were measured (inch), weighed (g), sorted, and planted into the 3 sections.

In order to account for effects of prior residency (Lohr 1993) all brook trout planted in the enclosures were obtained outside the study section. Of the 67 brook trout used, 29 were captured in Skinner Creek. These fish were captured by using handnets to drive the fish downstream into a live car fixed in the creek from bank to bank. The additional 38 brook trout were captured by hook and line 1-2 miles below the study section and transported in a live car by vehicle to the study section. Brook trout were held in a live car just below the study section and were tagged with individually numbered visible implant tags, fin clipped, and total length (cm) and weight (g) was recorded. On 3 and 4 August brook trout were introduced into sections 1 and 2.

Grayling and brook trout were allowed to acclimate for 7 days, from 4 to 10 August. During this period all fish captured in the out-migrant traps were returned to the study section. Beginning on 11 August, fish captured in the out-migrant trap were weighed, measured, identified by tag number, and deducted from enclosure biomass. Brook trout were released outside the enclosures and grayling were held between enclosures.

At the conclusion of the study (1 September), fish were removed from enclosures by electrofishing. We continued electrofishing until no additional grayling were captured and no brook trout > 10 cm were captured. We conducted an additional electrofishing pass on 2 September to ensure that all remaining fish were captured. Upon removal each fish was weighed (g), measured (cm) and identified by individual tag numbers.

Final biomass (g) was calculated for each section. Initial and final Fulton condition factor (K) (Anderson and Gutreuter 1983) was calculated and change (final K - initial K) in condition factor for species and section was determined. Specific growth rate by length (SPG) and weight (SPGW) was calculated for species and by section (Busacker et al. 1990). We compared initial and final total fish numbers to estimate loss due to mortality. Tag loss was also computed by species.

We used a nonparametric, rank-sum, two-sample (Mann-Whitney) analysis to test for differences in condition factor and specific growth between species in Section 1 and 2 and for differences between Section 1 and 2 for brook trout. A nonparametric, Kruskal-Wallis one-way ANOVA was used to compare condition factor and growth rates between sections for grayling and a Least Significance Difference (LSD) test was used if significant differences were detected.

Microhabitat Utilization

To test the hypothesis that brook trout exclude grayling from preferred habitats we compared microhabitat usages in allopatry and sympatry. Microhabitat sites were identified by snorkeling. Each section was snorkeled 5 times between 13 August and 30 August. Snorkeling occurred between 10:00 and 16:30 when lighting ensured the best visibility. To account for individual diver bias we randomly selected which of 3 divers snorkeled each section.

To measure fish positions the diver moved slowly upstream from side to side inspecting cover areas large enough to conceal fish. Upon locating a fish the diver waited 1 to 2 min to ensure the fish was maintaining its position undisturbed. Species was identified and fish location was marked with a numbered, colored stone. Focal point elevation (distance above the substrate) was estimated with a meter stick and fish activity was noted (e.g. feeding activities, aggressive behavior, proximity to other fish). The diver then relayed data to a recorder on the bank. During each snorkeling event, 15-20 fish were located in approximately the same ratio as the species composition in the section. To account for differences in focal point elevation measurements between divers, each diver was tested with dummy fish and measurement error was determined. Measurement error ranged from $\leq$ 2.5 cm for focal elevations < 25.0 cm and 1.25 to 7.5 cm for focal elevations > 25.0 cm.

Immediately following the completion of each snorkel event we measured habitat parameters at each fish location. Measurements included; water column (total) depth, mean water column velocity (0.6 depth), focal point water velocity, and distance to the nearest cover. Water velocities were measured using a Price Type

AA current meter. Cover was defined as any object that could conceal the fish from overhead view including water column depth or turbulence. We measured percent of substrate composition and vegetative cover within a radius of 0.5 m of the focal point. We also analyzed fish position using relative depth (focal elevation/total depth).

Data was entered into dBASE IV files (Borland International Inc. 1992), Lotus 1-2-3 spreadsheets (Lotus Development Corp. 1992) and analyzed statistically with STATISTIX 4.0 (Analytical Software 1992). To compare microhabitat use between species for sections 1 and 2 we used a nonparametric, rank-sum, two-sample (Mann-Whitney) test. To compare microhabitat use for the same species between sections we used Kruskal-Wallis one-way nonparametric ANOVA, and a LSD test if there were significant differences. Level of significance was held at P=0.05 for all tests.

RESULTS

Habitat

Upon completion of the initial habitat survey we established 3 sections based on total volume, pool and riffle volume, undercut bank area, total section length, and average width and depth (Table 1). To establish similar enclosures we sacrificed total riffle volume for similar total volume and pool volume. We perceived total volume for each enclosure should be as similar as possible and pool habitats were more important to these species. Thus, Section 2 has a smaller area of riffle habitat and less undercut bank area. Pools in Section 3 had a higher average quality rating (1) than Section 1 or 2 which had average ratings of 2 (Appendix 2). Substrate was dominated by gravel in all sections. The riparian area was dominated by sedges and banks were stable for all sections. Limited LWD was available for cover and algae cover averaged 0-25% for all sections. Temperature ranged from 3.9° to 13.3° C. Discharge ranged from 0.166 to 0.168 cms during the study period.

