HABITAT UTILIZATION AND THE BEHAVIORAL ECOLOGY OF RAINBOW TROUT (SALMO GAIRDNERI RICHARDSON) AND BROOK CHAR (SALVELINUS FONTINALIS (MITCHILL)) IN AVALON PENINSULA STREAMS

RICHARD ANTHONY CUNJAK

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Habitat Utilization and Behavioural Ecology
of
Rainbow Trout, *Salmo gairdneri* Richardson
and
Brook Char, *Salvelinus fontinalis* (Mitchill)
in Avalon Peninsula Streams

by

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A Thesis submitted in partial fulfillment
of the requirements for the degree of
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ABSTRACT

Recent range extension of introduced salmonid species in insular Newfoundland has caused concern over their effects on native fish species. The present study was designed to investigate the habitat utilization of the exotic rainbow trout and the native brook char in streams of the Avalon Peninsula. Underwater field observations were carried out in a stream where the two species coexisted. Brook char occupied positions with significantly lower water velocities, greater depth, and more cover than similar sized rainbow trout. Char showed similar microhabitat preferences regardless of the presence of trout. Behavioural observations of inter-specific pairs of fish at an in-stream viewing facility (Benthobservatory) showed that brook char were able to dominate rainbow trout in a slow flow (pool) environment. No species advantage was observed in a fast flow (riffle) environment. Subsequent experiments at the Benthobservatory provided evidence that trout preferred mid-stream stations in the main flow whereas char most often held station in slow flow areas usually associated with cover. Laboratory experiments designed to investigate the ability of one species, within its optimal temperature regime, to dominate another species indicated that brook char were most active, showed best growth, and were dominant over rainbow trout at 13°C. Trout showed their best growth and achieved dominance most often at 19 °C. The results suggest that rainbow trout may realize a metabolic and behavioural advantage over char at high stream temperatures.

The data indicate that microhabitat preferences of rainbow trout and brook char in the stream environment are sufficiently different to permit cohabitation with minimal interaction. This habitat segregation likely resulted from interactions with other salmonids in their indigenous ranges.

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GENERAL INTRODUCTION

The brook char, or mud trout, Salvelinus fontinalis (Mitchill) is indigenous to insular Newfoundland where it is the most common freshwater fish species. Its distribution is so widespread that Scott and Crossman (1964) noted, "Rarely does one encounter a body of water, regardless of size, which does not contain one or more forms of this fish". The life history strategy of this species is extremely variable consisting of stream resident, lake resident, or sea-run phases. It is a fall spawning species (late September to late October in the streams concerned in this study).

The rainbow trout, Salmo gairdneri Richardson is not native to Newfoundland. It was first imported from California and introduced to Long Pond, St. John's in 1887 (Scott and Crossman, 1964). From 1890 to 1901, further stocking of fingerling trout from the State of New York was carried out in numerous ponds of the Avalon Peninsula (Andrews, 1965). In later years, fry were obtained from established parent stock and distributed in these same ponds and others off the Avalon Peninsula. When anadromous, this species is known as the steelhead trout. Steelhead have been identified from as far away from the Avalon Peninsula as the west coast of the Northern Peninsula in insular

Newfoundland (Chadwick and Bruce, 1981). These occurrences are believed strays from aquacultural practices around the Gulf of the St. Lawrence such as that in Cape Breton, Nova Scotia and P.E.I. Both lake resident and stream resident populations have been identified for this species in addition to the sea-run forms. This variable life history pattern is dependent on location, stock type, and habitat (Scott and Crossman, 1973). Rainbow trout are typically spring spawners (March to May in Avalon Peninsula streams).

In recent years, fisheries biologists have expressed their concern regarding the ecological impact of such introduced species in Newfoundland, especially in light of the rapid spread of the other exotic salmonid, the brown trout (Salmo trutta Linnaeus) and its possible effects on brook char (Walters, 1954 ; Nyman, 1970) and Atlantic salmon, Salmo salar Linnaeus (Gibson et al., 1981). Aquacultural rearing of rainbow trout, such as that at Hopeall, Trinity Bay (Jamieson, 1978) and angler interest in the propogation of this species necessitate further research into the consequences of such introductions on native species like the brook char.

The present study was designed to investigate habitat use and the behavioural/ecological interactions of these two species in Avalon Peninsula streams during the spring to fall period (April to October). An understanding of species interactions at the juvenile fluviatile stage would provide background data for assessing the impact of recreational stocking programs or accidental introductions (in aquacultural practices) of rainbow trout on brook char. The study of salmonid interactions is a well known area of research (Newman, 1956 ; Kalleberg, 1958 ; Hartman, 1965 ; Jenkins, 1969b ; Nyman, 1970 ; Griffith, 1972 ; Schutz and Northcote, 1972 ; Gibson, 1973, 1981 ; Allee, 1974 ; Glova and Mason, 1977a,b ; Nilsson and Northcote, 1981 ; Fausch and White, 1981). However, except for the work in California by Newman (1956), no study of the stream interactions of rainbow trout and brook char specifically, has been documented.

The aims of this research were to identify stream habitat preferences of the two species and to determine the extent of resource competition in a number of different habitats and environmental situations. To meet these goals, field observations and collections were carried out at two stream sites where brook char and rainbow trout occurred in sympatry (but where instream habitats varied) and at another stream where only brook char were present. Manipulative experiments were conducted using an instream viewing facility (the Benthobservatory) to observe the behaviour of the two species in inter-specific and intra-specific situations. A series of laboratory experiments was also conducted at the Marine Sciences Research Laboratory (M.S.R.L.), Logy Bay to determine the effects of water temperature on the ability of each species to establish social hierarchies. Since the experimental temperatures used were within the range normally experienced in the stream habitat, and because each species had different temperature preferenda, it was believed one species would realize an advantage, given its optimal environmental temperature.

The thesis is organized into three sections : field studies ; the Benthobservatory studies, separated for the experiments in 1980 and 1981 ; and the M.S.R.L. experiments.

DESCRIPTION OF STUDY AREA

Three study sites were chosen on two different streams (Figure 1). The drainage basins of both streams are characteristic of the boreal heath ecoregion of the Avalon Peninsula (Meades, 1973). Geology of the respective areas is also similar. The rocks are of Precambrian age, equally divided between assemblages of intermediate to acidic volcanic rocks and those of sedimentary origin composed mainly of siltstone and sandstone (Rose, 1952). Pouch Cove Brook is located approximately 25 km north of St. John's at 47° 45′55" N, 52° 46′00" W and has a drainage area of 6.2 square km and an axial length of 6.0 km. The riparian vegetation at Pouch Cove Brook is dominated by *Picea* spp., *Abies balsamea*, *Betula papyrifera*, *Myrica gale*, and *Viburnum cassinoides*. This stream was chosen for its accessibility and because the brook char, *Salvelinus fontinalis*, is the only fish species present. The other two sites are located on the Piccos Brook system which is approximately 15 km north-northwest of St. John's at 47°42′30" N, 52°42′25" W. This stream has a drainage basin of 11.6 square km and an axial length of 10.0 km. The riparian community at the downstream station of Piccos Brook is composed primarily of *Alnus crispa*, *Myrica gale*, *Abies balsamea*, *Picea* spp., *Betula papyrifera*, and *Spiraea latifolia*, similar to the

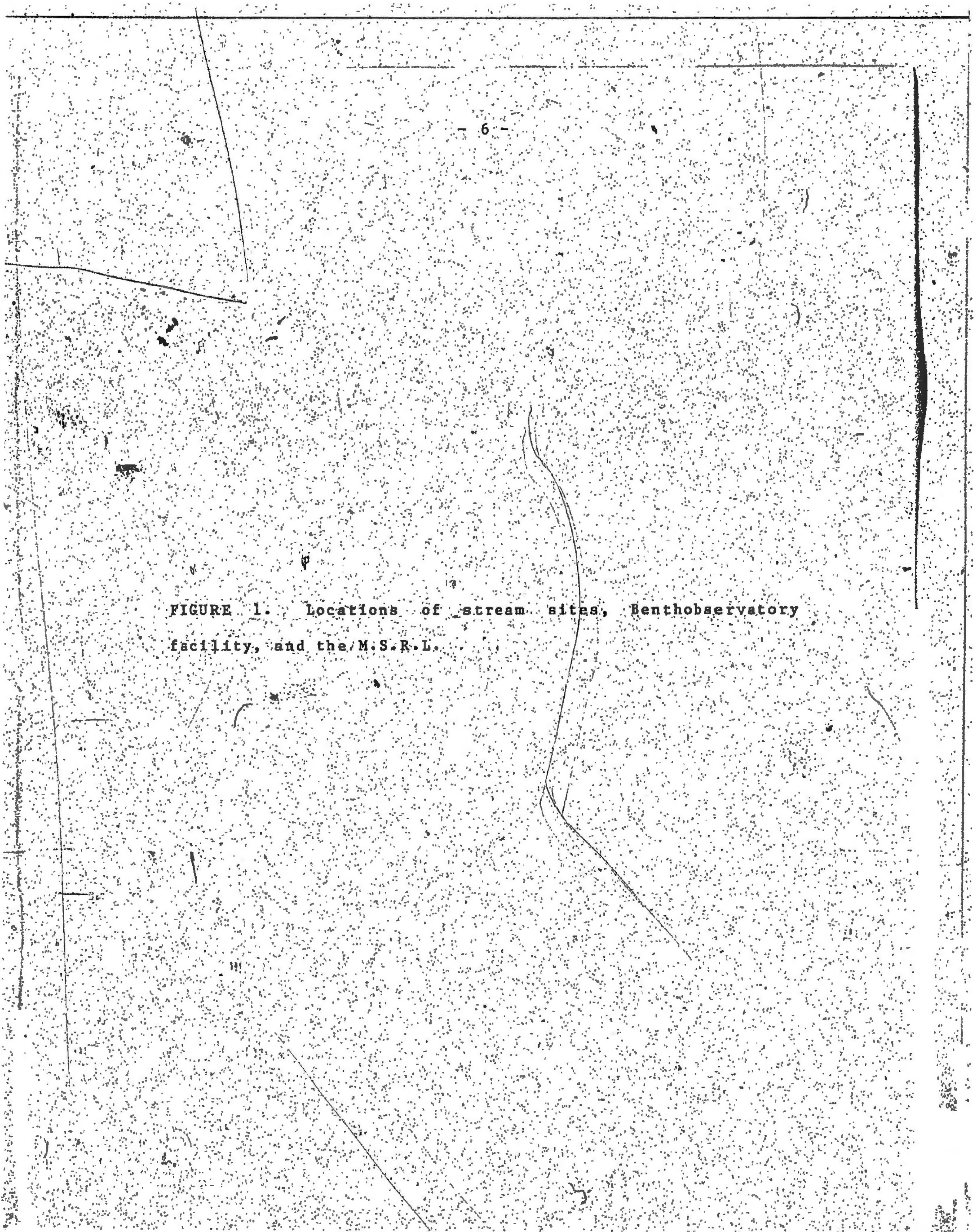
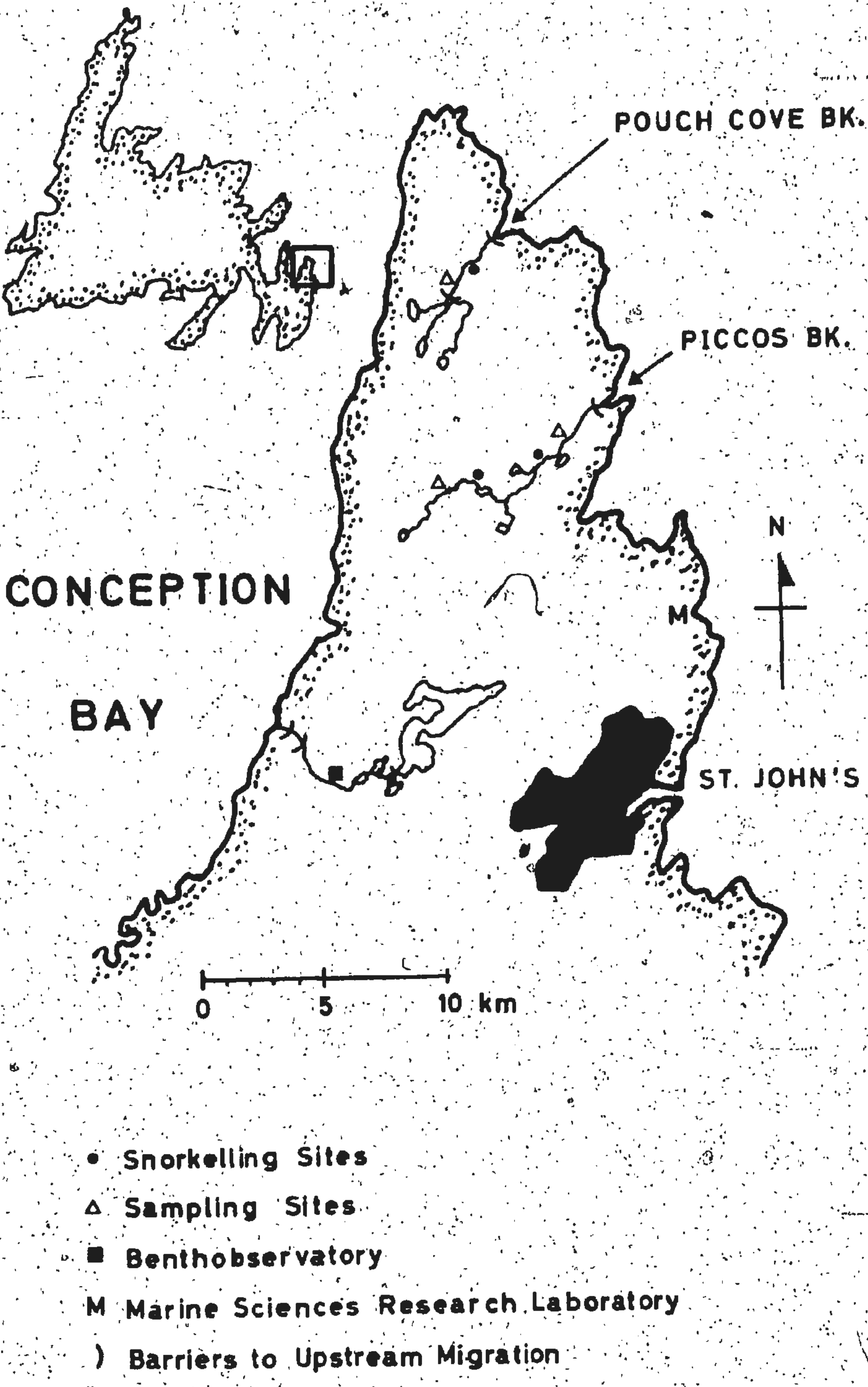


FIGURE 1. Locations of stream sites, Benthobservatory facility, and the M.S.R.L.


POUCH COVE BK.
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0
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10 km
• Snorkelling Sites
△ Sampling Sites
■ Benthobservatory
M Marine Sciences Research Laboratory
) Barriers to Upstream Migration

Pouch Cove Brook site. The upstream station has a riparian vegetation characterized by Myrica gale, Spiraea latifolia, Thalictrum spp.,Rosa nitida, and numerous species of grasses (Gramineae) while bankside trees and large shrubs were absent from here unlike the other two sites. The relative location of all three sites is shown in Figure 1.

Piccos Brook was chosen because it contains a mixed fish fauna that includes brook char, rainbow trout, and three-spined stickleback , Gasterosteus aculeatus Linnaeus. At Pouch Cove Brook, the only fish species present was the brook char. Since the downstream site on Piccos Brook was similar to that at Pouch Cove Brook in terms of its physical characteristics (Tables 1,2,3), this provided an opportunity for comparison of brook char in sympatry (with rainbow trout) and allopatry.

The specific choice of study sites and their respective lengths was based primarily on their suitability for snorkelling observations and that each site provided a combination of riffle and pool habitats. Generally, one hour of uninterrupted underwater observations was used to delineate the boundaries of each site. This accounts for the variations in the axial lengths, stream widths, and water surface areas between sites shown in Table 1. These values include only those stream sections in which snorkelling observations were made. Although these are variable, the amount of underwater habitat visible to the observer was approximately the same.

Discharge estimates at each site at extreme low and high flows during the 1981 field season (April to September) indicate the range of stream discharges during the field observations (Table 1). The 1980 season was a relatively high water year and consequently peak flows were probably higher than measured in 1981.

Stream substrate composition was determined for stream transects made at 25 metre intervals within each study section. Substrate composition within a transect was then determined as the percentage of each particle size category along successive 2 metre lengths of the transect. These values were then averaged for each stream site and are shown in Table 2. Riffle : pool ratios and the percentage of rooted vegetation were measured along each transect and likewise averaged for each stream site (Table 3).

Water samples for chemical analyses were collected in 1980 from each of the stream sites in the spring (May 20 - 30), summer (August 22), and the autumn (October 20). Total hardness, specific conductance, turbidity, total alkalinity, calcium concentration, pH, and chloride concentration were measured for each sample. All analyses were performed in the Water Analysis Laboratory of the Northwest Atlantic Fisheries Centre, St. John's. The results of these are shown in Table 1, Appendix A.

Table 1. Hydrological and morphological measurements for sites of snorkelling observations on Piccos Brook and Pouch Cove Brook.

Stream Site	Seasonal Low Discharge (m^3/sec) 26/07/81	Seasonal High Discharge (m^3/sec) 16/09/81	Mean Width (m)	Total Length (m)	Total Surface Area (m^2)	Stream Order*
Piccos Brook Downstream	0.16	0.89	5.7	92.5	527.3	4
Piccos Brook Upstream	0.05	0.30	3.5	105.0	363.5	3
Pouch Cove Brook	0.07	0.48	6.3	91.0	573.3	4

* based on classification scheme of Horton (1945)

Table 2. Stream substrate composition* at the Piccos Brook and Pouch Cove Brook study sites. Values are mean percentages for all stream bed transects (see text for explanation of methodology).

Study Site	Boulder > 256 mm	Cobble 64-256 mm	Gravel 2-64 mm	Sand 0.12-2.0 mm	Silt < 0.12 mm
Piccos Brook Downstream	20	35	27	9	9
Piccos Brook Upstream	0	11	51	21	17
Pouch Cove Brook	37	35	14	4	10

* Grain size dimensions modified from Hynes (1970)

Table 3. Riffle : Pool ratios and rooted vegetation component at the Piccos Brook and Pouch Cove Brook study sites. Values are means for stream bed transects.

Study Site	Riffles : Pools	Rooted Vegetation (%)
Piccos Brook Downstream	1.7 : 1	31.0
Piccos Brook Upstream	1 : 3.3	59.3
Pouch Cove Brook	1 : 1.7	9.2

FIELD STUDIES

During 1980 and 1981 periodic snorkelling observations were made at each of the study sites in order to observe the daytime behaviour and habitat use of each fish species under variable water levels, discharges, and water temperatures from spring to autumn. Knowledge of brook char and rainbow trout behaviour in their natural environs was considered prerequisite to the interpretation of the M.S.R.L. and Benthobservatory experiments.

In addition, fish samples were collected from both streams during 1980 (including two sites on Piccos Brook). This was done to obtain specimens for stomach content comparisons between species, age classes, and sites at different times of the year.

Materials and Methods:

Underwater observations were made using wet suit (or dry suit), mask, and snorkel. In 1980, these observations were made approximately once per month from early June until late October. In 1981, they were made approximately every two weeks, from April until September. Observations at each stream site covered the same sections. However, the duration of the observation period varied from 0.7 hrs to 1.2 hrs depending on the numbers of fish seen and water clarity. Water temperature, weather conditions, time, underwater visibility, and water level were recorded during each observation. Observations were only conducted if visibility was at least 1.5 metres. This value was determined as the minimum distance at which a fish could be approached from downstream before detection and flight by the fish. The maximum visibility was defined as that distance at which a dark-coloured underwater object disappeared from view. Each observation began at the downstream end of the study site, and was conducted by the observer moving cautiously in an upstream direction until the upstream boundary was reached. When a fish was encountered, species, life stage, age (underyearling or overyearling), and approximate length were noted on an underwater plastic writing slate. Further differentiation of overyearlings (i.e. fish of age I+ and older) was not attempted in this study. Separation of fry (underyearlings) and overyearlings was based on relative size and external body markings (eg. parr marks). Determination of fish length was made by associating snout and tail positions with adjacent objects and then measuring this distance. With practice, reliable estimates were possible without actual measurement. Behavioural observations of feeding, agonistic activity, movement, and position were also recorded.

The location occupied by a station-holding fish (i.e. one that maintained a stationary position on or off the substrate for at least a ten second period) was designated its 'focal point' (Griffith, 1972 ; Bustard and Narver, 1975 ; Rimmer, 1980 ; Fausch and White, 1981) and was marked with a small stone (colour specific for each species). Following each observation period, water velocity and water depth were determined at each marked focal point. Fry were an exception as their depths were recorded as depth of water at point of observation. This was because fry showed greater vertical movement than overyearlings in any particular location rather than maintaining a specific focal point. Care was taken not to record those fish believed to have been scared to a particular focal point by the observer. Consequently, positions of any visibly disturbed fish were disregarded. It was assumed that few if any fish were observed more than once during an observation period due to the tendency of stream salmonids to move downstream when frightened (R. J. Gibson, personal communication).

Water velocity was measured using an Ott current meter, Model 'C-2;10.150'. All water velocity measurements were taken at the focal point position above the substrate at the head position of the fish.

Each fish was also described in terms of its association with cover. Cover was defined as a 'broken' water surface due to turbulence and/or high water velocity, overhanging submerged riparian vegetation, riparian canopy less than or equal to 1.0 metres above the water surface, surface foam, undercut bank, and any form of instream cover beneath which a fish would be hidden from above (eg. boulders, logs). A fish was considered under cover if directly beneath any of the above, or near enough to one that it provided shade or shadow for the fish. Depth greater than or equal to 75.0 cm was also considered a form of cover. This value was determined as that depth at which the contours of a dark coloured stone became indistinguishable as it was lowered through the water column.

Fish collections were made a minimum of one km either upstream or downstream from the snorkelling site (Figure 1). Riffles, runs, and pools were sampled with approximately equal frequency. Both electro-fishing and angling with small flies were employed to capture the fish. Electro-fishing involved the placement of two barrier nets (1.25 cm 'stretch mesh') at the upstream and downstream boundaries of a stream section determined to have an approximately equal series of riffles and pools. Successive sweeps were made for a period of 30 minutes wherein fish were dip-netted, killed, and immediately placed in 10 % formalin. Due to the low conductivities experienced, electro-fishing was often ineffective in deep pools and during high water conditions. For this reason angling was also used to collect fish. Again, fish were immediately killed and stored in 10 % formalin. Sampling was done five times during the year (May 20 - 28 ; June 25 - July 8 ; August 4 - 9 ; September 16 - 18 ; and October 16 - 20) to determine if dietary changes paralleled invertebrate seasonal succession.

In the laboratory, each fish was measured (FL to nearest 0.1 cm), sexed, and stomachs removed. Stomachs were dissected out by severing them at the constriction of the duodenum and the esophagus. Each stomach was then washed with distilled water, immersed in a dish of 70 % ethanol and opened under a binocular dissecting microscope. Food items were removed and identified at least to Order for the terrestrial forms and to Family for the obligate aquatic forms. Many of the latter were identified to species. These were enumerated, grouped by taxon, and allotted 'points' according to the system devised by Hynes (1950). In this method, each food category (taxon) for a stomach is subjectively allotted a number of points based on its relative volumetric contribution to the entire stomach contents. These points are then scaled to percentages in order to give percentage composition of stomach contents for each fish. As noted by Hynes (1950), this method, "... is not influenced by frequent occurrence of a small organism in small numbers, nor of heavy bodies, like snail shells and caddis cases, and does not involve trying to count large umbers of small and broken organisms". Stomach fullness was also quantified for each fish. This was accomplished by giving point values for each 25 % of volume fullness. That is, 0 points for an empty stomach; 5 points - 25% full; 10 points - 50% full; 15 points - 75 % full; 20 points - completely full. A distended stomach was given a value of 30 points.

Results :

During the 1980 and 1981 field seasons, a total of 46 separate snorkelling observations were made between the three stream sites. This accounted for approximately 55 hours of underwater observations. The dates and summary of each are shown in Table 1, Appendix B.

Focal point velocity and water depth data were analysed by 1 - way analyses of variance (ANOVA) for unequal sample sizes (Sokal and Rohlf, 1973), utilizing the subprogram ONEWAY in SPSS, as outlined in Nie et al (1975). Each criterion variable (depth or velocity) was analysed separately for each of the Piccos Brook sites to determine if species differences existed. Since behaviour of salmonid fry is typically different from that of overyearlings, separate ANOVAs were performed for these two groups. Pouch Cove Brook data were tested separately as they were not statistically comparable to the Piccos Brook sites where a mixed fish fauna occurred. Rather, data from the former were tested for differences between age groupings. No statistical tests were made for a variable between the Piccos Brook sites as their respective stream morphologies were too dissimilar. The results of all tests are tabulated in Table 4.

At the Piccos Brook downstream site, there was a highly significant difference between species for mean focal point velocities at the fry stage (P < .001) and for overyearlings (P < .001). In both age groupings, mean focal point velocities of brook char were lower than that for rainbow trout. Also, mean velocities of fry were less than those for overyearlings within each species. This is probably due to the increased energy available to hold position in current with increasing size. Everest and Chapman (1972) found a strong positive correlation (r = .92) between lengths of juvenile chinook salmon (Oncorhynchus tshawytscha) and their focal point velocities.

At the downstream Piccos Brook site, no significant species differences were found for focal point depths among overyearlings (P > .05). Only fry showed a significant difference between species for depth at this site (P < .01) with rainbow trout occurring in deeper waters than brook char fry. The largest difference was between age groupings. Overyearlings of both species were in deeper water than fry

TABLE 4. Comparisons between rainbow trout and brook char for depth and velocity, at each of the stream sites, using analysis of variance (ANOVA).

$*p < .01$, $**p < .001$, ns - not significant

Stream Site	Criterion Variable	Independent Variable	Sample Size (n)	Mean[a]	F-ratio
Piccos Brook Downstream	Depth	Trout fry	51	33.05	7.175*
		Char fry	26	25.50	
		Trout overyearlings	75	45.80	0.771 ns
		Char overyearlings	31	42.88	
	Velocity	Trout fry	51	20.90	29.196**
		Char fry	26	10.56	
		Trout overyearlings	70	31.82	11.843**
		Char overyearlings	30	20.26	
Piccos Brook Upstream	Depth	Trout fry	11	41.82	—
		Char fry	2	22.50	
		Trout overyearlings	49	61.14	1.447 ns
		Char overyearlings	59	66.14	
	Velocity	Trout fry	11	10.46	—
		Char fry	2	12.10	
		Trout overyearlings	51	17.83	32.196**
		Char overyearlings	59	7.66	
Pouch Cove Brook	Depth	Char fry	29	25.01	19.345**
		Char overyearlings	78	37.01	
	Velocity	Char fry	29	10.69	1.219 ns
		Char overyearlings	78	10.20	

[a] Mean values for depths in cm; mean values for velocity in cm/sec

which were mainly restricted to the littoral areas and shallows.

Statistical results from the upstream Piccos Brook site differ somewhat from those at the downstream site. Species differences at the fry stage were not suitable for testing due to the small sample sizes (especially for brook char). However, rainbow trout fry (which were more numerous than char fry) were observed in deeper and slower water positions than rainbow trout fry downstream.

At the upstream site, rainbow trout overyearlings held stations in significantly higher water velocities (P < .001) than brook char overyearlings. This situation was similar to that downstream except that mean velocities were less. No significant difference was found between overyearlings of each species for depth at the upstream Piccos Brook site (P > .05). However, the mean depths occupied by both species were greater upstream as compared to the downstream site. These differences for mean depths and velocities between the two sites seem to be a function of site morphology. At the upstream site, the stream runs through an open boggy area (Figure 2) and is characterized by a narrow channel, almost rectangular in profile with steep banks. At the downstream site, the stream channel is much wider, gently sloping towards the centre, and discharge is considerably greater (Figure 3).

At the Pouch Cove Brook site, a highly significant

FIGURE 2. Piccos Brook (upstream) site where snorkelling observations were carried out.

FIGURE 3. Piccos Brook (downstream) site where snorkelling observations were carried out.

difference in focal point depths was found between age groupings ($P < .001$). Fry were found in shallower depths than were older fish, as was the case at the Piccos Brook sites. In fact, in the largest (and deepest) pool within the area, where large numbers of char were often seen, fry were observed only twice, and then only in the shallower margins. Mean depth values for each age grouping at Pouch Cove Brook were similar to those for char at the downstream Piccos Brook site.

No difference was found between age groupings at the Pouch Cove Brook site when tested for focal point velocities ($P > .05$). The mean water velocity positions of char fry were very similar to that at the downstream Piccos Brook site. However, mean focal point velocities of overyearling char were much lower than those measured for overyearlings at Piccos Brook (downstream). This seems to have been related to the stream morphometry at the Pouch Cove Brook site. Mean width was greatest here of all three sites yet discharge was lower. Consequently, the range of available water velocities here was quite low as water braided its way through various channels in this wide boulder and cobble strewn stream section (Figure 4).

Association with cover was tested between species and age groupings at all three sites, according to the format used for the depth and velocity variables. However, cover was treated as a discrete binary variable (associated with

FIGURE 4. Pouch Cove Brook site approximately 0.5 km upstream from the snorkelling section.

cover or not) and was analysed using the Chi - square test (Sokal and Rohlf, 1973). The results are shown in Table 5.

At the downstream Piccos Brook site, highly significant differences were found between the species ($P < .001$), for both age groupings. In each case, brook char were the species most associated with cover. At the upstream site, a similarly significant difference was found between the two species for overyearlings ($P < .01$) with brook char most associated with cover. However, the difference was not as pronounced as found at the downstream site. The reason for this was the physical differences between the two locations. The upstream site had a relatively small surface area, a deep, narrow channel, extensive riparian overhang, and dense instream vegetation in the shallows, all of which provided a situation where open water was limited. The low sample size of brook char fry upstream precluded any meaningful testing. It is however interesting to note that despite the paucity of open water stations, this is where all the rainbow trout fry (11) were observed.

At Pouch Cove Brook, fry were significantly less associated with cover than were overyearling char ($P < .01$). This was the only instance where less than 50 % of char observed (any age), were associated with cover. As mentioned earlier, the stream here is a wide shallow channel with relatively little riparian cover and virtually no aquatic vegetation which is a very important form of

TABLE 5. Comparisons between rainbow trout and brook char for cover association (percentages of fish associated with cover), at each of the stream sites, using chi-square tests. *p < .01, **p < .001, ns - not significant

Stream Site	Independent Variables	Sample Size (n)	Mean	X^2
Piccos	Trout fry	56	28.6	20.231**
Brook	Char fry	26	84.6	
Downstream	Trout overyearlings	80	23.8	27.896**
	Char overyearlings	31	80.6	
Piccos	Trout fry	11	0.0	—
Brook	Char fry	2	50.0	
Upstream	Trout overyearlings	64	46.9	10.363*
	Char overyearlings	60	76.7	
Pouch	Char fry	29	31.0	8.056*
Cove	Char overyearlings	78	64.0	
Brook				

instream cover to young stream salmonids (Boussu, 1954).

Gregarious behaviour (schooling or aggregating) was observed in both species. A `school' defined a group of fish which showed an approximately equal spacing between each of the members, a common geometric orientation, and a stereotyped behaviour (Shaw, 1962). An `aggregation' defined a group of fish in close association, within visual distance of one another, and generally displaying a common behavioural pattern but lacking the spacing homogeneity and polarity of the schooling fish. Keenleyside (1979) refers to such a group as a `non-polarized school'.

Schooling was only seen at the Pouch Cove Brook site where large schools of overyearling char were often seen in the largest and deepest pool within the study area. This phenomenon accounts for the majority of fish seen at this site. Schools of char were seen in this pool on seven occasions during 1980 and 1981 (Table 1c, Appendix B). Size of the schools varied from 8 to 60 fish with individuals usually within the body size range of approximately 10 to 15 cm FL. The behaviour appears to be related to a combination of fish density, local physical characteristics and environmental conditions. The large numbers of fish present in this stream section, coupled with the lack of access here to any large water bodies (i.e. ponds, lakes), has resulted in relatively high population densities in a limited spatial environment. In addition, schooling seems to show a strong correlation to periods of high water temperature, and to a lesser degree, low water levels. As brook char prefer cool water temperatures (Fry, 1948; Power, 1980) and because low summer water levels may reduce available habitat, a stream system such as Pouch Cove Brook might offer limited refuge during unfavourable conditions. Brook char seem to be utilizing those pools deep enough and/or shaded enough to offer the best refuge from high stream temperatures. The resultant high densities and reduced water velocities in these pools may have encouraged the schooling behaviour observed (Kalleberg, 1958).

Aggregations, although differing behaviourally from schools, appear to be a consequence of similar environmental factors (i.e. low water levels and high stream temperatures). Aggregations were observed at all three stream sites, by both species, and for both fry and older fish. They were most common at Pouch Cove Brook and the upstream Piccos Brook site, were predominantly composed of older fish, and were demonstrated more often by brook char than by rainbow trout.

At the downstream Piccos Brook site, only one incidence of an aggregation was observed (August 9, 1981), where six brook char fry held position under cover in a side-pool, all within one body length of each other. Water temperature was 19°C at the start of snorkelling but had risen to about 22 C by the end of observations. No aggregations of rainbow trout (any age) were observed here, despite their greater abundance.

At the upstream site, aggregations were seen most often. Brook char were most commonly involved but mixed species groups were also observed. Of the five aggregations seen, char accounted for 73 % of the fish involved (Table 1, Appendix B) and all were overyearlings.

At Pouch Cove Brook, aggregations were seen on three occasions. Both fry and overyearlings exhibited the behaviour but always separately.

General distribution patterns and relative species abundance can be roughly interpreted from the numbers observed during snorkelling (Table 6), assuming that both species reacted similarly to the observer's presence. It must be noted that these data are not conclusive and are based only on numbers of fish seen for those days and times of snorkelling. All observational enumeration was an underestimate of the actual population sizes.

Brook char fry were more abundant at Pouch Cove Brook than at the downstream Piccos Brook site. Their emergence time seems to be about mid May based on observations at both streams (Table 1a,c, Appendix B). The relative scarcity of fry of both species at the upstream Piccos Brook site appears largely a consequence of limited spawning substrate which is not available for at least one km upstream. Fry observed at the upstream study site were probably emigrants

TABLE 6. Numbers of rainbow trout and brook char recorded during snorkelling observations, at each of the stream sites (1980-1981). Values are for all observations combined. Aggregations (see text for explanation) not included.

Stream Site	Rainbow Trout				Brook Char			
	Fry		Overyearlings		Fry		Overyearlings	
	Holding Station	Swimming or Schooling	Holding Station	Swimming or Schooling	Holding Station	Swimming or Schooling	Holding Station	Swimming or Schooling
Piccos Brook Downstream	51	1	84	11	27	0	38	0
Piccos Brook Upstream	11	0	67	10	2	1	69	4
Pouch Cove Brook	–	–	–	–	50	1	120	250

from these upstream gravel beds. Rainbow trout fry appear to have emerged in late June in 1981. This difference in emergence times between the two species resulted in a size advantage for brook char which was quite obvious throughout the summer. By late October, size differences were negligible, a consequence of the faster growth rate of rainbow trout.

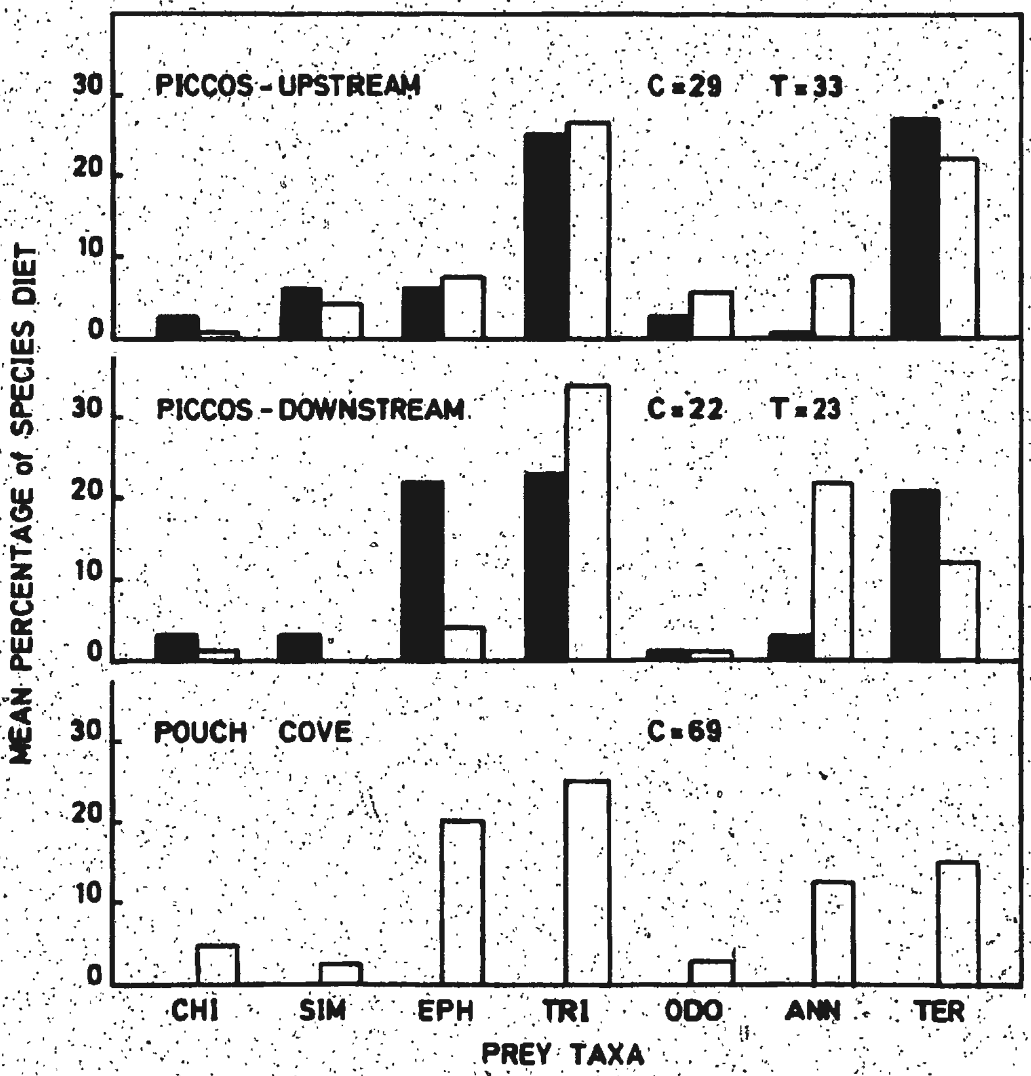
Distribution of overyearlings at the two Piccos Brook sites indicated a larger percentage of the population upstream were brook char. Similar results have been reported for other streams and rivers where the two species coexist and the differences have been attributed to temperature and/or gradient differences (Burton and Odum, 1945), stream size or physical barriers (King 1937, 1942 ; Kelly et al, 1980).