Fish Assemblages, Biomass and Condition

After introduction into the enclosures, grayling behaved as if they were still in a hatchery raceway. Although we planted fish throughout the sections, grayling quickly gathered at the downstream barrier. Initially, grayling exhibited no fright response when approached from the bank. In contrast, brook trout immediately dispersed and fled to cover when disturbed. Grayling became increasingly wary and dispersed as the study progressed, but

Table 1. Habitat summary for sections 1-3 in Skinner Meadows, August 1993.

SECTION	TOTAL VOL. (FT^3)	POOL VOL. (FT^3)	LGR VOL. (FT^3)	UNDER CUT AREA (FT^2)	TOTAL LENGTH (FT)	AVE WIDTH (FT)	AVE DEPTH (FT)
LOWER SEC 1 UNIT 3-7	4673	4233	440	344	212	13.2	1.6
MIDDLE SEC 2 UNIT 9-13	4741	4587	154	237	182	13.6	1.4
UPPER SEC 3 UNITS 16-21	4619	4194	425	309	213	12.0	1.5

still did not seek cover as readily as brook trout when disturbed. By the end of acclimation, grayling were still observed in loose aggregations, but were uniformly distributed throughout the sections.

These observations were reflected in emigration traps. On 4 August, the first day of the acclimation period, we captured approximately 50 grayling in the trap of Section 3, 15-20 grayling in Section 2, and none in Section 1. For the remainder of the acclimation period, only 7 more grayling were captured: all in the traps of Sections 2 and 3 where grayling densities were highest. No brook trout were captured in traps during the acclimation period.

We observed very little emigration from the study sections after the acclimation period. Four grayling were captured emigrating from Section 3, all within the first week after acclimation. No grayling were captured from Section 1 or 2. Three brook trout were captured emigrating from Section 1 on 22 August. Apparently, emigration was due to intraspecific (density dependent) rather than interspecific interactions.

We introduced 1.38-1.48 times the initial removed brook trout biomass (Table 2). Final total biomass was 1.53 times greater than initial planted biomass in Section 1, returned to approximately the same level in Section 2, and was 5% less than initial biomass in Section 3. Brook trout biomass increased over the period in both Section 1 and 2. Grayling biomass increased only in Section 1 and decreased in Section 2 and 3 (the higher density sections).

Table 2. Summary for removed, planted and final biomass by section for fish >10 cm in Skinner Meadows, Summer 1993.

SECT	REMOVED BIOMASS (g)	PLANTED EBT BIOMASS (g) %TOTAL	PLANTED GR BIOMASS (g) %TOTAL	TOTAL PLANTED BIOMASS (g)	FINAL EBT BIOMASS (g) %TOTAL	FINAL GR BIOMASS (g) %TOTAL	FINAL TOTAL BIOMASS (g)
SECT 1	1977	2232 76.5%	687 23.5%	2919 1.48x REMOVED	2336 77%	697 23%	3033 1.53X REMOVED
SECT 2	4058	1431 25.6%	4163 74.4%	5594 1.38x REMOVED	1506 33.9%	2932 66.1%	4438 1.09X REMOVED
SECT 3	5739	-	7925 100%	7925 1.38x REMOVED	-	5473	5473 0.95X REMOVED

Mortality substantially affected final biomass (Table 3). Upon final removal from the enclosures we assumed that all introduced fish were captured and missing fish were mortalities. Grayling mortality rate was higher than that of brook trout.

Approximately 36% (n=102) of the grayling introduced could not be accounted for at the end of the sampling period. In contrast, only 4.5% (n=3) of the brook trout introduced were not accounted for at the end of the sampling period. Sections 2 and 3, with higher densities of grayling, recorded a greater loss in biomass than Section 1 which was dominated by brook trout (Table 3). In contrast to mortality rates, grayling lost fewer tags than brook trout. Of 184 grayling recaptured at the end of the study only 3 (1.6%) lost tags. Twenty-seven (42%) of the 64 brook trout recaptured had lost tags.

Table 3. Total introduced and final number of grayling and brook trout and percent mortality by section in Skinner Meadows 1993.

	SECTION 1	SECTION 2	SECTION 3	TOTAL
PLANTED EBT	40	27	0	67
NO. EBT MORTALITY (%)	0 (0)	3 (11)	-	3 (4.5)
PLANTED GRAYLING	16	91	179	286
NO. GRAYLING MORTALITY (%)	3 (18.8)	32 (35.2)	67 (37.4)	102 (35.7)

Growth rates during the study period also reflected intraspecific effects. In Section 1, where brook trout dominated species composition, grayling condition factor increased significantly more (P=0.002) than brook trout, which decreased in condition factor (Table 4). Specific growth by length did not differ between species, although grayling gained significantly more weight (P=0.0002) than brook trout.

In contrast, in Section 2 where grayling dominated, brook trout had a significantly greater increase in condition factor than grayling (P=0.02). Again there was no significant difference in specific growth by length, but specific growth of brook trout by weight increased significantly more than for grayling (P=0.003).

Average change in condition factor of grayling was not significantly different between sections. While initial condition factors did not vary between sections, mean final condition factors for Section 1 and 3 were significantly higher than Section 2 (P=0.002). However, under low densities in Section 1, specific growth of grayling was significantly greater by length (P=0.006) and weight (P=0.01) than in either Section 2 or 3.