Feeding was observed at all sites and for both species. Drift feeding was most common (93% of observations). Feeding from the substrate was minimal (7%) and mostly seen by char. Most observations of feeding by char at Pouch Cove Brook were made on schooling fish or those in aggregations. Feeding was observed even as water temperatures exceeded 20 °C. On May 30, 1981, schooling char were feeding at the surface on a 'mayfly hatch' at a water temperature greater than 22°C. Rainbow trout were observed feeding throughout the day and often from mid-stream positions. In general, feeding was opportunistic. Regardless of environmental conditions, aquatic invertebrate emergences ("hatches") stimulated feeding by both species.

The stomach content data were grouped for overyearlings of each species and analysed separately from stomach data for the fry (0+). This was done for two reasons : (1) for compatibility with the results of the snorkelling observations where the same groups were used ; and, (2) because salmonid fry generally feed on different organisms than do overyearlings (Griffith, 1974 ; Wurtsbaugh et al, 1975 ; Bisson, 1978 ; Tippets and Moyle, 1978). Comparisons were made between species where they occurred in sympatry and between char from both streams.

Figure 5 shows the diet composition for each species (overyearlings) at each of the three stream sites, for all samples combined (May to October). Where the species were sympatric, Trichoptera were the most important component of the brook char's diet with terrestrial invertebrates and aquatic Annelida, of secondary importance. Rainbow trout overyearlings preyed mainly on terrestrial species and Trichoptera, although Ephemeroptera were equally important at the downstream Piccos Brook site. A monthly breakdown of the data (Figures 1 - 3, Appendix B) shows that the Ephemeroptera were most important (to trout) early in the season whereas the Trichoptera became increasingly important to both species as the season progressed. This pattern reflects the species emergence dates of those Avalon

FIGURE 5. Prey consumed by overyearling rainbow trout (solid bars) and brook char (open bars) at Piccos Brook (upstream and downstream sites) and at Pouch Cove Brook. Only those prey taxa comprising > 5% (by volume) of a species' diet, for any sampling date, are included. Data include all sampling dates. T = sample size of rainbow trout , C = sample size of brook char ; CHI = Chironomidae larvae, SIM = Simuliidae larvae, EPH = Ephemeroptera nymphs, TRI = Trichoptera larvae/pupae , ODO = Odonata nymphs, ANN = aquatic Annelida, TER = terrestrial invertebrates (includes obligate forms and aerial stages of aquatic species).



MEAN PERCENTAGE of SPECIES DIET
PICCOS - UPSTREAM
C = 29
T = 33
PICCOS - DOWNSTREAM
C = 22
T = 23
POUCH COVE
C = 69
30
20
10
0
CHI
SIM
EPH
TRI
ODO
ANN
TER
PREY TAXA

Peninsula ephemeropteran taxa (Heptagenildae, Leptophlebildae, and Ephemerellidae) most utilized by the two salmonid species (D. Larson, personal communication). Larval Trichoptera (numerous species) were present throughout the season which explains their longer period of utilization as prey species. Terrestrial species were most important to each species from mid-summer through to the fall with negligible use in the spring.

At the Pouch Cove Brook site, brook char showed a wider utilization of prey species than where they were sympatric with trout. Ephemeropteran nymphs and trichopteran larvae/pupae were the major taxa consumed, the former mainly in the spring and the latter through the summer and the fall.

Fry stomachs were also analysed. The low numbers of individuals of this group in the samples, especially at the upstream Piccos Brook site, makes species comparisons difficult. Generally, fry relied on smaller sized organisms especially those most available in the drift since this is where they primarily feed. Chironomidae, Ephemeroptera, net-spinning Trichoptera, terrestrials (primarily winged baetids and homopterans), and collembolans were the most frequently ingested prey.

Agonistic activity (intra-specific and inter-specific) was observed at all sites. However, it was not common (seen only in 15% of observations). Approaches, chases, and retreats were the most common acts. The low frequency of aggressive interactions observed is probably due to the ability of subordinate individuals to escape unlike laboratory situations (Chiszar et al, 1975).

Weather had little noticeable effect on behaviour during underwater observations. Focal point depths and velocities were approximately the same, over the range of weather conditions experienced. This was true of both species. However, brook char utilized cover more often and behaved slightly more secretively during a few hot sunny days but this was not a regular observation.

Certain seasonal differences in species behaviour and distribution were obvious. By late October, 1980, both species were absent from the upstream Piccos Brook site where water temperatures were between 6.0° C and 8.0°C. Rainbow trout and juvenile brook char probably had moved downstream to Goose Pond whereas maturing brook char had moved upstream to spawning areas. At the downstream site, rainbow trout were absent and probably had emigrated to deeper overwintering pools or ponds. Most of the brook char observed here were in spawning condition and situated over suitable spawning substrate, in higher water velocities than frequented earlier in the season. Courting behaviour and aggressive displays were observed.

In late April at Pouch Cove Brook, brook char were found under rocks in the deepest parts of pools. At the

Piccos Brook sites char were not observed, presumably because they were still in overwintering areas. Only rainbow trout were seen. These were mainly between 15 cm and 25 cm FL and presumed to be spawners.

Discussion :

Three variables : depth, velocity, and cover indicate different microhabitat preferences between species and age groups. The extent to which these preferences were displayed, was largely affected by local stream morphology and hydrology.

Brook char showed a strong preference for cover and low water velocity, at least during daylight hours when my observations were made. Gibson (1966) and Power (1980) noted that brook char often use cover during the day but come out into the open to feed at dawn and dusk. In an experimental study, Gibson and Keenleyside (1966) found char in the open only under low light intensity ; at higher intensities they were always under cover. My observations did not extend beyond the daylight hours so different diel responses were certainly possible. Similar cover and flow responses by brook char are documented (Boussu, 1954 ; Griffith, 1972) and this fact has been used to increase char production by stream alteration (Saunders and Smith, 1962 ;

White and Brynildson, 1967 ; Hunt, 1969).

Cover (as defined in this study) was a limited resource at the Pouch Cove Brook site. This would explain the lower percentage of underyearlings associated with cover here. Fry were probably being displaced from the few areas of cover that do exist (boulders and deep pools) by the larger and more dominant older fish which also showed a lower percentage association with cover as compared to the other two sites. Fausch and White (1981) found cover to be a limited resource in Michigan streams where brook char and brown trout, Salmo trutta, coexisted. They found that the more dominant brown trout displaced brook char from more favourable instream cover positions. In this study, where species were sympatric (Piccos Brook), brook char fry were primarily distributed along stream margins utilizing cover in the form of instream vegetation and overhanging (or submerged) riparian vegetation - both of which were in short supply at the Pouch Cove Brook site.

Brian (1956) noted that where a species occurs alone, it may increase its habitat utilization as opposed to when it coexists with another species. That the reduced cover association by brook char at Pouch Cove Brook was due to a niche expansion in allopatry (as compared to Piccos Brook where they were sympatric with rainbow trout) was discounted. Considering the large amount of open water available, brook char still showed a strong preference for positions associated with cover.

Cover and water velocity can be inter-dependent and therefore difficult to separate as independent variables. For example, a bottom of a pool > 75 cm depth can provide both cover and a slow flow microhabitat for brook char. The problem then is determining whether char are selecting for slow flow or cover or both. The two variables were treated as separate entities in this study because a turbulent surface in riffles, and shade from riparian overhang or mid-channel boulders in a fast flow, also sufficed as cover (according to my criteria), yet these areas were generally avoided by brook char at all stream sites. Rather, brook char preferred cover positions in slow flow situations.

Rainbow trout, in comparison, showed strong preference for higher water velocities and open water stations (downstream site). It is more difficult to infer preference for these same variables at the upstream site where only 53 % of the trout held open water stations, but open water was comparatively scarce here. Rainbow trout often held open water positions in the fastest velocities available and when utilizing cover, did so in the main flow or by holding riffle stations below surface turbulence. Cover positions, characterized by slow water flow, were rarely utilized by trout. Butler and Hawthorne (1968) found that wild rainbow trout in a California stream showed lower use of cover and greater movement from shaded areas than brook char and brown trout.

The possibility that rainbow trout held open stations because of displacement by brook char from cover locations, was discounted. At both Piccos Brook sites, many more 'potential cover' stations were identified during each snorkelling observation than could be accounted for by the numbers of fish seen. These 'empty' cover stations were assumed suitable as they were utilized by both species during other observations. At the upstream Piccos Brook site where available open water was limited, less than 50 % of the rainbow trout overyearlings showed an association with cover. The rainbow trout fry here, which might be expected to be most restricted in their position choice by size subordinance and the dense growth of vegetation in the shallows, always occupied open water stations. Since cover was only limiting at the Pouch Cove Brook site where rainbow trout did not occur, these results seem to indicate a volitional residence of open water stations by rainbow trout. Other salmonids have also been found to prefer open water more than areas with cover. Ruggles (1966) suggests that juvenile coho salmon may even avoid areas of dense shade and Gibson and Keenleyside (1966) found that Atlantic salmon parr showed preference for open water if suitable cover was nearby where they could hide when frightened.

MacCrimmon and Kwain (1966) found no significant preference for either covered or open areas of tanks by rainbow trout fry during tests with various light intensities. Yearling trout showed a significant preference for the covered portion of the tank under all light intensities, except darkness. The discrepency of their results with mine may be due to the laboratory conditions (i.e. standing water environment), use of hatchery fish (Vincent, 1960 ; Moyle, 1969 ; Fenderson and Carpenter, 1971), or lack of submerged cover (Gibson and Keenleyside, 1966).

Cover could serve many functions. Shade cover can create a cooler, less stressful microenvironment during periods of high water temperature. Cover positions behind instream objects might require less energy for holding station. Overhead cover might reduce predation, especially from birds. The use of riffles as cover would presumably protect rainbow trout in midstream stations. Another possible function of cover, particularly as it relates to brook char, was demonstrated by Helfman (1981). He found that shade producing objects in lakes attracted fish because a fish hovering in the shade was better able to see approaching objects and is simultaneously more difficult to see, especially under sunny conditions.

Water depth was not a critical factor for differentiating species microhabitat preferences in these streams. Rather, water depth appeared most important, with respect to char, where it served as cover (defined as 75 cm in this study). In stream tank experiments, Gibson and Power (1975) speculated that 50 cm depth could provide cover for brook char and Atlantic salmon in the brownish coloured waters of the Matamek River.

At the downstream Piccos Brook site, rainbow trout fry were in significantly deeper water than brook char fry. Rather than being a differential depth preference, the shallower water positions were probably more a response to cover. Since cover positions in deep water were often occupied by overyearling char, the fry of this species may have been selecting the next available areas. These were the stream edges where riparian vegetation provided shade cover or amongst the thick growths of <u>Fontinalis</u> sp. and/or <u>Juncus bulbosus</u>, which were characteristic of the shallow water zones. Conversely, the rainbow trout fry, in selecting for open water areas, moved away from the stream margins and into deeper water but not as deep as that occupied by overyearling fish.

The smaller initial size of the rainbow trout fry did not appear to affect their habitat choice. Soon after emergence, they were seen in significantly faster water than occupied by brook char fry. Johnson and Ringler (1981) noted rainbow trout fry (within 2 - 3 weeks of emergence) preferred faster water velocities than cohabiting coho salmon fry. Perhaps the different microhabitat preferences for cover and velocity reduced interaction between brook char and rainbow trout fry as no field observations of inter-specific agonistic activity were recorded for underyearlings of these species.

An interesting behaviour was observed during 1981 which may also have reduced interaction of the fry of these two species. From the time of emergence until approximately early July, brook char fry maintained positions high in the water column (often just below the surface). By early July, they showed a marked preference for positions close to the substrate. Rainbow trout fry showed a similar 'vertical shift' moving close to the substrate during late July. It is interesting that the shift to the substrate by brook char corresponds with the emergence of rainbow trout and their movement to the 'high' vertical position. Since brook char fry showed a similar vertical position shift at Pouch Cove Brook, the phenomenon is likely not related to species interaction. Perhaps a dietary change to benthic invertebrates with larger body size or a preference for substrate positions with increasing body size of the fry can explain the observations. Regardless of the reason, such behaviour would tend to minimize inter-specific interaction.

At Pouch Cove Brook (and possibly at the downstream Piccos Brook site), high water temperatures (> 19°C) seem to be the environmental factor most often associated with gregarious behaviour. The aggregation of fish in deeper water or under cover suggested an avoidance reaction to unfavourably high water temperatures. This appeared to be best accomplished in a pool environment which presumably was also a less energy demanding habitat as compared to positions in a current. Elson (1942) observed char congregating in areas of cooler water at high stream temperatures (> 20°C) and Gibson (1966) observed both brook char and salmon moving into areas of cool spring seepage at similar high water temperatures. King (1937) observed over 100 rainbow trout (3 to 15 inches in length) aggregated in one pool near a small spring inlet when stream temperatures reached 29 °C in a Tennessee stream. These data and my observations suggest that when high temperature is the cause of aggregations, brook char will show this tendency at a lower water temperature than rainbow trout. This is probably related to the higher temperature tolerance of the latter (Fry, 1951). The higher number of aggregations seen at Pouch Cove Brook seems to confirm this although the high fish density and limited cover availability here, increased the probability of such behaviour occurring.

The aggregation of brook char fry at Pouch Cove Brook on October 21, 1980 was also apparently related to temperature but in this case, low water temperature. Fry were absent from shallow stream sections and aggregated in a large pool (for the first time all season). This behaviour may have been due to lowering temperature and seasonal change in behaviour as fry were moving to overwintering areas. Similar autumnal behaviour has been recorded for Atlantic salmon (Rimmer, 1980), steelhead trout (Hartman, 1965), coho salmon (Bustard and Narver, 1975), brook char (Cooper, 1953 ; Benson, 1955), brown trout and rainbow trout (Benson, 1955).

At the upstream Piccos Brook site, aggregation behaviour was most often associated with low water levels and consequent reduced habitat availability. At this site, dense mats of Fontinalis sp. and Juncus bulbosus occur in the shallow riffles between pools. During low water conditions in the late spring and summer, pools were virtually isolated from one another by these 'vegetation barriers' and the fish appeared to be restricted to a relatively small area of the stream. The question arises as to why the fish did not move downstream to more favourable locations (such as Goose Pond) as water levels started falling ? Two possible explanations are : (1) stream fishes tend to show restricted non-reproductive movement within their 'home range' (Gerking, 1959 ; Edmundson et al. 1968 ; Lewis, 1969 ; Cargill, 1980) ; and (2) stream species tend to respect riffle areas as boundaries of their home range (Gerking, 1953) and this tendency was probably reinforced by the occurrence of the dense growths of aquatic macrophytes. Following severe spates such as occurred on June 10 and July 9, 1981, water levels rose and aggregations were not evident at this site during the subsequent snorkelling observations. Apparently, high water conditions resulted in emigration, actively by swimming (Gerking, 1959) or passively by displacement during flooding (Onodera, 1962).

The differential longitudinal distribution of brook char between the Piccos Brook sites was not believed due to water temperature. Thermograph recordings showed a maximum temperature increase of less than 2 °C from upstream to downstream during the warmest summer period. Neither was it believed due to species displacement (Nyman, 1970). Species specific preferences for localized habitat characteristics were probably more important for explaining the longitudinal distribution. The greater cover availability and low gradient at the upstream site (providing a smaller riffle : pool ratio) suggest preferred brook char habitat. In his evaluation of instream variables on salmonid habitat, Waters (1976) found that rainbow trout were better adapted to a higher range of channel gradients whereas brook char increased in population density as pool quality ratings increased.

It is difficult to conclusively assess the data from the stomach analysis. Sample sizes were small for each sampling date, especially at the sympatric sites and may only reflect the diets of a few fish only a few hours prior to capture (Nilsson and Northcote, 1981). Grouping of the data such as performed for Figure 5 can result in misinterpretation since the effects of seasonal invertebrate availability are masked. Grouping of age classes (> 0+) makes no distinction between the diets of yearlings and older fish which have been known to be different (Klemetson and Grotnes, 1975 ; Tippets and Moyle, 1978). All sampling of fish species was during the daylight hours. This may have introduced a diurnal bias to the feeding data (Eggers, 1977 ; Johnson and Johnson, 1981) especially since invertebrate drift composition has been found to be different during daylight and darkness. The data are however useful for between species comparisons at each site, in terms of daylight feeding.

Trichoptera were the most important invertebrate order in the diet of both fish species (based on stomach volume contribution) whether living sympatrically or allopatrically. No apparent differences between char and trout were found for the types of Trichoptera consumed. The Hydropsychidae and Philopotamidae (net - spinners) and the Limnephilidae (case - builders) were the groups most utilized. These groups are generally found in a variety of stream microhabitats from riffles to pools (Wiggins, 1977; Merritt and Cummins, 1978) and therefore available to both char and trout on this basis.

Some seasonal diet variation was indicated from the stomach content data which appeared to reflect seasonal availability of the invertebrates. Ephemeroptera were consumed more in the spring whereas terrestrials and Trichoptera were fed on more often in the late summer. Wiseman (1969) noted a similar trend in brook char sampled from various locations in insular Newfoundland (mainly ponds). He found that the benthic component of the diet decreased but the pelagic and terrestrial components increased from spring to fall.

The most obvious diet variation between the two species was their differential utilization of aquatic annelids and terrestrial species. Aquatic annelids (oligochaetes and hirudineans) were fed on by brook char to a much greater extent than by rainbow trout which consumed terrestrial species more often. This preference for terrestrial invertebrates by rainbow trout has been documented by other researchers (Metz, 1974 ; Johnson, 1981) and may be a consequence of their position in shallow riffles where they can exploit the surface drift (Glova and Mason, 1977a), their propensity for daytime feeding (Jenkins, 1969c ; Bisson 1978) when these invertebrates are most common, or their preference for moving prey (Waters, 1969 ; Ware, 1972) since they are primarily visual feeders (Ware, 1972 ; but see Jenkins, 1969a and Tanaka, 1970). Brook char, on the other hand, are more closely associated with the bottom (Newman, 1956) and may rely more on midwater drift and bottom prey (Griffith, 1974), although they can feed substantially on terrestrial surface drift (Reed and Bear, 1966).

At the Pouch Cove Brook site, the more generalized pattern of feeding may be due to the absence of a competing species, especially as char were found occupying a wider range of depths and were less associated with cover than at the other sites. To infer that the more generalized feeding pattern is a result of wider habitat utilization in allopatry suggests that a certain degree of interactive segregation (Brian, 1956 ; Nilsson, 1967) was occurring between the species at Piccos Brook, especially at the downstream site where diet differences were the greatest. This type of species segregation also implies that food is limiting since a superabundance of food should still allow almost identical resource utilization (Nilsson, 1956, in Kalleberg, 1958). An indication of the scarcity of the food resource is suggested from measures of stomach fullness. In August and September, stomachs averaged between 50 % and 75 % full (both species), less than that observed earlier in the season. However, no definite conclusions were possible especially in comparing between sites since information on invertebrate composition was not collected in this study.

It is possible that the more similar habitats at the fry stage (i.e. shallow littoral margins) may result in greater inter-specific competition for food than occurs among the older age classes, if this resource was limiting. Since greatest diet overlap occurs among similar sized fish

(Bisson, 1978 ; Johnson, 1981), the potential for competition might be most obvious for fry, especially by late summer once fish lengths of the two species are approximately equal. Diet overlap could be realized even earlier if morphological differences (eg. smaller gape by char) negated any size advantage conferred by prior emergence, as suggested between sympatric Atlantic salmon and brook char (Williams, 1981).

The data indicate considerable overlap in the feeding of these two species among all age classes, whether allopatric (brook char) or sympatric and supports the contention that these salmonids are opportunistic feeders (Tebo and Hassler, 1963 ; Waters, 1969 ; Nyman, 1970). Certain differences were identified such as the greater utilization of aquatic annelids by char, and small terrestrial spp. and Heptagenid Ephemeroptera by trout. These differences complement the microhabitat differences observed during snorkelling. That more distinct feeding differences were not observed may be due to the lack of a limiting food resource or the small sample sizes. More likely, the reason is the small size of the study stream resulting in specific resource overlap in most stream microhabitats. The most obvious and clear evidence for interactive segregation (for food) has been found in large rivers (George and Hadley, 1979) and mainly in lakes (Nilsson, 1965 ; Schutz, 1969 ; Swift, 1970 ; Klemetson and Grotnes, 1975 ; Nilsson and Northcote, 1981). Such habitats provide more potential for isolating mechanisms with little necessary overlap. In small streams, such as those in this study, food items in the drift can be accessed from most microhabitats. In fact, Waters (1969) suggested that drift allows the utilization of insects to fish predators in a wide variety of discrete microhabitats (eg. riffles and pools). For example, a pool dwelling fish may utilize drift once it has settled onto the bottom in the slow flow of its habitat. To complicate the matter even further, much of the variation may be due to food specialization of individual fish, rather than species. Bryan and Larkin (1972) found this to be the case among individual rainbow trout, cutthroat trout, and brook char in a small stream and experimental ponds and attributed much of this specialization to interactions between individuals. Ringler (1979) noted that these behavioural differences may have resulted from initial learning experience of individuals for different prey species encountered by chance.

In conclusion, the field studies found rainbow trout and brook char to occupy different daytime stream microhabitats. These specific habitat preferences were mostly related to differential responses to cover and water velocity, and to a lesser degree, depth. Rainbow trout were most often observed in open main flow positions. Brook char were closely associated with cover and generally occurred in deeper water and slower flows than trout. The diet differences and longitudinal distributions of the two species seemed to reflect their respective microhabitat preferences. However, the degree of expression of these preferences was dependent on many factors including site morphology, water temperature, season, and fish age (and size).

BENTHOBSERVATORY EXPERIMENTS

The Benthobservatory is a semi-submerged 1.5 m X 2.1 m concrete shelter. It is located on Broad Cove Brook 7 km west of St. John's at approximately 49°34'N ; 52°52'W. By entering through the top of the structure, an observer can view the underwater stream environment through each of the four windows. Water is supplied to the structure via a diversion channel from the main stream approximately 10 metres upstream. A technical description and construction details were given by Laird et al (1974).

During 1980 and 1981, behavioural observations were made on brook char and rainbow trout in both inter- and intra-specific situations. The Benthobservatory provided an excellent opportunity for experimentation in a near natural setting. Water level, discharge, and temperature fluctuated normally as in the main stream. No supplemental feeding was necessary as natural food resulted from invertebrate drift, in-stream benthic production, and/or terrestrial invertebrates which lighted on or fell into the stream.

(i) The 1980 Experiments:

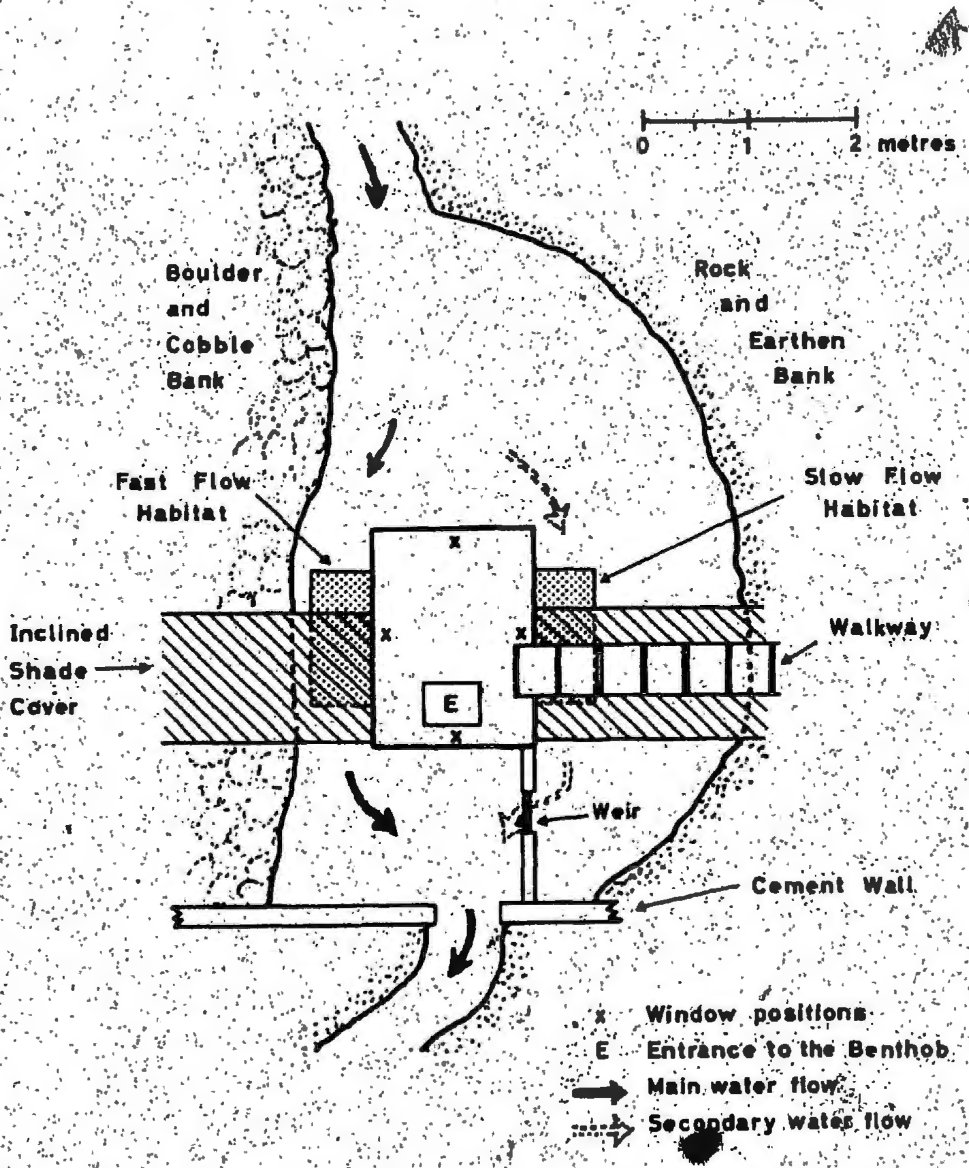
The Benthobservatory experiments of 1980 were designed to determine the effects of fast and slow microenvironments on the establishment of social hierarchies in inter-specific pairs of fish, and to correlate these results with field observations. The slow flow and fast flow enclosures (Figure 6) were assumed to simulate pool and riffle habitats, respectively. Agonistic activity, feeding frequency, position choice, and social status were recorded in an effort to determine if there was any evidence of species dominance in a particular flow regime.

Materials and Methods:

Two screen enclosures of 1.25 cm X 1.25 cm mesh were constructed and were placed in front of two of the windows of the Benthobservatory. These screens were fitted as tightly as possible against the sides of the Benthobservatory structure to prevent the escape of the experimental fish. Each enclosure extended above the water to a height of 30.0 to 40.0 cm. These were covered with a fine nylon mesh screen to prevent fish from jumping out and to prevent predation, particularly by kingfishers which were common in the area.

The underwater dimensions of the enclosures were 1.6 m

FIGURE 6. Diagrammatic view of the Benthobservatory facility during the 1980 experiments.


0 1 2 metres
Boulder and Cobble Bank
Rock and Earthen Bank
Fast Flow Habitat
Slow Flow Habitat
Inclined Shade Cover
Walkway
x
E
Weir
Cement Wall
x Window positions
E Entrance to the Benthob
Main water flow
Secondary water flow

X 1.0 m X 0.25 m deep for the pool habitat (slow flow) and 1.6 m X 0.8 m X 0.23 m deep for the riffle habitat (fast flow). Above the downstream half of each enclosure, a sheet of plywood measuring 2.0 m X 1.3 m was situated approximately 1 m above the water surface to provide shade cover. The substrate was primarily gravel within the riffle habitat and silt/sand in the pool habitat. Water velocity profiles were determined by periodic flow measurements (Ott meter) in both sides and are shown in Figures 1 and 2, Appendix C.

All fish used in the experiments were from natural populations : rainbow trout from Piccos Brook ; brook char from Pouch Cove Brook. The different locations precluded prior recognition of individuals used in the experiments which might have affected eventual hierarchial determination. Only overyearlings were used in these experiments. Initial lengths and weights of the fish are shown in Table 1, Appendix C.

Initially, all fish were captured by a plexi-glass fyke trap. It consisted of a 1.5 metre nylon mesh leader, two 0.8 metre adjustable plexi-glass wings and a two compartment trap body, measuring 0.9 m X 0.4 m X 0.4 m. This method was used in securing both species for the first five experiments. However, by mid August, the trap proved ineffective and angling with small barbless flies was used to provide fish for Experiments 6 to 9. Once captured, each species was kept in separate retainer boxes in the stream for a minimum of 8 hours to allow them to recover from the stress of capture and handling. Next, pairs of fish (one of each species) of approximately the same size (length and weight) were chosen. Each fish was anesthetized using 'Alka-seltzer' (1 tablet per litre of water), weighed on a triple beam balance (to nearest .1 g), and fork length (FL) measured (to nearest .1 cm). One pair of fish was then introduced, into the fast flow habitat and one pair into the slow flow habitat. Observations were started no sooner than one hour after introduction to allow for a period of adjustment and recovery. Experiment 1 was an exception. A period of five days acclimation between introduction and first observation was allowed and three fish were used in the slow flow habitat (2 brook char and 1 rainbow trout) rather than a pair.

Thirty minute observations were made on the fish in each habitat every second day with five observations per experiment. Again, Experiment 1 was an exception with five observations made over a period, of only seven days. In total there were nine experiments running from June 5, 1980 to October 17, 1980. Observations were carried out at various times between 0630 and 2000 hrs. To minimize any diurnal behavioural variation.

To avoid visual disturbance of the fish during the observations, they were viewed from behind a blind of dark plastic within the Benthobservatory. Water and air temperatures were recorded on a 8-day continuous recording thermograph. Water levels were regularly recorded in the main stream and the study area.

During all observations, fish position and orientation , agonistic behaviour, hierarchial status, and number and type of feeding moves were recorded for each species. In order to describe fish position, each enclosure area was subjectively divided into equal segments of a 3 X 3 X 3 matrix thereby providing 27 sub-sections. The flow measurements used to construct the velocity profiles (Figures 1 and 2, Appendix C) were taken at the mid-point of each of these sub-sections. A portable casette tape recorder was employed to record qualitative observations.

Agonistic behaviour was recorded on an Esterline-Angus event recorder using a multiple channel keyboard. Nine displays were identified and recorded per species. These were similar to those described by Kalleberg, 1958 ; Hartman, 1965 ; and, Jenkins, 1969b, and are listed below :

Lateral Display - a prolonged erection of the dorsal fin often in conjunction with extension of the paired fins although the degree of extension of the latter was variable and dependent on the intensity of the action (Baerends and Baerends-van Roon, 1950). The dorsal line of the body was either straight or slightly recurved. Duration of the lateral display varied from a minimum of 1 sec. to 15 sec. Orientation was such that the full lateral body surface was presented to the opponent.

Frontal Display - characterized by an arched back posture, extension of the basihyal apparatus with concomitant gape, and the dorsal fin fully retracted against the body. Orientation was usually 'head on' to the opponent and duration was variable but usually less than 5 seconds.

Nips - contact of one fish on another with an open mouth for the assumed purpose of biting.

Threat Nips - similar to nips but without apparent contact and no obvious intention of biting because the distance separating the fish often precluded this possibility.

Chase - an accelerated movement by one fish in pursuit of another. This action often terminated in bodily contact such as a nip.

Approach - a deliberate swimming movement or orientation by one fish toward another which may or may not have resulted in a retreat by the latter.

Backward Displacement - a movement of one fish anteriorly to another fish, followed by the former fish drifting back towards the other and resulting in its displacement.

Retreats - an abandonment of some previously occupied position resulting from one (or a combination) of the above described aggressive acts. Retreats were primarily oriented away from the displaying fish and consisted of either slow or accelerated swimming, the speed often directly related to the intensity of the aggressor's act. A retreat was described by Jenkins (1969b) as a submissive action.

Submissive Posture - an obvious retraction of the dorsal and paired fins and, if position was close to the substrate, a lowering of the body position such that the ventral surface came in contact with the stream bottom. These were always made in response to one of the above acts (excluding retreats). Submissive postures were often (but not always) effective in deterring further aggression by a dominant fish. Jenkins (1969b) termed this an 'appeasement' strategy.

Dominant hierarchial status was based on a fish showing a minimum of three of four 'dominance criteria' during one observation period. There was never an observed reversal of status once a fish was assigned a status rank.

The criteria used for dominance were :

(1) Initiating all aggressive acts in an observation period. Aggressive acts included all the behavioural acts previously described except for retreats, submissive postures, and lateral displays. Since dominant individuals are most often the aggressors (Lorenz, 1966 ; Manning, 1972), this was considered a reliable indicator of higher social rank. Newman (1956), Yamagishi (1962), and Noakes and Leatherland (1977) based their estimations of dominance

on the frequency of aggressive acts by one fish on another in a type of 'nip right' relationship, thereby assuming that these represented unit expressions of dominance.

(2)Colour change : This was most obvious for the rainbow trout where subordinate ranking fish assumed a dark colour band extending along the lateral line from tail to opercula and occasionally continuing through the eye imparting a dark colour or type of 'eye-stripe'. Brook char colour changes were more difficult to distinguish. A slight darkening of the overall body colour generally occurred in subordinate individuals as was noted by Newman (1956).

(3)Continuous anterior position relative to the other fish : Since anterior feeding positions within a given space are favoured positions of dominant individuals (Hartman, 1965 ; Butler and Hawthorne, 1968), this was considered a good indicator of status. However, positions must have been comparable at that point in time when the determination is made. That is, a position high in the water column in turbulent flow necessitating apparently great expenditures of energy to maintain position was not considered desirable even though it may be anterior relative to the other fish. Likewise, anterior substrate positions in sheltered corners which were obviously not feeding positions were not considered as dominance criteria.

(4)Mobility within the enclosure space : This criterion was based on the premise that the dominant ndividual showed more 'unchallenged freedom of movement' within all areas of the enclosure whereas a subordinate was restricted to a minimal space and often moved only posteriorly to the dominant (criterion 3). This distinction precludes the existence of territories and site-specific hierarchies (Noakes, 1978) and assumes that the social structure formed is of a dominance hierarchy. In fact, this was found to be the case. None of the experiments showed evidence of simultaneous territoriality by both fish in a pair. That is, the dominant fish (when a hierarchy was established) apparently treated the entire enclosure as its territory with no observable spatial defence exhibited by the subordinate. Most likely this was a function of the small space of the enclosures which had bottom areas of 1.3 square metres and 1.6 square metres, for riffle and pool sides respectively. Both these values were below the estimated territory sizes for overyearling stream salmonids for a number of different species and locations (see Allen, 1969, for review).

Feeding was also quantified. A feeding move was defined as any movement by a fish towards an item and the subsequent ingestion of that item. Therefore, the ingestion and possible later rejection of an item was still treated as a feeding move whereas movement to an item, without ingestion, was not.

After the series of observations constituting an experiment were completed, fish were removed , weighed, measured, and preserved in 10 % formalin for later sex determination.

On August 23 and September 15, a series of observations were made throughout the day for groups 6 and 8, respectively. Observations were started at 0630 hrs and were continued every three hours with the last occurring at 1830 hrs. Experimental procedure was the same as described above except no event recorder was used. The purpose of these day-long observations was to determine if any variation in behaviour occurred between dusk and dawn.

Results :

All quantitative data were analysed using one factor and two factor analyses of variance (ANOVA) for unequal sample sizes (Sokal and Rohlf, 1973). These tests were intended to test for differences in a number of measured variables between species, status levels, and flow situations. Some non-parametric correlation analyses were also performed. All statistical testing was accomplished with the SPSS computer package (Nie et al, 1975).

Data from the 1980 experiments are shown in Table 1,

Appendix C. Nine experiments were conducted between June 5 and October 17, 1980. In the fast flow (riffle habitat), eight experiments resulted in social hierarchies. Each species established dominance four times. In the slow flow (pool habitat), six of the nine experiments resulted in social hierarchies. Only one rainbow trout became dominant (Experiment 2). In some of the experiments, no social hierarchy resulted. This was due to the failure of satisfying the prescribed dominance criteria or because of escape of the experimental fish prior to any hierarchial identification. Such escapes were usually a consequence of high water flows during spates which damaged the screen enclosures (Experiment 3, brook char - Riffle habitat ; Experiment 7, both habitats ; Experiment 9, Riffle habitat).

Statistical tests showed that no significant difference existed between species for initial fork lengths ($P > .05$) or for initial weights ($P > .05$). Likewise, no significant difference was found between dominants and subordinates with respect to initial fork lengths ($P > .05$) or initial weights ($P > .05$). Therefore, these variables were not considered important in affecting eventual social status in these experiments. Both species were able to attain dominance even when they were at a slight size disadvantage.

Sex was determined for only 36 % of the experimental fish after observations. All these were immature and no apparent effect of sex on status determination was recognized.

No significant difference was found between species with respect to weight change ($P > .05$) but it was greatly affected by social status. A good correlation ($r = .6761$; $P < .01$) was found between status and weight change. Dominant fish, regardless of species, showed a significantly different ($P < .01$) weight change (net positive) from subordinates which showed a net weight loss. The dominant's weight gain was realized in every experiment in the fast flow habitat and in 67 % of the experiments (where a hierarchy was identified) in the slow flow habitat.