Micro-Habitat Utilization

Qualitatively, we observed that grayling and brook trout selected different habitats. Although often in close proximity, brook trout generally positioned themselves closer to the substrate and to cover. No aggressive interactions were observed directed at grayling by brook trout. However, grayling were very aggressive toward other grayling and brook trout. Grayling were aggressive and exhibited agonistic behavior during feeding. On one occasion a smaller grayling was observed as a dominant aggressor over larger grayling and larger brook trout.

Table 4. Initial, final, and change in Condition factor, SPG and SPGW summary for grayling and brook trout by sections. A Mann-Whitney U test was used to identify significant differences (P=0.05) for and between grayling and brook trout in sections 1 and 2. A Kruskal-Wallis ANOVA was used to identify differences for grayling between sections 1, 2 and 3.

SECTION	INITIAL K	FINAL K	DELTA K	SPG	SPGW
1 EBT 75% GR 25%	1.01y 0.80	0.99 0.85z	-0.02 0.05*	0.10 0.12	0.24 0.58*z
2 EBT 25% GR 75%	0.95 0.78	1.01 0.80	0.05*y 0.02	0.08 0.06	0.42*y 0.26
3 GR 100%	0.79	0.82z	0.02	0.08	0.33

* Significant difference between grayling and brook trout in the same section.
y Significant difference between brook trout for sections 1 and 2
z Significant difference between grayling for sections 1, 2 and 3.

In sympatry we found limited use of riffles by both species. However, grayling used riffles more (10% of observations) than brook trout (1% of the observations) (Table 5). Within pools grayling occupied positions of higher velocities and focal elevations in shallower water and further from cover than brook trout. In both sections 1 and 2 grayling had significantly higher focal (P=0.00) and mean column velocities (P= 0.00) than brook trout (Figures 2A and B). Grayling also used shallower areas (Sec. 1, P=0.05; Sec. 2, P=0.00) and higher focal elevations (Sec. 1, P=0.02; Sec. 2 P=0.03) than brook trout. Relative depth was also higher (Sec. 1 and 2, P=0.00) for grayling than brook trout. In both sections, brook trout maintained positions closer to cover than grayling, although not statistically significant (Sec. 1, P=0.09; Sec. 2, P=0.19). Our observations indicate that grayling did not use cover and the lack of significance is probably may be due to measuring distance to cover rather than actual cover usage.

Brook trout used microhabitats irregardless of the density of grayling (Figure 3). There was no difference in measures of stream position between Section 1 and 2 except for total depth. Brook trout were located in deeper areas (P=0.04) in Section 2 than in 1. However, focal elevation and relative depth did not significantly differ. Both grayling and brook trout maintained positions closer to cover in Section 1 than in 2; however, this may be due to less undercut bank cover available in Section 2 and was not statistically significant (Table 3).

In allopatry, grayling utilized riffles more than in sympatry. In Section 3, grayling utilized positions with significantly lower focal and mean column velocities than in Section 1 or 2 (P=0.00 for both)(Figure 4). Focal elevation and relative depth were higher in Section 3 than in Section 2 and 1 but not significantly. There were no significant differences for total depth and distance to cover between sympatry and allopatry.

Table 4. Micro-habitat measurements for grayling and brook trout by section. A Mann-Whitney U test was used to identify significant differences (P=0.05) for and between grayling and brook trout in sections 1 and 2. A Kruskal-Wallis ANOVA was used to identify differences for grayling between sections 1, 2 and 3.

SECTION	RIFFLE OBSER NO. (%)	POOLS OBSER NO. (%)	FOCAL DEPTH FT	FOCAL VELOC FT/S	TDEPTH FT	TOTAL VELOC FT/S	RELAT DEPTH FT	DIST COVR FT
1 EBT 75% GR 25%	1(2) 4(10)	46(98) 36(90)	0.26 0.44*	0.33 0.65*	2.13* 1.84	0.45 0.76*	0.13 0.23*	1.26 1.72
2 EBT 25% GR 75%	0(0) 6(11)	44(100) 50(89)	0.33 0.51*	0.34 0.59*	2.41*y 1.76	0.35 0.66*	0.14 0.27*	1.66 2.02
3 GR 100%	35(25)	105(75)	0.59	0.43z	1.79	0.50z	0.30	1.77

* Significant difference between grayling and brook trout in the same section.
y Significant difference between brook trout in sections 1 and 2.
z Significant difference between grayling for sections 1,2 and 3.

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 this study, we found little evidence to suggest that brook trout interfered with the ability of grayling to utilize preferred positions. In sympatry, grayling used positions of higher velocity, closer to the surface, and in shallower depths than brook trout. Brook trout, in contrast, positioned themselves in deeper, slower water and were more substrate and cover oriented. Apparently, the preferred habitats of grayling and brook trout differ enough to minimize the affects of shared resources.

Removal of the dominant species should induce a shift in resource usage by a subordinant species (Fausch 1984; Hearn 1987). In allopatry grayling utilized significantly lower focal and mean column velocities than in sympatry. This may indicate some competitive interference by brook trout for lower velocity positions. However, depth related parameters such as focal elevation, total depth, and relative depth did not differ significantly between the control and sympatric sections. Differing velocities may be an artifact of channel morphometry. Grayling utilization of depths and velocities did not differ between the two levels of brook trout densities.

In allopatry, grayling used a greater diversity of available habitats than in sympatry. Grayling were distributed in riffles, backwater areas, and higher in the water column in the control section. Similar positions were not used as frequently by grayling or brook trout in either of the sympatric sections. With high grayling densities, saturation of preferred habitats may have resulted in forced utilization of less preferred habitats. Intraspecific competition in Section 3 may have resulted in greater diversity in usage of habitat types.