Table 2, Appendix C shows the total number of agonistic acts per experiment for each flow situation. Generally, the frequency of agonistic encounters was higher in the riffle side than in the pool side but the difference was not significant ($P > .05$). The fact that subjects were prevented from leaving the enclosures may have increased the potential for interactions (Chiszar et al., 1975). The higher frequency of agonistic acts in the slow flow habitat in Experiment 1 was likely due to the presence of three fish which would increase the probability of interaction. No significant differences ($P > .05$) were found between species with respect to total agonistic activity and each species' behavioural displays were apparently understood by the other as if they were the same species (Newman, 1956).

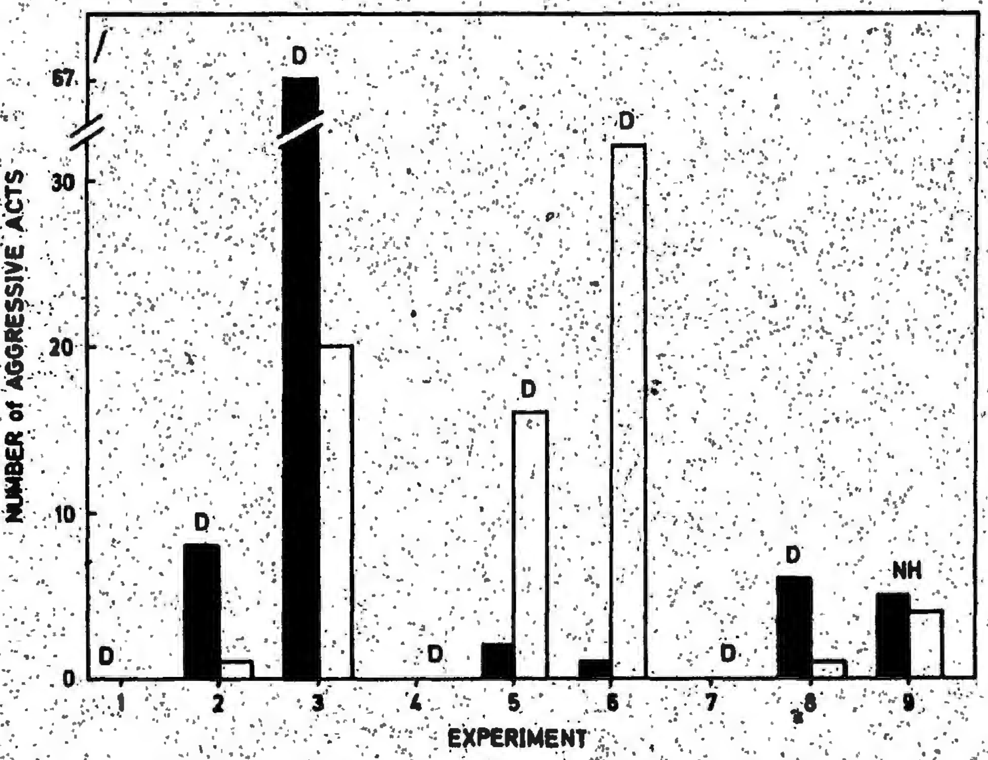
It was assumed that one fish would affect the behavioural expression of another, once a hierarchy was established. Therefore, it was decided that a measure of agonistic activity before dominance would give a more meaningful estimate for species comparisons. Figures 7 and 8 show the results for riffle and pool habitats, respectively. Only aggressive acts were included for these calculations, thereby omitting the data for 'retreats' and 'lateral displays', which were considered submissive (Jenkins, 1969b) or ambivalent acts containing elements of both attack and escape behaviour (Manning, 1972 ; Chiszar et al, 1975).

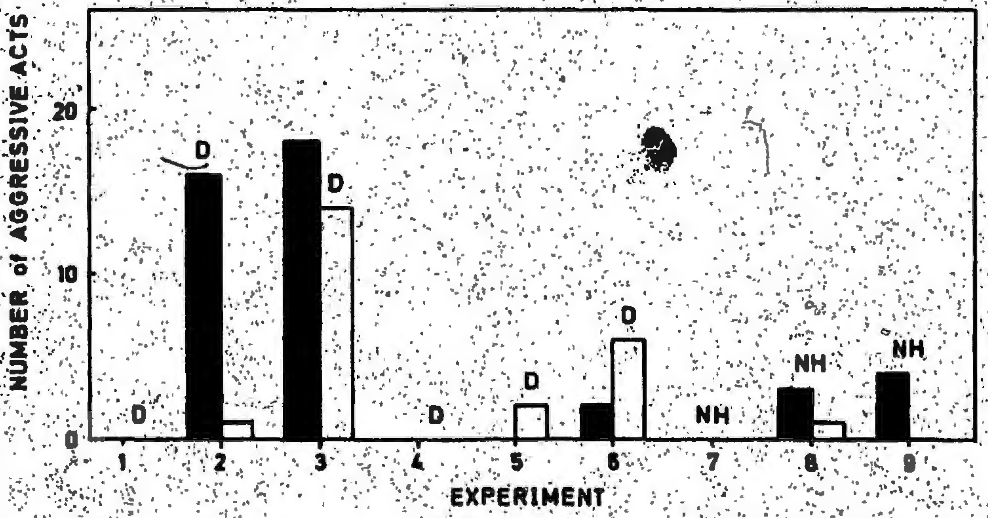
In all cases but one (Experiment 2, pool side), the eventual dominant fish initiated most of the aggressive acts. This suggests that the social status was determined prior to recognition of it by my criteria. If true this supports the need for extreme caution and equalization of conditions for each fish prior to behavioural observation since initial encounters may be the most important determinant of ultimate social structure. No species differences for aggressiveness were apparent from Figures 7 and 8. Most of the variation was attributed to social status differences.

The types of agonistic acts observed showed some differences between species and flow situations. In the fast flow habitat, lateral displays, approaches, and

FIGURE 7. Frequency of aggressive acts per experiment by rainbow trout (solid bars) and brook char (open bars) before hierarchial determination in the fast flow habitat of the Benthobservatory in 1980. D = eventual dominant fish ; NH = no heirarchy identified. For Experiment 1, the hierarchy was established prior to any observations (see text).

FIGURE 8. Frequency of aggressive acts per experiment by rainbow trout (solid bars) and brook char (open bars) before hierarchial determination in the slow flow habitat of the Benthobservatory in 1980. D = eventual dominant fish ; NH = no heirarchy identified. For Experiment 1, the hierarchy was established prior to any observations (see text).


NUMBER of AGGRESSIVE ACTS
67
30
20
10
0
D
D
D
D
D
D
D
D
NH
1
2
3
4
5
6
7
8
9
EXPERIMENT


NUMBER of AGGRESSIVE ACTS
20
10
0
D
D
D
D
D
D
NH
NH
NH
1
2
3
4
5
6
7
8
9
EXPERIMENT

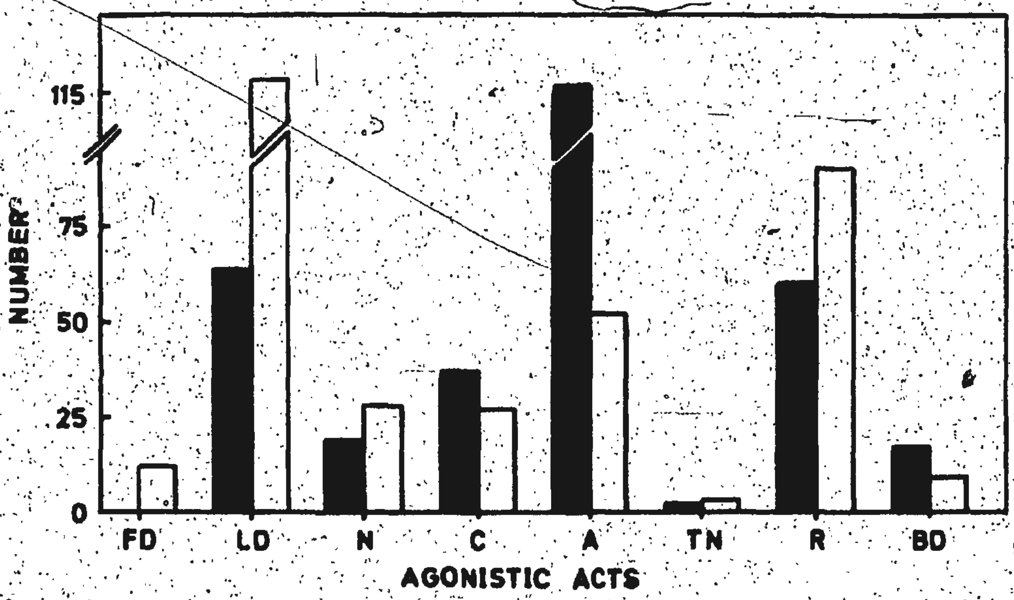
retreats were the most common agonistic acts observed (Figure 9). Brook char showed the most lateral displays and rainbow trout showed the most approaches. Newman (1956) also found brook char to use more elaborate threat displays (eg. lateral displays) than rainbow trout and suggested that this indicated a more advanced social behaviour where non-injurious acts predominate.

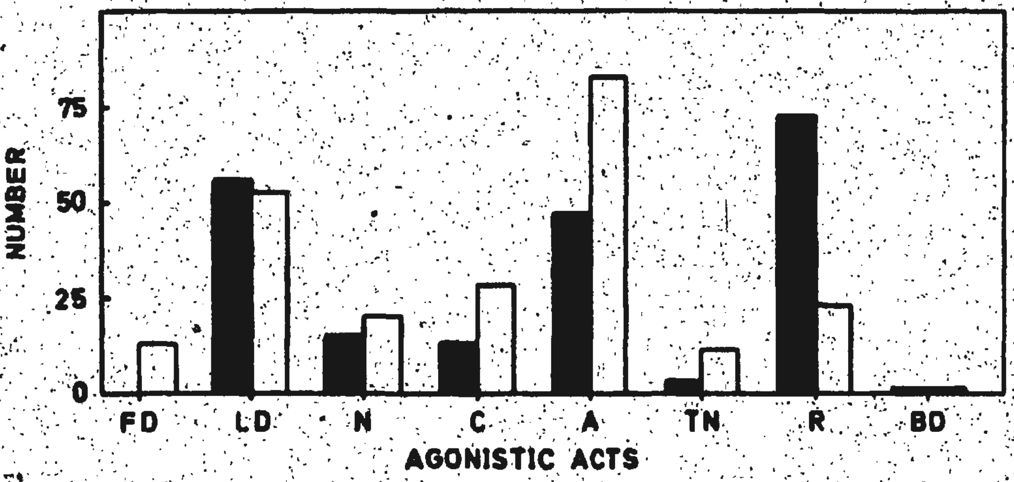
In the slow flow, approximately the same pattern of agonistic behaviour occurred but the frequency of each act was less (Figure 10). Lateral displays, approaches, and retreats were again the most common acts. The comparatively low frequency of aggressiveness by trout in the slow flow can be explained by the dominance of char here and the resultant suppression of such acts as chases (and nips) by the subordinate trout which instead, showed a high number of retreats. In fact, 53 % of all nips and 54 % of all the chases recorded for trout, occurred in Experiment 2, the only time a rainbow trout was the dominant fish in the slow flow habitat.

The frontal display was the only behavioural act unique to the brook char. It was observed with approximately the same frequency in both flow situations. This is an aggressive display associated with the attack response (Kalleberg, 1958 ; Keenleyside and Yamamoto, 1962) and was never initiated by a subordinate char. No behavioural displays unique to rainbow trout were observed in these

FIGURE 9. Frequency of agonistic acts for rainbow trout (solid bars) and brook char (open bars) in the fast flow habitat of the Benthobservatory during the 1980 experiments. Values are for all experiments combined. FD = frontal display , LD = lateral display , N = nip , C = chase , A = approach , TN = threat nip , R = retreat , BD = backwards displacement.

FIGURE 10. Frequency of agonistic acts for rainbow trout (solid bars) and brook char (open bars) in the slow flow habitat of the Benthobservatory during the 1980 experiments. Values are for all experiments combined. FD = frontal display , LD = lateral display , N = nip , C = chase , A = approach , TN = threat nip , R = retreat , BD = backwards displacement.


115
75
50
25
0
NUMBER
FD
LD
N
C
A
TN
R
BD
AGONISTIC ACTS


75
50
25
0
NUMBER
FD
LD
N
C
A
TN
R
BD
AGONISTIC ACTS

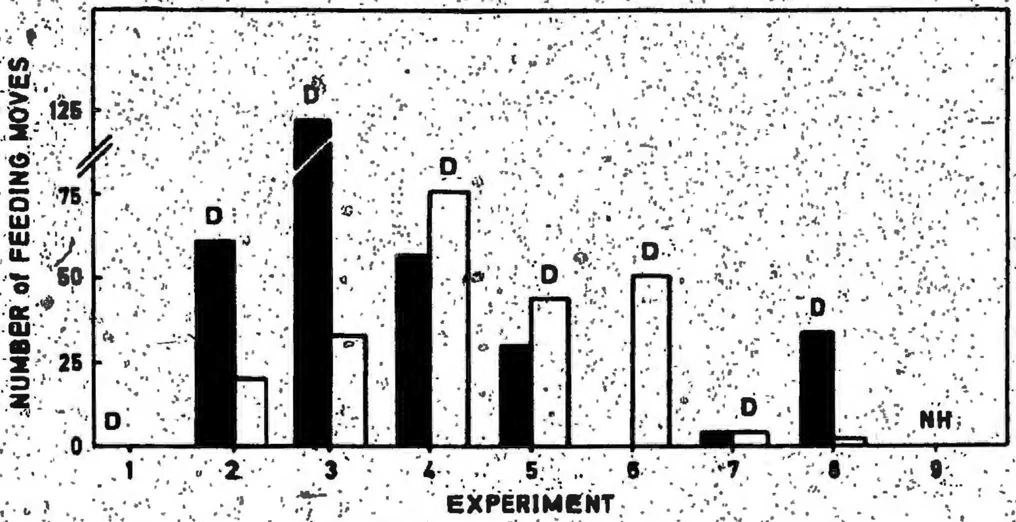
experiments.

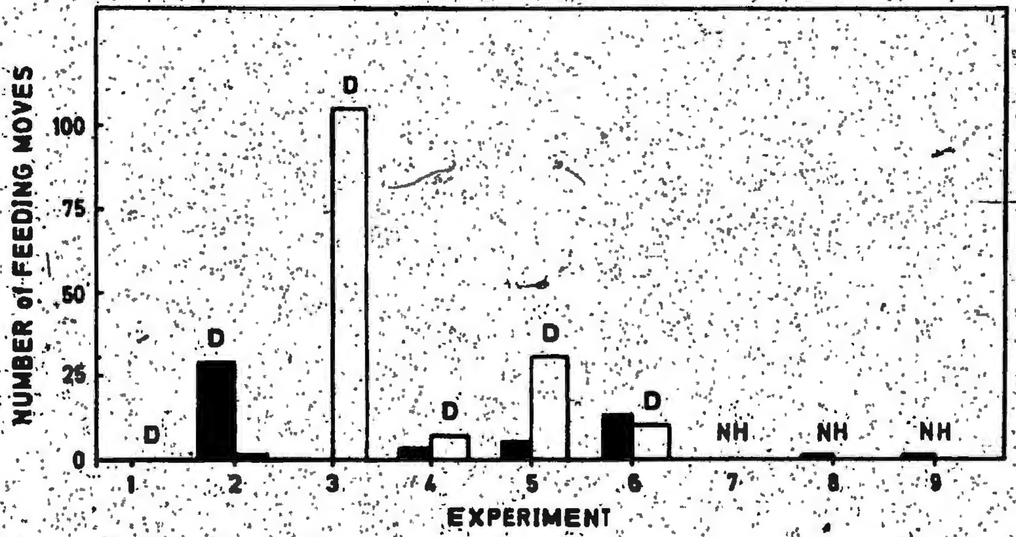
Table 3, Appendix C shows the total number of feeding attempts observed per experiment in each flow habitat. Feeding attempts were much more frequent in the fast flow habitat but the difference was not significant ($P > .05$). The increased feeding resulted in greater general activity in the fast flow habitat often resulting in interaction which may explain the more numerous agonistic activity observed here. No significant species differences were identified for numbers of feeding attempts (both sides combined, $P > .05$) but brook char did have a higher mean frequency probably because of its dominance and subsequent greater feeding within the pool side since dominant fish made significantly more feeding attempts than subordinates ($P < .05$) in both the riffle side (Figure 11) and the pool side (Figure 12). Feeding was also greater for the eventual dominants in both sides before any hierarchy was recognized. This is similar to the results for agonistic activity before dominance and again indicates that hierarchies were established prior to my recognition of them.

Generally, water temperature was not an important factor in most of these experiments because of the cool and wet summer experienced in 1980. Only experiments 2 and 5 were subjected to adversely high water temperatures which may have affected results. Brook char have a lower temperature tolerance than rainbow trout (Fry, 1948) and 20

FIGURE 11. Frequency of feeding moves per experiment by rainbow trout (solid bars) and brook char (open bars) in the fast flow habitat of the Benthobservatory during the 1980 experiments. D = dominant fish , NH = no hierarchy identified. Feeding was not recorded in Experiment 1.

FIGURE 12. Frequency of feeding moves per experiment by rainbow trout (solid bars) and brook char (open bars) in the slow flow habitat of the Benthobservatory during the 1980 experiments. D = dominant fish , NH = no hierarchy identified. Feeding was not recorded in Experiment 1.


NUMBER of FEEDING MOVES
0
25
50
75
125
D
D
D
D
D
D
D
D
NH
1
2
3
4
5
6
7
8
9
EXPERIMENT


NUMBER of FEEDING MOVES
0
25
50
75
100
D
D
D
D
D
D
NH
NH
NH
1
2
3
4
5
6
7
8
9
EXPERIMENT

C is generally considered the maximum tolerable temperature (Fry, 1951). The 36 hrs. > 20°C experienced during Experiment 2 (Table 7) may have negatively affected brook char, presumably to a greater degree than it would rainbow trout. This may have been part of the reason for the dominance of the rainbow trout in Experiment 2 (both sides). It should be noted that temperatures in the slow flow habitat tended to be between 0.5°C and 1.0°C warmer than those measured in the riffle side due to the lower flushing rate and therefore the effect may have been greater than in the fast flow habitat.

The results of Experiment 5 seem contradictory to the preceeding observations as brook char dominated in both water flows, although water temperatures were even higher than recorded in Experiment 2. The reason may have been the differential treatment of the fish prior to observations. Brook char were captured by fyke trap and allowed to recuperate (in retainer boxes) for two days prior to observations. Difficulty in capturing rainbow trout by trap resulted in their being angled only six hours prior to observations. It is very likely that they were much more stressed than the char at the start of the experiment. Degree of stress can be a major factor in dominance ranking (Ejike and Schreck, 1980) even though the effects are not readily apparent (Wedemeyer, 1972 ; Mazeud et al, 1977) and may have contributed significantly to the hierarchial

TABLE 7. Water temperatures recorded in Broad Cove Brook, at the inflow of the benth-observatory, during the 1980 experiments.

Temperature Category	Experiment								
	1	2	3	4	5	6	7	8	9
Number of Hours >20°C	0	36	1	0	74	0	0	0	0
Maximum Daily Temperature (°C)	16.0	23.6	20.1	19.0	24.7	18.1	18.9	17.9	11.5
Minimum Daily Temperature (°C)	9.8	15.0	14.0	15.1	17.8	15.0	15.0	13.0	9.0

outcome especially since initial encounters can be an important determinant of dominance (as noted earlier).

Position choice was similar for both species, that being a preference for the most anterior position facing into the current. This was true for both sides and was always the position of the dominant individual. In such a confined space as these experimental habitats, the ultimate position of a subordinate was 'dictated' by the dominant. Generally, they appeared to hold positions which minimized the probability of interaction. Experiment 5 provided the opportunity to test the position choice of a subordinate once a dominant was removed. After the third observation, the dominant brook char died and was removed. During the remaining observations, the rainbow trout lost its dark subordinate colouration, held positions at the upstream end of the enclosure and showed a substantial increase in feeding. This behaviour indicates the preference of an anterior position and the disadvantage of being a subordinate.

The only noticeable species difference for position choice was the affinity for substrate positions by dominant char. Dominant rainbow trout showed a preference for positions higher in the water column. These differences were only obvious in the slow flow of the pool side. Newman (1956) also found rainbow trout to prefer mid-water stations and brook char to prefer the substrate in slow flow conditions. No vertical position differences were apparent in the riffle side. High water velocity here seemed to require both species to hold positions close to the substrate where water velocity is less (Morisawa, 1968).

The results of the day-long observations (August 27 and September 15) suggests no direct relationship between position choice, frequency of feeding, or frequency of agonistic acts with time of day or weather conditions (Table 5 a,b, Appendix C) at least for these experiments. Feeding was observed by both species throughout the day whether water temperatures were high and the sun was shining (August 27) or when the sky was overcast and it was raining (September 15). Feeding responses in the fast flow habitat were more numerous than those in the slow flow habitat, a function of drift preponderance here. The slightly higher feeding response of fish in both sides at dusk (September experiment) was probably due to the increased drift caused by heavy rains, rather than to drift periodicity (Waters, 1969).

Discussion :

The hierarchial results indicate a superior ability by brook char to achieve dominance over similar sized rainbow trout in a slow flow (pool) situation. The assumption here was that each fish in a pair was in the same relative physiological and physical condition prior to observations. The dominance of brook char in a pool type environment would be advantageous since field observations indicate this species prefers such a habitat. In the fast flow (riffle) situation, no clear species advantage was apparent as both species attained dominance with equal frequency. My field observations suggest that trout were more common than char in riffle habitats. Therefore, the ability of brook char to achieve dominance in the fast flow situation, as often as did trout, was not expected. Newman (1956) studied these two species in the lab and in the field and found that in confined or concentrated conditions, brook char were more aggressive and more likely to dominate rainbow trout. His lab and stream observations were made in near static conditions and pools, respectively, which may partially explain the greater dominance of char. Nevertheless, the confinement of the Benthobservatory enclosure may have provided the char with a competitive advantage by differentially increasing their aggressiveness, as suggested by Newman, even in the fast flow habitat.

It is also possible that the relative success displayed by char in the fast flow habitat was because water velocities experienced here were not outside their preferred range (according to the focal point velocities measured at the three stream sites). The position choice of the dominant char was mainly close to the substrate and often near the glass window where flows would be minimized due to frictional drag (Morisawa, 1968). Figure 1, Appendix C shows that the greatest mean velocity recorded in those positions favoured by dominant brook char (i.e. near substrate in upstream two-thirds of enclosure) was only 33.8 cm/sec., which was within the range of focal point velocities measured in the field for this species (Table 1, Appendix B) although higher than their mean values (Table 4).

General agonistic behaviour and feeding in these experiments, indicated no species differences with respect to these variables. The only statistical differences were between flow situations and hierarchial status. In the fast flow habitat, feeding and agonistic activity were greatest as expected from the greater drift availability here and the close association of these two behaviours (Keenleyside and Yamamoto, 1962 ; Symons, 1968 ; Dill, 1977). Dominant fish fed more frequently and were more aggressive than subordinates, regardless of species. This explains the greater frequency of weight gain among dominant individuals than subordinates. The lower number of dominants showing a weight gain in the slow flow habitat was likely due to less food availability, especially invertebrate drift, as compared to the fast flow habitat. Yamagishi (1962) suggested another reason which could explain the dominant's lower growth rate in the slow flow habitat. In his experiments, he found that dominant rainbow trout did not show a faster growth rate than subordinates until a social status was firmly established, which he estimated at 2 - 4 weeks. My experiments lasted a maximum of 2 weeks and in the 2 experiments where the dominants did lose weight, the times to hierarchial establishment were among the longest recorded.

A positive weight change would be expected if dominant status conferred a superior feeding position, often indicated by most anterior station within a habitat (Hartman, 1965 ; Gibson, 1981 ; McNicol and Noakes, 1981). This was very obvious in these experiments. Initial species interactions often involved competition for an anterior position relative to the other fish, orientation being positively rheotactic. This response was most common and stereotyped in the fast flow habitat, a function of water velocity. However, even the low flows in the slow flow habitat were sufficient to stimulate preference for an anterior position facing into the current. Once a hierarchy was established, the dominant fish always maintained an anterior feeding position and the subordinate could feed only on items which passed by the dominant. Attempts by the subordinate to feed anterior to the dominant resulted in immediate aggression by the latter eventually resulting in the subordinate being driven back to its original position.

Difficulty can arise in interpretation of the results of the Benthobservatory experiments beyond the range of their limitations. Confinement and crowding are serious factors requiring careful consideration prior to behavioural interpretation. The stress of handling and manipulation of the fish throughout the experiments was assumed to have affected both species equally but this may not have been true although general behaviour indicated it was. There was some evidence that rainbow trout may have shown a greater dominance in the fast flow habitat under more standardized sampling procedures and in less confined situations. Despite the limitations, the results contribute to an understanding of the social interactions, and habitat preferences of these two species.

The ability of brook char to dominate rainbow trout in a slow flow (pool-type) situation correlates with my field observations of the preference by char for slow flow stream habitats. The ability of rainbow trout to achieve dominance as often as char in a fast flow situation suggests at least an equal ability by trout to compete for preferred positions in riffle habitats. Likewise, indications are that at high stream temperatures (i.e. > 20°C), rainbow trout may show a behavioural and physiological advantage over char which could increase the ability of trout to dominate in lotic habitats.

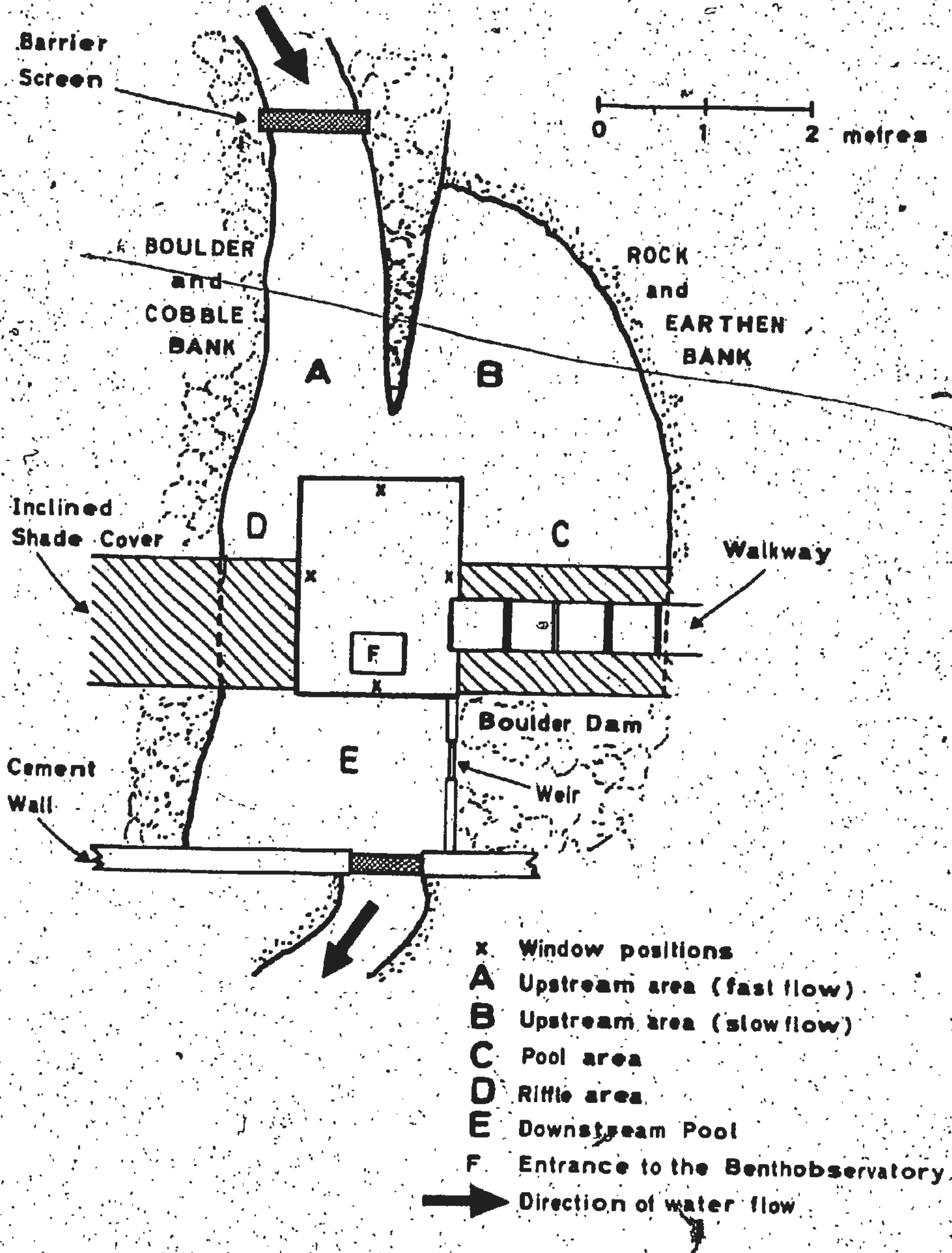
(ii) 1981 Experiments:

In 1981, the Benthobservatory was used for a different set of experiments. The area immediately around the Benthobservatory was arranged to provide a variety of microhabitats of variable velocity, depth, cover availability, and substrate type. The purpose was to provide each species with a range of habitats and then to record their frequency of occurrence within the different habitats. Experiments were performed to observe distribution and microhabitat choice in intra-specific and inter-specific situations. Comparisons were made between these results and the field observations.

Materials and Methods:

With a system of weirs, boulder dams, and wood/rock deflectors, a 16.6 sq. m. area, that could be viewed from within the Benthobservatory, was divided into four sections : an Upstream area with variable flow habitats ; a Pool with negligible flow ; a Riffle ; and a Downstream Pool with variable substrate type and current patterns (Figure 13). Differentiation of the Upstream area into fast flow and slow flow habitats was by an imaginary boundary running

FIGURE 13. Diagrammatic view of the Benthobservatory facility and the surrounding area during the 1981 experiments.


Barrier Screen
0 1 2 metres
BOULDER and COBBLE BANK
ROCK and EARTHEN BANK
A
B
D
C
Inclined Shade Cover
Walkway
F
Boulder Dam
Weir
E
Cement Wall
x Window positions
A Upstream area (fast flow)
B Upstream area (slow flow)
C Pool area
D Riffle area
E Downstream Pool
F Entrance to the Benthobservatory
Direction of water flow

from the upstream window to the apex of the wood/boulder deflector. Overhead cover was provided by two 1.3 m X 2.0 m plywood sheets placed approximately one metre above the water surface (as used in the 1980 experiments). One of these was situated over the Riffle area and the other over the Pool area. Instream cover was provided by turbulent water surface, rubble/boulders, aquatic vegetation (mainly Sparganium sp. and Juncus bulbosus L. especially in the later experiments due to seasonal growth), and the Benthobservatory structure itself.

Substrate type varied from predominantly gravel/rubble in the riffles and runs to silt/sand/detritus in the Pool area and gravel/rubble/boulder in the Downstream Pool (Table 1, Appendix D).

Water velocity and depths were recorded throughout the study area during low water conditions (August 14, 1981) and again during peak seasonal discharge (September 16, 1981). Water velocity was measured at 0.60 of the water depth (Hynes, 1970) with an Ott flow meter.

To prevent fish movement to or from the experimental area, a series of barrier screens (1.3 cm X 1.3 cm mesh) were situated at both its upstream and downstream ends. These screens extended approximately one metre above the water surface at the inflow and 1.5 m at the outflow.

Inter-specific and intra-specific experiments were carried out between May 6 and August 11, 1981. Three intra-specific experiments (two with rainbow trout only and one with brook char) were conducted, followed by three inter-specific experiments.

As in 1980, the rainbow trout were from Piccos Brook and the brook char were from Pouch Cove Brook. Sampling was done with a Smith Root Type V backpack electrofisher. Fish were selected for similarity of size, generally between 10.0 and 15.0 cm FL. Numbers of fish introduced for the intra-specific experiments were 27 (Expt 1 - trout), 27 (Expt 2 - char), and 19 (Expt 3 - trout). For the inter-specific experiments, the numbers of each species were identical but totals differed between experiments : 26 (Expt 4), 26 (Expt 5), and 20 (Expt 6). The variable number of fish introduced for the different experiments was a reflection of the availability of the fish during the different sampling dates. In all cases the resultant densities were greater than the densities of overyearling stream salmonids that have been recorded elsewhere (see review in Allen, 1969). High densities were used for two reasons : (1) to increase the probability of interaction ; and, (2) to ensure that a representative number of fish would be observed throughout an experiment since losses were to be expected from escape or predation and to account for those fish out of sight of the observer.

Before the start of an experiment, fish were kept in retainer boxes (1.0 m X 1.0 m X 1.0 m) for a minimum of six hours. Prior to the inter-specific experiments, each species was held in a different box. Fish were then anesthetized, measured (FL to nearest 0.1 cm), weighed (to nearest 0.1 g), and individually branded with a hot Nichrome wire on each side dorsal to the lateral line. Following their recovery in the retainer boxes, they were introduced en masse to the Downstream Pool area.

Observations began the day following introduction (minimum of 12 hrs). Each experiment consisted of six observations made on alternate days and at variable times during daylight hours from 0800 to 2000 hrs. All observations were made through a 5.0 cm X 20.0 cm 'eye - slit' behind a dark plastic blind within the Benthobservatory. Each observation was of 15 min duration for each of the four window areas. Upon entering the Benthobservatory, a minimum of 30 min was allowed prior to any observation. This was to give fish time to recover from any disturbance resulting from the observer's entry into the structure. Individual identification, position, feeding behaviour, residence time (i.e. number of minutes within a particular area or station), and agonistic activity were noted for all fish seen.

After an experiment, subjects were recaptured by electro-fishing. Each fish was identified, measured, weighed, and preserved in 10 % formalin for later sex determination and stomach analysis.

Results :

The one way ANOVA test for unequal sample sizes (Sokal and Rohlf, 1973) was used for data analysis. Data were grouped by species, distinguishing between intra-specific and inter-specific experiments.

During the first intra-specific experiment (A), many of the fish (rainbow trout) escaped after the fourth observation period resulting in a recovery of only 30 % of the subjects at the end of observations. Consequently, another intra-specific experiment (C) with rainbow trout was performed and the data from both experiments (A and C) were grouped for statistical comparison with the intra-specific char experiment (B).

For all the intra-specific experiments, no significant difference was found between species for initial fork length ($P > .05$) or for initial weights ($P > .05$) although the mean length of brook char (9.70 cm) was slightly greater than that for rainbow trout (9.59 cm) and the latter had a larger initial mean weight (Table 8).

For the inter-specific experiments, no significant species difference was found for initial fork length ($P > .05$). However the initial weights of rainbow trout were significantly heavier ($P < .05$) than those for char (Table 8). Despite the significant weight difference, it was assumed no differential advantage was realized by rainbow

Table 8. Comparisons between rainbow trout (T) and brook char (C) for initial lengths and weights during intra-specific and inter-specific benthobservatory experiments in 1981, using analysis of variance (ANOVA).

n - sample size; * p < .05, ns - not significant

Criterion Variable	Species	Intra-specific Experiments			Inter-specific Experiments		
		n	Mean	F-ratio	n	Mean	F-ratio
Initial Fork Length (cm)	T	46	9.60	0.042 ns	36	12.20	3.076 ns
	C	27	9.71		36	11.59	
Initial Weight (g)	T	46	12.55	0.292 ns	36	22.28	5.754*
	C	27	11.03		36	17.91	

trout over brook char in these experiments due to this factor alone.

The weight change of each fish during an experiment was determined and statistical comparisons were made between species. To compensate for any differences in specific growth rates, final weights were also expressed as percentages of the initial weights, and similarly analysed. No difference was found between the results of either procedure (Table 9). In the intra-specific experiments (A - C), there was a significant difference ($P < .01$) between species, for weight change. Brook char showed a mean weight gain whereas rainbow trout showed a mean weight loss.

Weight change was also significantly different ($P < .05$) between species in the inter-specific experiments (Table 9). Rainbow trout showed a net weight loss as in the intra-specific experiments. Brook char also showed a net weight loss but not as great as shown by trout. Mean final weights of trout were approximately the same as initial weights in both sets of experiments - i.e. approximately 92% of the initial weight. Char final weights averaged greater than 100% of the initial weight in the intra-specific experiments but only 95% of the initial weight in the inter-specific experiments (D - F).

The frequency of occurrence of each species within the various habitat areas was tested (Table 10). Only station holding fish (maintaining stationary position on or off the

TABLE 9. Comparisons between rainbow trout and brook char for weight change during the 1981 benthobservatory experiments, using analysis of variance (ANOVA). $^{*}p < .05$, $^{**}p < .01$

Experiments	Criterion Variables	Independent Variables	Sample Size[a] (n)	Mean	F-ratio
Intra-specific	ΔWt_1[b]	Trout	17	-1.006	7.668**
		Char	21	+0.291	
	ΔWt_2[c]	Trout	17	92.40	10.238**
		Char	21	100.1	
Inter-specific	ΔWt_1	Trout	27	-1.559	4.366*
		Char	27	-0.907	
	ΔWt_2	Trout	27	92.07	5.298*
		Char	27	95.13	

[a] Numbers of fish recovered at the end of experimental observations

[b] Final weight - Initial weight; gram units

[c] (Final Weight ÷ Initial Weight) x 100

Table 10. Comparisons between rainbow trout and brook char for numbers of fish observed in each of the experimental habitats at the Benthobservatory in 1981. All statistical testing was by analysis of variance (ANOVA).

*p < .05, **p < .01, ns - not significant

Experimental Habitat	Independent Variable	Intra-specific experiments: Mean Number of fish per observation	Intra-specific experiments: F-ratio	Inter-specific experiments: Mean Number of fish per observation	Inter-specific experiments: F-ratio
Upstream area (fast flow)	Trout	3.00	2.846 ns	1.00	6.760*
	Char	0.17		0.28	
Upstream area (slow flow)	Trout	0.39	1.427 ns	0.0	4.208*
	Char	1.17		0.28	
Pool	Trout	0.23	10.757**	0.0	—
	Char	2.00		0.0	
Riffle	Trout	0.31	3.442 ns	0.50	2.033 ns
	Char	0.83		0.22	
Downstream Pool	Trout	6.08	4.828*	4.17	4.203*
	Char	9.67		6.22	

substrate for a minimum of five min.) were used for these analyses.