Condition factor also indicates intraspecific competition may have been more important than interspecific competition. Brook trout in Section 1 lost condition under high intraspecific densities; whereas, grayling gained condition under low intraspecific densities. Grayling in Section 1 also had higher specific growth rates, by length and weight, than sections with higher grayling densities. We observed similar results in Section 2 where high densities of grayling resulted in lower weight gain and lesser increase in condition for grayling, while low densities of brook trout resulted in higher specific growth by weight and improved condition for brook trout. Grayling in higher densities in Section 2 and 3 had very similar growth parameters in spite of the absence of brook trout in the control.

For salmonids, density is partially regulated by limited food and space and competition for these resources may result in the displacement of fish into less suitable habitats or emigration (Chapman 1966, McFadden 1969, Bachman 1984). In our study, grayling in allopatry used a broader range of habitats, perhaps indicating intraspecific competition due to saturation of preferred habitats. If dominance hierarchies and efficient foraging sites limit grayling under high densities, we would have expected emigration to occur. Interspecific competition did not appear to cause emigration from sympatric enclosures after acclimation. Four grayling were captured emigrating from the control section with highest densities of grayling. Similarly, three brook trout were captured emigrating from the section with the highest densities of brook trout. Although inconclusive, the emigration would indicate intraspecific more so than interspecific interactions.

Mortality of grayling, assumably due to predation, was high in Section 2 and 3. Predation may have regulated densities and assumed the function of emigration. This contention is supported by the apparent density dependence of predation rates and the return of biomass to near pre-experiment levels in those sections.

Our results indicate spatial segregation occurs between juvenile grayling and adult brook. Skaar (1989) also found distinct differences in habitat usage for age 1+ grayling and brook trout. In his study, brook trout used faster water closer to cover, while grayling occupied slower runs and pools often associated with backwaters. Our results differ: we found brook trout use deeper water with slower velocities than grayling. Our results concur with regard to brook trouts' affinity for cover. However, our techniques of marking microhabitat sites differed. Future studies should compare preferred positions of grayling and brook trout in wild, resident, sympatric populations in the upper Big Hole River.

McMichael (1990) concluded grayling preferred surface food items while brook trout preferred subsurface items. We found grayling positioned themselves higher in the water column than brook trout and were very aggressive surface feeders. Brook trout were not as aggressive surface feeders and positioned themselves closer to the substrate and to cover. Our observations support McMichael's conclusions that there appears to be limited direct competition for food during the summer months.

One objective of the Fluvial Arctic Grayling Recovery Program is to expand the distribution of grayling throughout their native range. Many of the streams identified by Kaya (1992B) for reintroduction were disqualified because of presence of exotic species including brook trout. Our data does not indicate extensive competition for food and space between brook trout and grayling. However, competition for resources may occur under different conditions, seasons, and life stages. Our study explored only one life phase and season. Results may be biased by using hatchery-reared grayling, although their change in behavior and increased fright response overtime suggested otherwise. Effects of recent drought and critical thermal regimes on competitive interactions are unknown.

Other possible interspecific interactions, such as predation on grayling fry by brook trout may affect wild populations. Predation by brook trout on young grayling has been documented in the Red Rock River (Nelson 1954). Although Streu (1990) and McMichael (1990) found limited predation of grayling fry by brook trout in the upper Big Hole River, their studies were conducted during summer months when young of the year grayling were not as vulnerable as newly emerged fry. Future studies should address predation of newly emerged fry.

Our findings have additional implications for potential reintroductions. Mortality was much higher for grayling (36%) than brook trout (4.5%) for the first 30 days after introduction. This may be due to the effects of hatchery learned behaviors. During the acclimation period, grayling congregated and did not seek cover when disturbed increasing vulnerability to predation. As acclimation proceeded, grayling became more wary and dispersed. Wild brook trout, in contrast, immediately sought cover and were less visible when disturbed. In planning future grayling introductions, managers should be aware of potentially high mortality the first month after introduction. Grayling should be acclimated within the stream for up to a week prior to release. Managers should monitor introduced populations to estimate mortality so that future introduction plans can incorporate a mortality factor.

RECOMMENDATIONS

1) Observations and measurements of micro-habitat use for grayling and brook trout in the Upper Big Hole River where sympatric populations now coexist.

2) Compare observations and measurements of micro-habitat use for grayling, brook trout and other native and exotic species in other drainages.

3) Study predation of grayling fry by brook trout in the upper Big Hole.

4) Possible competition between grayling and brook trout during other life-stages and seasons.

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Figure 1. Skinner Meadows study site with enclosure sections, out-migrant traps, barriers, pools, riffles, and species composition.