In intra-specific experiments, rainbow trout showed a higher mean frequency of occurrence than brook char in the fast flow section of the Upstream area and in the Riffle area but the differences were not significant (P > .05). In the slow flow section of the Upstream area, brook char were observed more often than trout but again the difference was not significant (P > .05). Despite the lack of conclusive statistical data, observations suggest different microhabitat preferences within these particular areas especially with respect to localized flow patterns. Within the Riffle area, isolated `pockets' of low flow were more often used by char than trout, with the latter mainly seen holding station in the main flow of midstream. In the Upstream (fast flow) area, as many as 13 trout were seen during a single observation. There was never more than one char seen here per observation.

Within the Pool and the Downstream Pool areas, during the intra-specific observations, there were significant species differences (P < .01 and P < .05, respectively) for frequency of occurrence. In both cases, brook char were the more numerous species. Both species were observed most often in the Downstream Pool and consequently this was the area of highest concentration. Microhabitat segregation between species within the Downstream Pool was also _emonstrated according to position of fish relative to the flow pattern. Rainbow trout showed a preference for stations at the head of the pool and in the main current. Brook char were mostly observed in the central and back-eddy sections where water velocity was the lowest. Since the largest and most aggressive individuals of both species were observed in these respective microhabitats, it was assumed to be a position preference rather than a secondary choice due to inferior social status. Even so, subordinate rainbow trout have been observed to show a similar position choice to dominants even when displaced (Jenkins, 1969b).

For the inter-specific experiments, the species also showed different habitat preferences within the study area. In the Upstream area, rainbow trout were observed significantly more often than char in the fast flow section ($P < .05$) whereas char were seen significantly more often in the slow flow section ($P < .05$). In fact, rainbow trout were never seen in the latter. Within the Pool area, neither species was seen during any of the observations. This is probably due to the higher water temperatures experienced here compared to the other areas. Lack of detectable flow created near stagnant conditions and water temperatures rose quickly, occasionally exceeding 25°C on hot, sunny days.

No significant difference was found between species for frequency of occurrence within the Riffle area ($P > .05$) but qualitative differences between species were the same as noted in the intra-specific observations. Trout often held open main flow stations wheras brook char utilized back-eddies and instream cover out of the main current.

In the Downstream Pool, char were observed significantly more often than trout (P < .05) preferring the central and low flow sections. Trout were most often seen in main current stations, especially at the head of the pool. The similarity of the results from both the intra- and inter-specific experiments suggests that distribution patterns are the result of species preferences rather than species interactions.

Lower water levels and higher water temperatures were experienced in the inter-specific experiments compared to the intra-specific experiments (Table 2, Appendix D). This was believed the reason for the low numbers of fish observed in the Upstream, Pool, and Riffle areas as compared to the intra-specific experiments. The Downstream Pool was used more often than any other area, by both species, during the inter-specific experiments. However, the numbers of fish observed were lower than that seen in the Downstream Pool during the intra-specific observations. This was because many of the fish were hidden from view by the abundant macrophytic growth which was not as pronounced during the earlier experiments (A - C).

Aggregations were seen during most observations in

Experiments D and E. They were mainly composed of char although trout were also present. The occurrence of the aggregations was often associated with high stream temperatures and low water levels. Similar conditions were suggested for aggregation formation observed during snorkelling observations at Pouch Cove Brook and the upstream Piccos Brook sites. The Benthobservatory aggregations were variable in number (8 to 15 fish) and were always observed in the central back-eddy section of the Downstream Pool where flows were negligible (< 3.0 cm./sec. - the minimum detectable flow rate with the Ott meter). This latter characteristic may explain the preponderance of char in the aggregations (Figure 14) since this species preferred areas of low water flow.

Territories were established by a small number of fish of both species but their enumeration or measurement was not attempted. Brook char territories tended to be in slower water velocities than those of rainbow trout, reflecting respective flow preferences. Most of the territories were seen in the Downstream Pool area, near the head of the pool, for trout , and along the back-eddy margins, for char. Both species abandoned territorial behaviour as daytime water temperatures exceeded 20°C.

As the water within the study area warmed above 20 ° C, char became lethargic, reduced feeding, and were more cryptic, often holding substrate positions beneath cover.

Rainbow trout showed similar behavioural changes but at higher temperatures (>23-24 ° C). Rather than becoming secretive, as did char, trout reacted to high temperatures by holding station in lower water velocities than usual - presumably to reduce energy expenditure. The tendency by trout to form aggregations was likewise observed at a higher temperature than that seen for char. These observations agree with field observations and with the work of other researchers who have found trout to be tolerant of higher temperatures than char (Cherry et al , 1975, 1977 ; Peterson et al, 1979).

An interesting behaviour was observed throughout these observations which further differentiated microhabitat preferences of the two species. In slow water areas, resting positions on the substrate were sometimes seen and these were almost exclusively characteristic of brook char. Often they would be observed alternating between 'hovering' just above the substrate and settling down onto the bottom on erected fins, apparently resting. Duration of these substrate positions was variable, exceeding 15 min. on occasion. Rainbow trout rarely rested on the bottom, except when disturbed at which time they hid beneath rocks. Mostly, they held stationary 'hover' positions close to the substrate in moderate current. The comparative lack of substrate positions by trout in low flow areas may be due to a stereotyped 'hover' behaviour from its more typical riffle habitat. In these fast flow environments, substrate positions would be difficult to maintain due to the force of the current, unless special morphological adaptations were present, as in Atlantic salmon parr (Kalleberg, 1958).

Stomach contents of the experimental fish were superficially examined. The low sample sizes (eg. only 4 char recovered in Experiment F) make the conclusions speculative. Nevertheless, some interesting information can be derived from the results.

Generally, both species were opportunistic foragers, feeding on similar prey items whether allopatric or sympatric. During the early experiments, the main food items were chironomids and trichopterans (mainly hydropsychids and philopotamids) with ephemeropteran nymphs of less importance. These were mainly taken in the drift and often just prior to emergence as evidenced by the many pharate adults consumed. Terrestrial forms (obligate and aerial stages of aquatic species) were also important in the early experiments and became even more important during the later experiments, probably as a result of late summer species emergence and late summer declines in invertebrate biomass (Hynes, 1970 ; Bradt, 1977). This seasonal change in prey availability may also account for the general decline in the stomach fullness values and is comparable to the feeding decline observed in the previous year's observations at the Benthobservatory.

The only obvious species difference in feeding was the utilization of aquatic annelids (hirudineans and oligochaetes) by brook char. This group was a major dietary component for char in all experiments but was entirely absent from the diet of rainbow trout. Since this group of organisms is characteristic of pools and low flow areas of streams and ponds where mud and debris can accumulate (Pennak, 1978), its utilization by char may be a reflection of occurrence in the same habitats rather than differential prey selectivity.

Discussion :

The results of the 1981 Benthobservatory experiments corroborate many of the findings of habitat preference derived from the 1980 experiments and the snorkelling observations. Preference of main flow stations by rainbow trout and low flow conditions with associated cover by brook char were observed in both intra-specific and inter-specific experiments. No observed displacement to a different habitat could be attributed to either species in the inter-specific experiments. The only discernible effect of sympatry was the 'tightening' of the respective habitat distributions to those niches in which species were apparently best adapted. Feeding differences were few but were similar to those found from the stomach analyses of the field samples, and these differences could be related to preferred habitat positions of the two species.

The habitat preferences of the two species were even more obvious when relative positions of each were considered within the respective sections. In the Riffle area, rainbow trout generally held midstream stations close to the substrate in the main current whereas brook char were often in the shade and in positions out of the main flow. Likewise, in the Downstream Pool, trout preferred stations at the head of the pool where water velocity was the greatest ; char were most often positioned in the quieter water of the back-eddies and usually under cover of rocks or aquatic macrophytes.

The only major difference between the two sets of experiments with respect to habitat distribution was the obvious lack of utilization of the Pool area by both species in the inter-specific experiments. This was believed due to the much higher water temperatures experienced within this section during the mid-summer when the inter-specific experiments were run.

Both species utilized the Downstream Pool area more than any other, whether sympatric or allopatric. This seems to be related to the type of habitat that existed here, specifically its greater diversity. This section was the deepest and had the most aquatic vegatation. These factors and the large rocks provided the most instream cover in the study area which would be of great importance to brook char, as already demonstrated. That this section was also used most often by rainbow trout may indicate a preference by this species for potential cover positions nearby, perhaps for refuge when frightened.

Results of weight change for both species during the intra-specific experiments indicated more favourable growth by brook char for the experimental period. Available food within the study area was believed comparable between these experiments and both species were observed feeding. The inference, then, is that conditions within the study area may have favoured char more than trout, the assumption being that all other factors (eg. physiological state, behaviour in confinement) affected each species equally. Velocity measurements and flow patterns within the study area indicated that there was a greater percentage of habitat characterized by low water velocities and back-eddy currents. Based on data from the snorkelling observations and the results from the Benthobservatory experiments in 1980, this type of 'pool' environment would be more typical of preferred brook char habitat. This aspect of species differences was supported by the results of the species distribution observations made at the Benthobservatory in 1981. However, this 'available habitat bias' was mainly a problem of the intra-specific experiments. During the inter-specific experiments, the high stream temperatures in the Pool area precluded its use by char, thereby making the amounts of available riffle and pool habitats approximately equal.

The relatively poor final condition of the trout was attributed to lack of preferred habitat in the intra-specific set of experiments and was at least part of the reason for the poor condition of trout in the inter-specific experiments. However, on the basis of weight change alone, the presence of char did not affect the ultimate condition of trout in the inter-specific experiments since their weight change values were approximately the same for both sets of experiments. The relatively poor final condition of char in Experiments D - F was likewise not attributable directly to the presence of rainbow trout but rather the different environmental conditions experienced. Water levels were lower and stream temperatures much higher in the latter set of experiments. This resulted in reduced habitat availability, increased density, and probably thermally stressful conditions to char which prefer cooler water temperatures than trout.

MSRL EXPERIMENT

Brook char and rainbow trout have different temperature preferenda (Fry, 1951). It was the purpose of this part of the study to test the hypothesis that one species would realize a physiological advantage within its optimal thermal regime and that this condition would be measurable through behavioural observation. If such a situation were to exist , it could provide one species with a differential advantage over the other, given its thermal preferendum, and assuming such temperatures were realized in the stream environment. In the case of the brook char , Salvelinus fontinalis , a temperature between 12°C and 15°C is generally considered the optimal thermal regime (Baldwin, 1957 ; McCormick et al, 1972 ; Power, 1980). Rainbow trout , Salmo gairdneri , on the other hand, prefer warmer water temperatures than char (Fry, 1948 ; McCombie and Berst, 1975 ; Peterson et al, 1979) with an optimal temperature range between 17°C and 20°C (Horak and Tanner, 1964 ; McCauley and Pond, 1971 ; Dickson and Kramer, 1971 ; Cherry et al, 1977). For this study, three experimental temperatures were used : 8 °C (below both species' optima); 13°C (considered the optimal temperature for brook char); and, 19 ° C (the optimal temperature for rainbow trout). A temperature of 20°C could have been used as the optimal temperature for rainbow trout but it was feared that this temperature would be detrimental to brook char (Hokanson et al, 1973) because it is outside the tolerable range of water temperatures for this species and would therefore confuse the results.

Materials and Methods:

The experiments were carried out at the Marine Sciences Research Laboratory (M.S.R.L.). In order to isolate temperature effects, all other variables were kept as constant as possible. The laboratory facility was fed by a natural water source (a nearby pond). Four experimental fibreglass tanks with glass fronts and identical inside dimensions (1.18 m X 0.56 m X 0.60 m) were used. A large fibreglass holding tank (1.63 m X 0.96 m X 0.80 m) retained fish until they were needed. In order to prevent mixing and interaction of the two species, a wood frame and nylon mesh (0.62 mm mesh size) 'divider' separated the holding tank into equal halves. Wood / nylon covers were constantly in place on all tanks to stop fish from jumping out. All tanks were aerated continuously and provided with gravel bottoms. Inflow rates were standardized at 2.3 litres per min. Outflow valves in the four experimental tanks were located on the side walls. Each of these tanks had a 55 cm high stand pipe set in one corner which permitted water flow to the sub-gravel filter and contained the `air stone'. Water depths were maintained at 50 cm during experiments. Water depth of the holding tank was 70 cm.

In order to maintain a constant water temperature during an experiment, two NESLAB heat exchanger units (type SWHX) with attached 2000 watt heaters and switching relays, were utilized. As one NESLAB unit could only control the temperature in one tank, only two tanks had temperature control. These were used for inter-specific experiments. The other two tanks were used for intra-specific experimentation and showed temperature fluctuations similar to that in the outside pond though slightly `dampened'. In order to make the temperature in the four tanks roughly comparable, the experimental temperatures used followed the natural seasonal thermal progression. The paralleling of seasonal temperature change was also necessary to reduce the behavioural complications of seasonal temperature acclimation (Sullivan and Fisher, 1953 ; Hartman, 1966 ; Javaid and Anderson, 1967). For this reason, the 8°C experiment was run from December 8, 1980 to March 6, 1981 ; the 13 °C experiment from April 11, 1981 to June 1, 1981 ; and the 19°C experiment from June 27, 1981 to August 9, 1981. All intra-specific experiments were also referred to as X temperature experiments (where X = 8, 13, or 19 ° C) as for the inter-specific experiments, although the former showed greater fluctuations from X. In fact, the maximum temperature within the '8°C' intra-specific experiments was only 6°C, but will be referred to as the 8°C experiment for ease of comparisons between the intra- and inter-specific sets of observations. Except for the last portion of the 19 °C experiment, the heating unit maintained the desired temperature. During the later period of incoming warm water, cooling units (model PBS 75 - S) were substituted for the heaters.

Both fry and overyearlings of each species were used in these experiments. These were obtained by electo-fishing from Piccos Brook (rainbow trout) and Pouch Cove Brook (brook char) and introduced to separate sides of the holding tank. This was done at least two weeks prior to the start of observations. All observations were made from behind cardboard 'blinds' in front of the tanks and through a 20.0 cm X 5.0 cm eye-slit. Dark plastic covered the observer and 'blind' to prevent detection. Photoperiod was held constant within each temperature experiment but varied between experiments according to the natural daylight cycle.

Before the start of each group of observations, a pair of similar sized fish was selected for use in each tank : one rainbow trout and one brook char for each of the two inter-specific temperature control tanks; and two rainbow trout or two brook char for each of the two intra-specific tanks. Each fish was anesthetized, measured (FL to nearest 0.1 cm), and weighed on an electronic Mettler PC 4400 balance (to nearest 0.1 g). They were then allowed to recover in fresh water. In the inter-specific experiments, since the tanks were temperature controlled and the holding tank was not, the temperature gradient between the two was occasionally > 5 °C. In these cases, the temperature controls on the NESLAB units were set in gradual 3 °C increments until the desired temperature was reached. During this acclimation period in the experimental tanks, the fish were separated by a wood frame/nylon mesh divider (0.56 cm X 0.65 cm) thus preventing any interaction. Once the experimental temperature was reached, the fish were dip-netted from each of the two inter-specific tanks, dividers removed, and fish introduced into opposite tanks from those in which they were acclimating. This 'switching' procedure was necessary so that prior residence effects would not be a problem in interpreting results (Payne, 1975). Observations began after a minimum of one hour. The intra-specific methodology was slightly different. After anesthetizing, weighing, and measuring, one fish of each pair was marked for individual recognition by clipping the caudal lobe of the dorsal fin. Fish were allowed to recover and then introduced into their respective tanks. No acclimation period was necessary since tank temperatures were the same as that for the holding tank. Observations were begun a minimum of 12 hrs after introduction to allow fish to adjust to the experimental tanks. The introduction of a pair of fish to each of the four tanks was denoted as one group.

Each observation period was 15 min per tank. Five observations were made per group of fish, on alternate days and usually between 0900 and 1700 hrs. In the 8° C experiment, there were five groups whereas only four groups were tested in each of the 13°C and 19°C experiments.

At the end of observations for each group, fish were removed, weighed, measured, and preserved in 10% formalin for later sex determination.

During each observation period, agonistic behaviour was recorded for each fish on an Esterline-Angus event recorder. Social status was recorded when hierarchies were established and feeding moves were enumerated and categorized. Qualitative information such as position, colour, and general appearance were recorded on casette tape.

Six agonistic displays were identified. These included the frontal display, lateral display, nip, chase, approach, and retreat. All acts were the same as defined for the Benthobservatory experiments.

Social status was determined in the same manner as for the Benthobservatory experiments. That is, a fish was denoted as the dominant only if it exhibited at least three of the four dominance criteria in any one observation period. Afterwards, it was considered the dominant unless the subordinate exhibited three of the four dominance criteria in any following observation period. Such a hierarchial reversal was never observed in these experiments. When a dominant could not be recognized (as defined by my criteria), the experimental group was described as having 'no hierarchy identified'.

Two types of feeding moves were distinguished ;

(1) pelagic - a feeding attempt within the water column or at the water surface.

(2) grope - any feeding attempt off the tank bottom or the tank sides.

As in the Benthobservatory experiments, a feeding attempt was defined as the actual opening of the mouth and ingestion of a potential food item.

At the end of each observation period, water temperatures were recorded in each tank. Continuous records of water temperature were taken from December 10, 1980 to March 6, 1981 in one of the intra-specific experimental tanks, and from December 7, 1980 to July 6, 1981 in one of the inter-specific experimental tanks. These were recorded on 8 - day or 30 - day Peabody-Ryan thermographs.

Fish in the experimental tanks were fed only after observations and at the rate of once every second day during the 8°C experiments and once every day during the remaining experiments. The amount of food given per tank was between 5.0 and 10.0 g. The food was a standard moist pellet made at the M.S.R.L. where it has been found a successful food for these species. Its composition was 35.0% fresh capelin, 48.8% capelin meal, 10.0% wheat middlings, 5.0% fish oil, 1.0% vitamin mix, 0.1% choline chloride, and 0.1% vitamin C. The fish in the holding tank were fed at the same rate as those in the experimental tanks but the amount used was approximately 60.0 g.

Results :

Summary tables for all experimental groups are shown in Table 1 (a,b,c), Appendix E.

Statistical analyses of the data were performed using one-way and two-way analyses of variance (ANOVA) as described by Sokal and Rohlf (1973).

Twenty fish of each species were used in the 8°C experiments (inter- and intra-specific). In the other two temperature experiments (13°C and 19°C), 16 fish of each species were used in each of the inter-specific and intra-specific experiments. No significant difference ($P > .05$) was found for initial fork length between individual fish used in any of the three temperature experiments. Likewise, there was no significant difference ($P > .05$) for initial weight of the experimental fish (Tables 11 and 12). Mean values for length and weight were higher for the 19°C experiment than at the other two experimental temperatures.