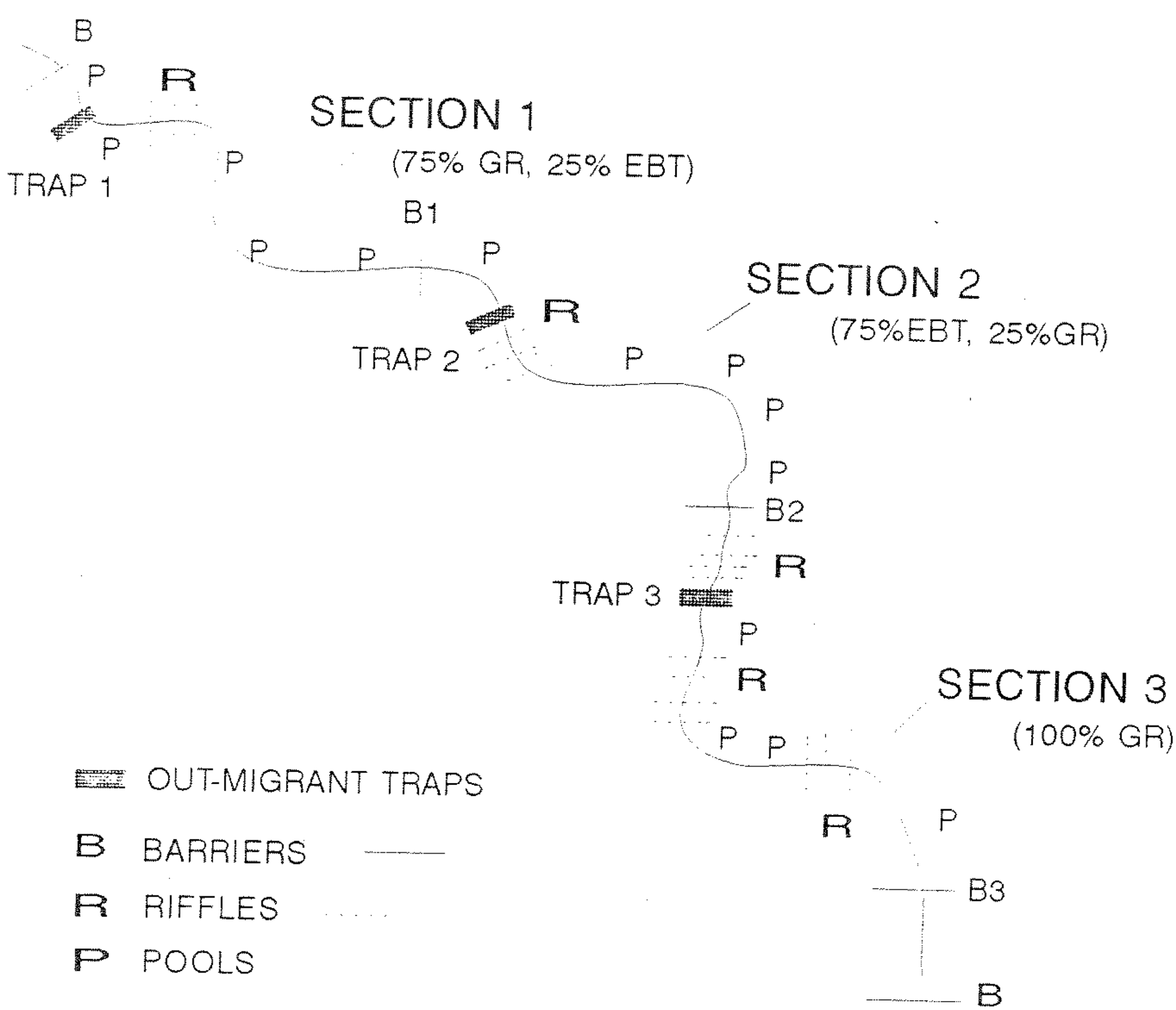
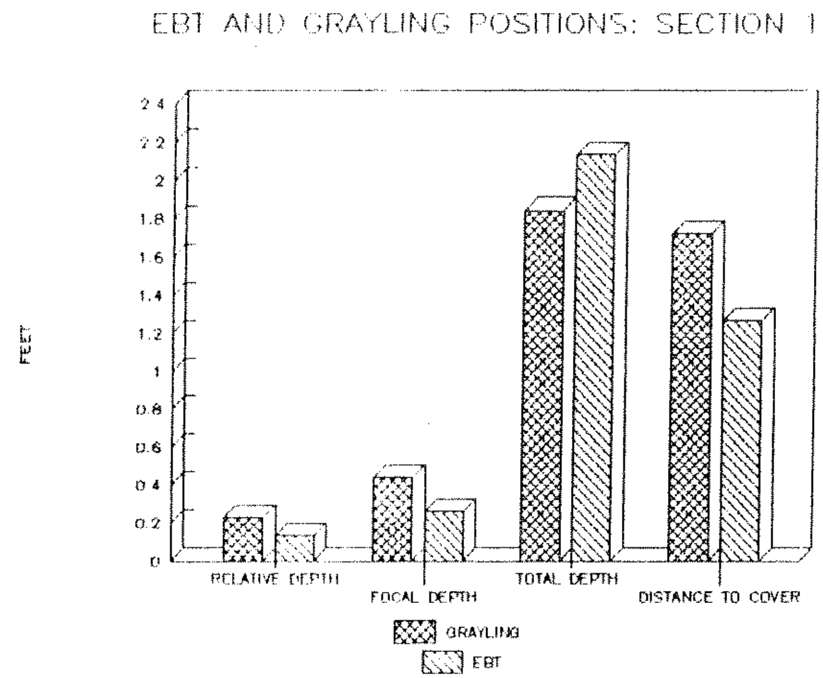


Figure 2A. Micro-habitat positions, and velocities of grayling and brook trout in Section 1, Skinner Meadows, 1993.



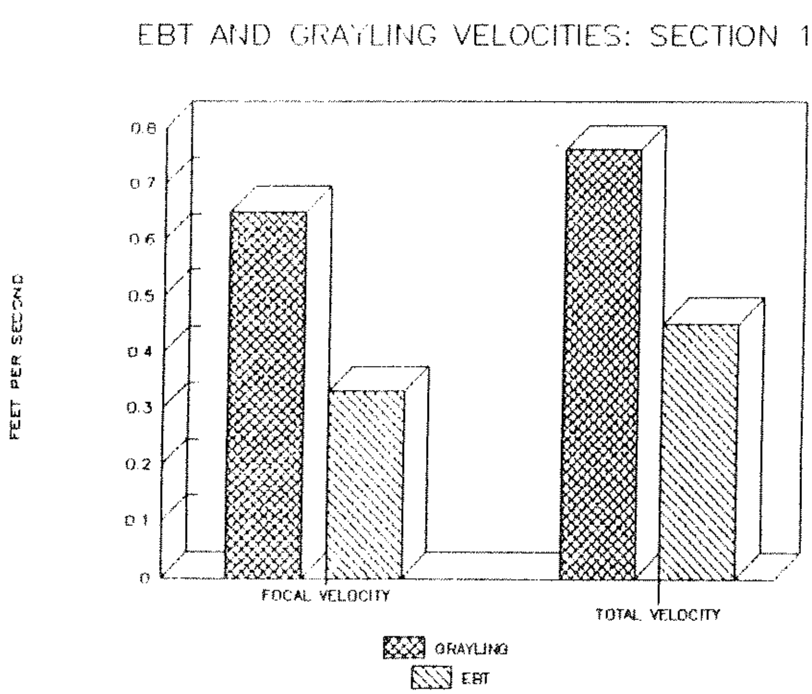
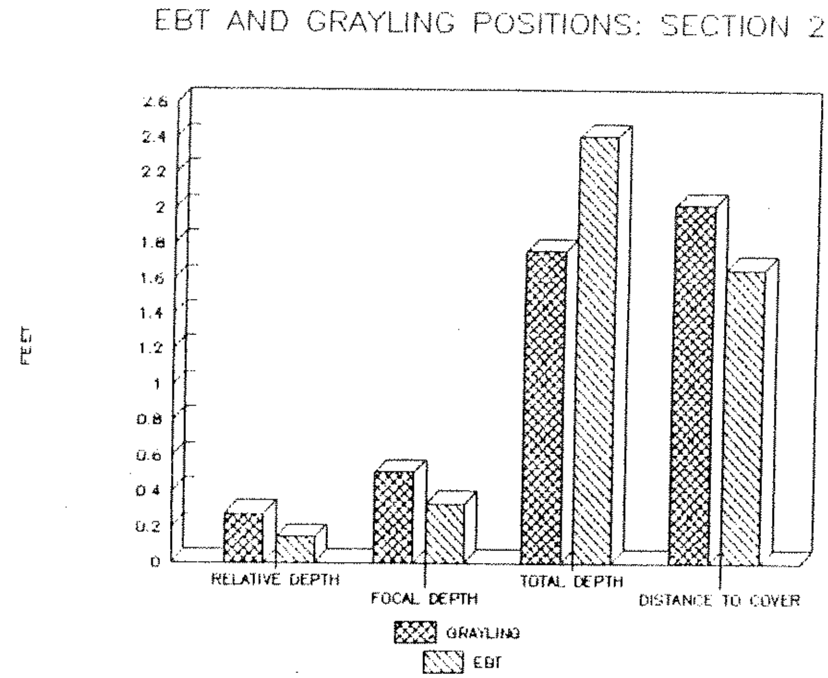


Figure 2B. Micro-habitat positions, and velocities of grayling and brook trout in Section 2, Skinner Meadows, 1993.



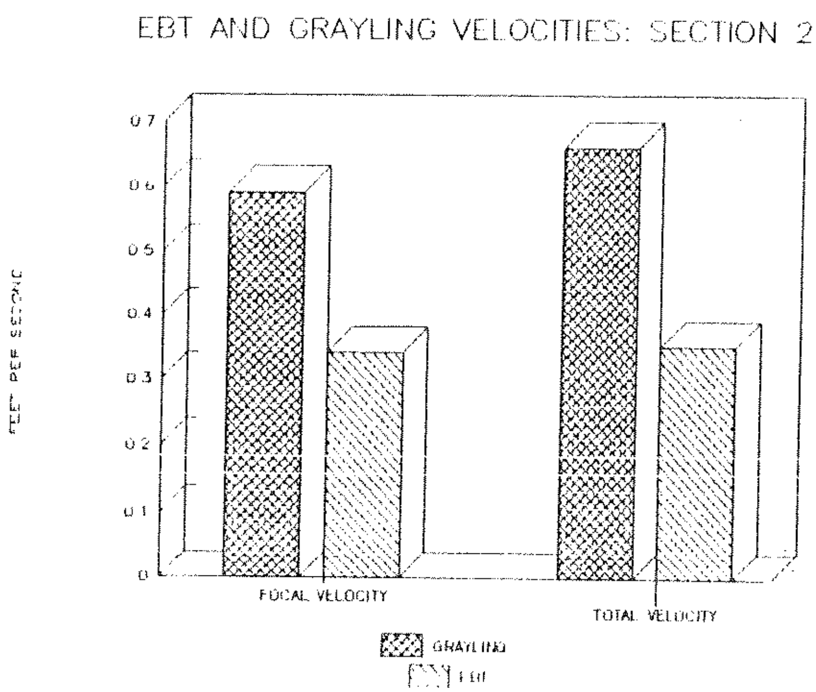
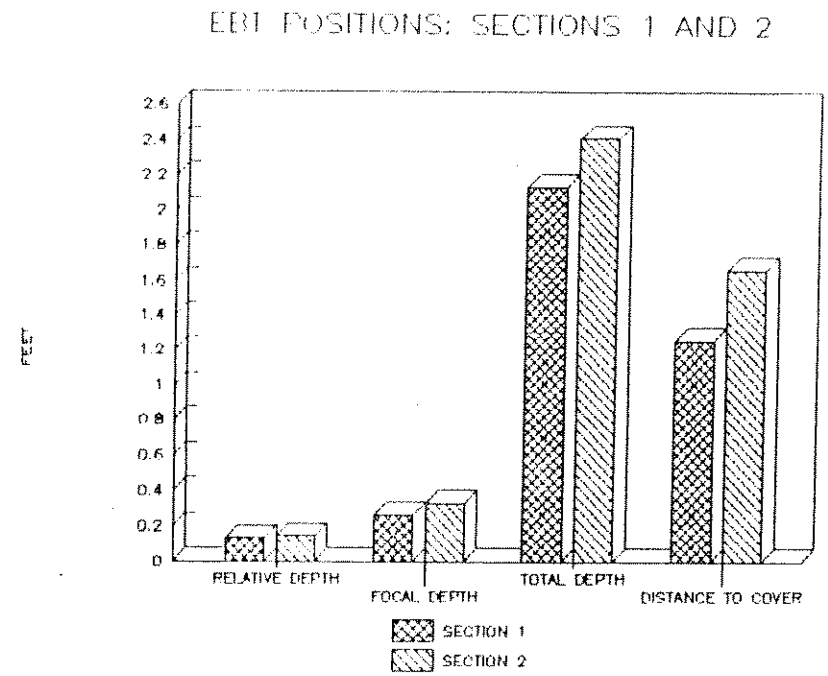


Figure 3. Micro-habitat positions and velocities for brook trout Sections 1 and 2, Skinner Meadows, 1993.



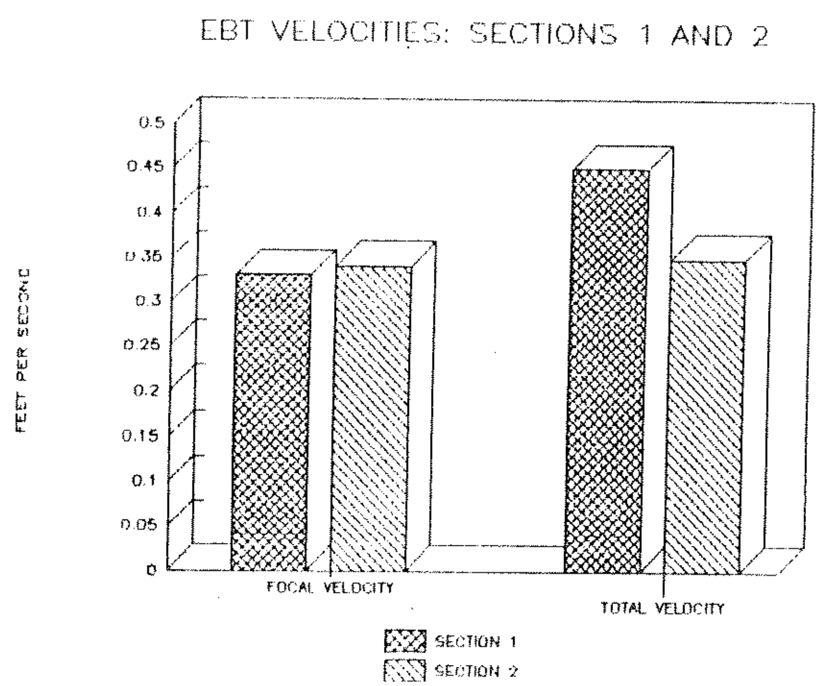
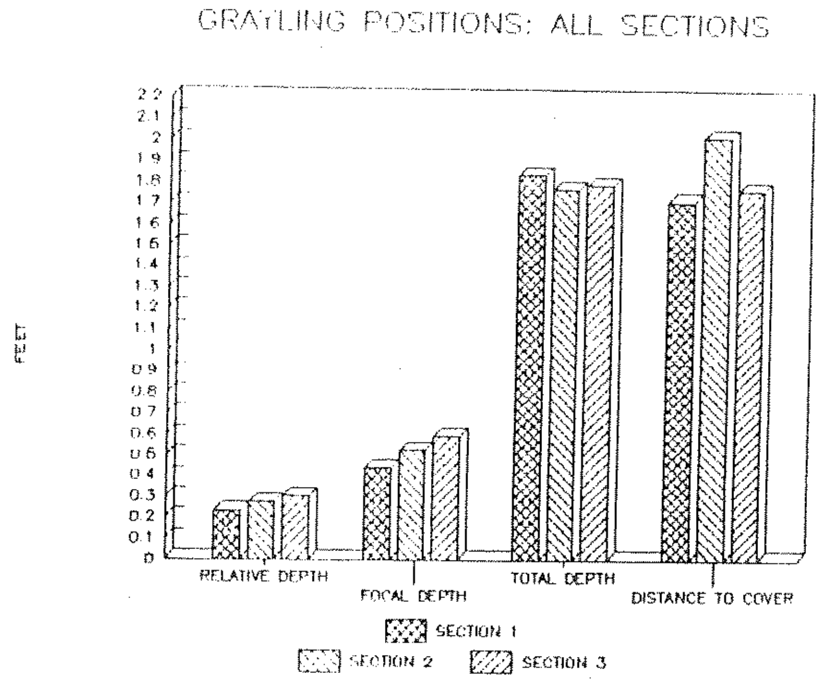
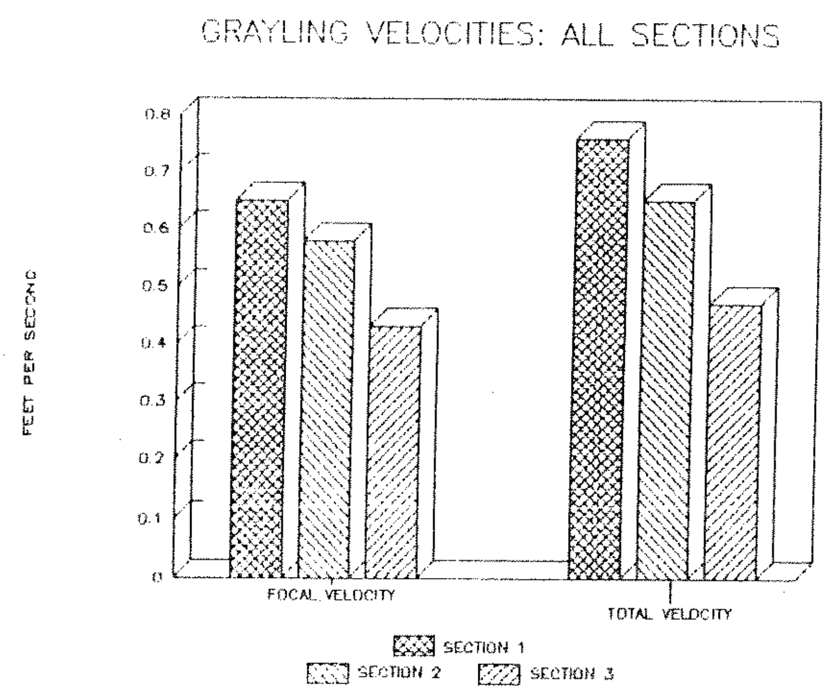


Figure 4. Micro-habitat positions and velocities for grayling in





APPENDIX 1
Wentworth Scale for Classification of Substrate (Welch 1948)

Substrate Class	Particle Diameter (mm)
Sand/Silt	<2.0
Peagravel	2-6
Gravel	6-7.5
Rubble	7.5-15
Cobble	15-30
Boulder	>30
Bedrock	

Appendix 2

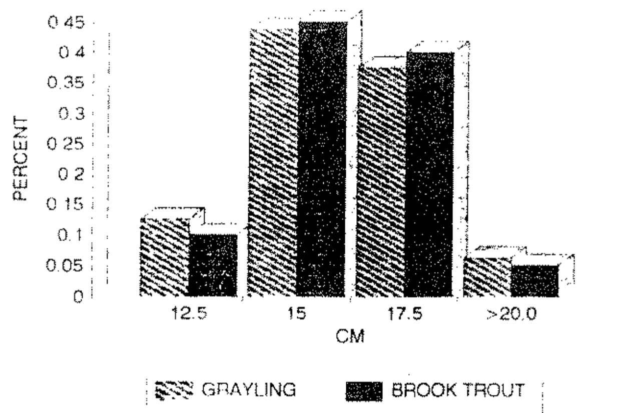
Pool quality rating from Platts et al. (1983).

Rating	
Pool Size	
3	Pool much longer or wider than average width of stream.
2	Pool is as long or wide as average width of stream.
1	Pool much shorter or narrower than average width of stream.
Pool Depth	
3	Deepest part of pool >0.9m
2	Deepest part of pool 0.6-0.9m
1	Deepest part of pool <0.6m
Pool Cover	(Turbulence, logs, boulders)
3	Abundant >30% of pool bottom obscured.
2	Partial 10-30% of pool bottom obscured.
1	Exposed <10% of pool bottom obscured
Total Score	**Pool Classification**
8 or 9	1
7	2
6	3
4 or 5	4
3	5

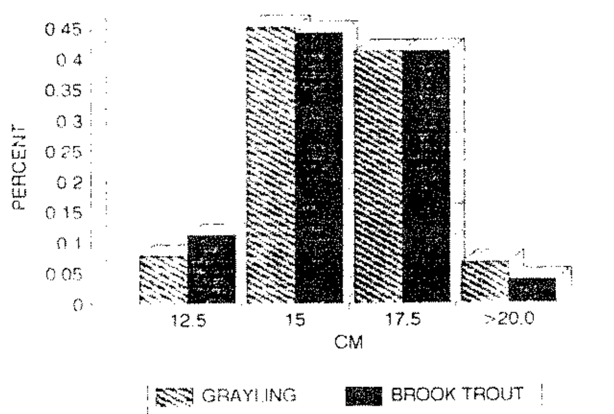
Appendix 3

Length-Frequency of introduced grayling and brook trout by section in Skinner Meadows, August 1993.

SECTION 1



SECTION 2



SECTION 3