TABLE 11. Comparisons between rainbow trout (T) and brook char (C) for morphometric variables measured at each test temperature during intra-specific experiments at the MSRL. All statistical testing was by analysis of variance (ANOVA). Subscript numbers refer to particular fish in an experimental pair.

ns - not significant; n - sample size

		8°C			13°C			19°C		
Variable	Species	n	Mean	F-ratio	n	Mean	F-ratio	n	Mean	F-ratio
ΔWt_1[a]	T	9	-0.089	0.303 ns	7	-0.086	0.067 ns	6	-1.900	4.057 ns
	C	10	-0.170		8	-0.013		8	-0.600	
ΔWt_2[b]	T	9	96.54	0.198 ns	7	95.82	3.692 ns	6	93.19	1.796 ns
	C	10	97.48		8	102.57		8	96.68	
Initial Fork Length (cm)	T_1	5	6.70	0.516 ns	4	5.93	3.306 ns	4	11.70	0.006 ns
	T_2	5	6.78		4	6.38		4	11.88	
	C_1	5	9.24	0.000 ns	4	9.73	0.024 ns	4	11.20	0.281 ns
	C_2	5	9.22		4	9.45		4	10.88	
Initial Weight (g)	T_1	5	2.54	0.397 ns	4	1.65	2.888 ns	4	19.18	0.029 ns
	T_2	5	2.64		4	2.13		4	21.10	
	C_1	5	7.70	0.068 ns	4	10.0	0.031 ns	4	11.20	0.040 ns
	C_2	5	8.50		4	9.0		4	10.88	

[a] ΔWt_1 = Final Weight (g) - Initial Weight (g)

[b] ΔWt_2 = (Final Weight + Initial Weight) x 100

TABLE 12. Comparisons between rainbow trout (T) and brook char (C) for morphometric variables measured at each test temperature during inter-specific experiments at the MSRL. All statistical testing was by analysis of variance (ANOVA).

*p < .01, **p < .001, ns - not significant; n - sample size

		8°C			13°C			19°C		
Variable	Species	n	Mean	F-ratio	n	Mean	F-ratio	n	Mean	F-ratio
ΔWt_1[a]	T	10	-0.260	8.544*	6	-0.267	3.389 ns	7	-0.171	0.241 ns
	C	10	+0.500		7	+0.114		7	-0.471	
ΔWt_2[b]	T	10	95.56	20.053**	6	93.96	3.281 ns	7	97.22	0.277 ns
	C	10	106.84		7	102.10		7	94.73	
Initial Fork Length (cm)	T	10	8.32	0.123 ns	8	8.35	0.010 ns	8	9.96	0.200 ns
	C	10	8.64		8	8.24		8	10.21	
Initial Weight (g)	T	10	6.26	0.000 ns	8	6.79	0.029 ns	8	10.63	0.181 ns
	C	10	6.27		8	6.11		8	11.54	

[a] ΔWt_1 = Final Weight (g) - Initial Weight (g)

[b] ΔWt_2 = (Final Weight ÷ Initial Weight) x 100

This reflects the use of fish captured in the spring (June 17, 1981) as compared to the winter when fish for the 8°C and 13°C experiments were captured. All experimental fish were immature and no relationship was identified between sex and eventual hierarchial status.

Weight change values were determined for all fish used in these experiments. As in the Benthobservatory experiments, statistical results were the same when measured as a direct weight difference or when final weight was expressed as a percentage of the initial weight (Tables 11 and 12). However, the latter method was more meaningful for between species comparisons.

In the intra-specific experiments, water temperatures measured during observations ranged from 3.3 to 6.0°C (8°C experiment), 6.6 to 16.7°C (13°C experiment), and 15.4 to 20.3°C (19°C experiment).

(1) Intra-specific Experiments :

At 8°C, brook char established hierarchies in four of the five groups whereas rainbow trout established a hierarchy only once. No significant difference ($P > .05$) was found between species for weight change as both species showed a net weight loss. Trout showed the greatest weight loss when expressed as a percentage of the initial weight.

The number of days to the establishment of a hierarchy was estimated and then tested between species (Table 13). At 8°C, no significant difference ($P > .05$) was found. Char averaged 5.5 days to reach dominance, whereas trout required 5.0 days.

At 13°C, seven hierarchies were established (4 by char, 3 by trout) from a possible eight groups, much more than occurred at 8°C. Weight change was not significantly different between species ($P > .05$) but trout showed a mean weight loss whereas char showed a mean weight gain (when final weight was expressed as a percentage of the initial weight). No significant difference ($P > .05$) was found between the species for the number of days required to establish dominance but brook char did average less time (2.25 days) than rainbow trout (3.0 days).

At 19°C, six hierarchies were established of a possible seven. One group's observations (Group 1, trout only) were terminated due to the death of one of the subjects. Char established hierarchies four times whereas trout did only twice (of the three groups). Weight change values were not significantly different between species ($P > .05$) as both showed net weight losses, greater than found at either 8°C or 13°C and trout showed the greatest weight loss. Hierarchies were established significantly faster ($P < .001$) by trout (avg = 1.0 days) than char (avg = 6.75 days).

Based on these data, brook char did better than rainbow

TABLE 13. Mean number of days* to the establishment of a dominance heirarchy for each species during the temperature experiments at the MSRL. Values are only for those experiments where a heirarchy was identified according to the prescribed criteria (see text).

Experiment	Species	Temperature		
		8°C	13°C	19°C
Intra-specific	Rainbow Trout	5.0	3.0	1.0
	Brook Char	5.5	2.3	6.8
Inter-specific	Rainbow Trout	10.0	5.0	4.0
	Brook Char	3.8	3.6	9.0

* Values are means for all heirarchies per species per experimental temperature.

trout at the lower water temperatures and especially at 13° C (approximate). This was the only time that mean final weight of char exceeded their initial weight. Rainbow trout also had their best weight change (although negative) at 13 °C. Both species showed their greatest weight losses at 19 °C. It is worth repeating here that water temperatures fluctuated in the intra-specific experiments and generally were lower than the controlled temperatures in the corresponding inter-specific tanks.

Size (length or weight) was not found to be important in these experiments in determining eventual hierarchial status. Weight change at the end of each group's observations, was significantly different between dominants and subordinates ($P < .05$), with dominant individuals usually showing the least weight loss.

If it is assumed that the number of days required to establish a hierarchy is related to an individual's 'fitness' (since hierarchial status is often dependent on the outcome of interaction), then one can infer that within an individual's preferred environmental conditions, time to dominance should be shortest. This presumes that an individual's fitness (i.e. physical, behavioural, and metabolic condition) is greatest within its preferred temperature range. The results of such an analysis are shown in Table 13. Although sample sizes are probably too small to justify statistical testing, the results show some interesting trends. In the 13°C experiment where temperatures varied about the optimal range for brook char, the number of days to hierarchial establishment was less than that for trout and much less than found for char at the other test temperatures. Rainbow trout, on the other hand, which have a higher preferred temperature range than char required significantly less time to reach dominance in the 19°C experiment.

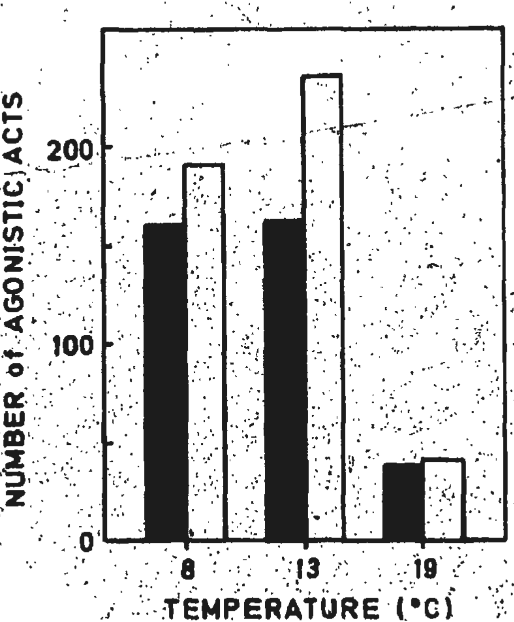
Total agonistic activity was recorded for both species during these experiments and is shown in Figure 15. The results clearly indicate that the majority of agonistic activity observed during the 8°C and 13°C experiments was between brook char. Rainbow trout showed virtually no agonistic interaction at 8°C reflecting their general inactivity at these colder temperatutes (which were actually lower than 8°C) and probably related to their higher preferred temperature range. Both species showed their greatest amount of agonistic interaction at 13°C. At 19°C, both species showed approximately the same amount of agonistic activity but brook char showed their lowest amount at this temperature.

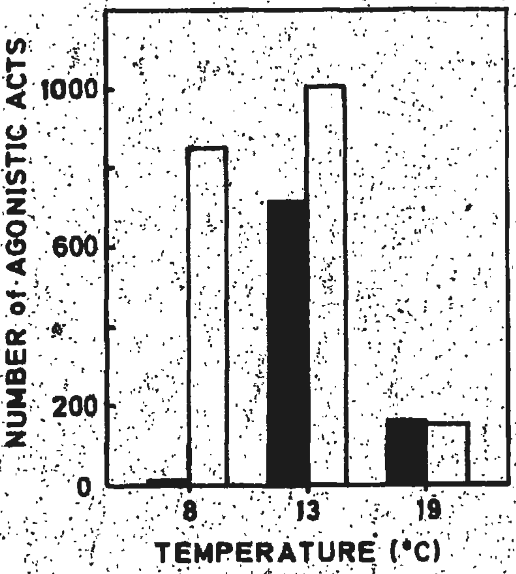
(ii)Inter-specific Experiments :

At 8°C, five of the ten groups developed hierarchies.

FIGURE 15. Frequency of agonistic acts by rainbow trout (solid bars) and brook char (open bars) at 8°C, 13°C, and 19 °C during the intra-specific experiments at the M.S.R.L. Values for the 8°C experiment were based on observations of five groups ; values for the 13°C and the 19°C experiments were based on observations of four groups.

FIGURE 16. Frequency of agonistic acts by rainbow trout (solid bars) and brook char (open bars) at 8°C, 13°C, and 19 °C during the inter-specific experiments at the M.S.R.L. Values for the 8°C experiment were based on observations of five groups ; values for the 13°C and the 19°C experiments were based on observations of four groups.


NUMBER of AGONISTIC ACTS
200
100
0
8
13
19
TEMPERATURE (°C)


NUMBER of AGONISTIC ACTS
1000
600
200
0
8
13
19
TEMPERATURE (°C)

Of these, four were by brook char and one was by a rainbow trout. Weight change over the course of observations was significantly different between the two species ($P < .01$). Brook char showed a mean weight gain whereas trout tended to lose weight. Likewise, the number of days to hierarchial establishment for char was much less than that for trout although the difference was not significant ($P > .05$). The comparatively better results of weight change of char in inter-specific observations at 8 °C than in the intra-specific 8°C observations was believed more a function of a constant (and higher) water temperature in the former rather than the effect of inter-specific interaction. Intra-specific temperatures were consistently below 8°C during these observations and approaching those temperatures where salmonids show least growth and worst condition (see review in Carlander, 1969).

At 13°C, brook char again displayed a competitive advantage over rainbow trout, achieving dominance five times ; trout were dominant in only one group. As at 8 °C, char showed a mean positive weight difference over the course of observations while trout lost weight, although the difference was not significant ($P > .05$). In comparison to the intra-specific 13 °C observations, char showed approximately the same degree of weight change (percentage values). Trout, however, showed a higher percentage weight loss in the inter-specific 13°C observations as compared to results for this species in intra-specific observations. This seems to be due to the presence of char as water temperatures were comparable in both sets of observations (Table 1b, Appendix E). This would be expected, if the optimal temperature of char (circa 13 ° C) conferred a competitive advantage to this species. A further indication of the dominance of char at 13°C , was the time required to establish social hierarchies. Brook char averaged 3.6 days while the one rainbow trout which achieved dominance took 5.0 days, but the difference was not significant ($P > .05$).

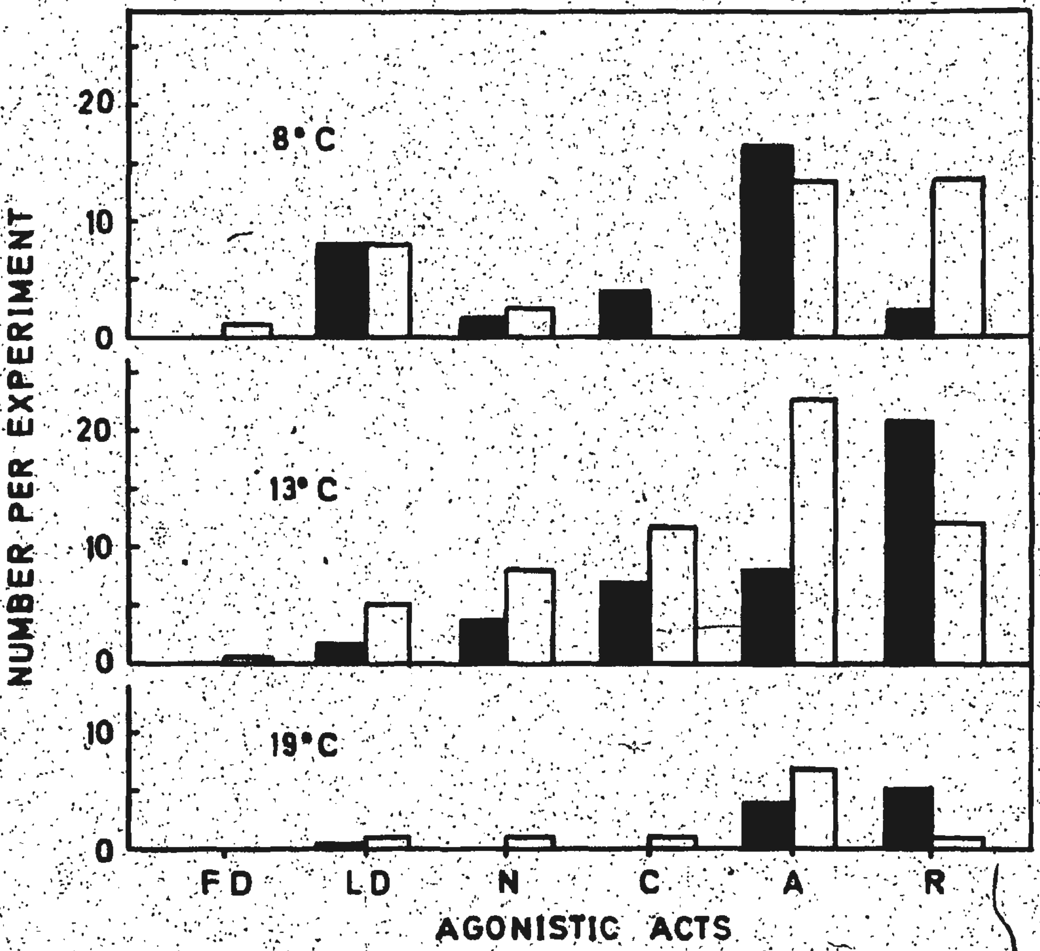
At 19°C, the results were slightly different from the previous two experimental temperatures. Brook char achieved dominance more times (3) than trout (2) but the difference was the lowest of the three experiments. Of all the experiments (both inter- and intra-specific), rainbow trout showed the best mean weight change (percentage value) at 19 °C, although still a net weight loss. Brook char showed their greatest mean weight loss of all experiments at 19°C. These data suggest that rainbow trout were able to do best at this temperature. This is further supported by the results of the time to hierarchial establishment . Brook char required an average of 9.0 days, the longest of any experiments (inter- or intra-specific). Rainbow trout averaged significantly less ($P < .01$).

Figure 16 shows the total amount of agonistic activity recorded for each species at each of the three experimental temperatures. Brook char showed higher values than rainbow trout at both 8 ° C and 13 ° C. Both species showed approximately the same amount at 19°C and the values were the lowest recorded of the experiments. The main difference compared with the intra-specific observations was that rainbow trout showed much more agonistic activity at 8°C in the inter-specific experiment. It appears that this was due to a combination of inter-specific interaction and increased activity at the higher temperatures (i.e. intra-specific temperatures were lower than 8°C). Rainbow trout actually showed more aggressive acts than char at 8 ° C in the inter-specific experiments (Figure 17) as the latter showed more retreats. This was not expected since trout were less active than char which usually dominated trout in the inter-specific experiments. However, most of this aggression was attributed to the interactions recorded in Group 3 (Tank A) where no hierarchy was identified and, in fact, brook char showed the better weight change at the end of this group's observations.

Discussion :

The results of the intra-specific and especially the inter-specific experiments support the hypothesis that brook char display a competitive advantage over rainbow trout at

FIGURE 17. Individual agonistic acts by rainbow trout (solid bars) and brook char (open bars) at 8°C, 13°C, and 19 °C during the inter-specific experiments at the M.S.R.L.



NUMBER PER EXPERIMENT
8° C
13° C
19° C
20
10
0
FD
LD
N
C
A
R
AGONISTIC ACTS

cooler water temperatures. This was most obvious at 13°C, the supposed optimal temperature for brook char. However, the results could not show that rainbow trout realized a competitive advantage at 19°C (the supposed optimal temperature for this species), only that trout showed less of a weight loss than char and achieved dominance fastest at this water temperature. Three possibilities could explain the inability of rainbow trout to demonstrate a competitive advantage over char in the 19°C experiment. First, and probably most important, both species showed a general decline in condition from the time of capture to the termination of the experiments. This was most pronounced in the rainbow trout which displayed mean weight losses in each experiment. Rations were not limiting as evidenced by the surplus amounts remaining in tanks throughout the observations and also in comparison to ration levels used by other researchers (Yamagishi, 1964 ; Glova and Mason, 1977a). The continuous weight loss and deteriorating condition of many of these fish (especially the trout) seems to have been due to a reluctance to consume the pellet food. Consequently, rainbow trout may have been more adversely affected by captivity than were char. If trout were initially in worse relative condition than char, it is reasonable to assume that their competitive ability would be less, especially at the higher water temperatures where more food intake would be necessary to balance the greater energy expenditure (Wurtsbaugh and Davis, 1977). Javaid and Anderson (1967b) demonstrated that starvation experiments on rainbow trout and brook char resulted in lowered selected temperature ranges. If both species were in a state of poor nutrition in my experiments, it might explain why rainbow trout were not able to demonstrate a clear competitive advantage over char at 19°C. The optimal temperature of the trout may actually have been lower than 19° C, given their poor physical condition.

The second possible reason for the lack of evidence of trout dominance at 19°C, is the experimental design. Although both species did show a minimal rheotactic orientation within the aquaria, water flow was negligible. As noted in the previous sections, brook char showed a preference for and dominance in slow flow (pool) habitats. These static aquarium conditions simulated a pool environment and therefore may have favoured char over trout.

The differential species habitat preferences found in the streams may also explain the different types of feeding moves observed in the experiments (Table 2, Appendix E). Presumably a 'grope' type feeding move would be typical for a pool dweller which actively searches out its prey while swimming close to the bottom. A riffle dweller, which maintains a fixed station, would more likely feed on food particles drifting by in the water column or on the water surface.

Finally, the confined conditions in the tanks may have promoted increased aggression in the char and therefore increased the likelihood of this species dominating trout (Newman, 1956). Char generally showed a greater amount of agonistic activity than did trout in both sets of experiments, even at 19°C.

Problems inherent to laboratory experimentation can influence the results. The experimental design, the poor feeding displayed by the subjects, and behavioural interpretation in aquarium habitats are all factors which must be taken into consideration. Likewise, the temperature variability between intra- and inter-specific experiments makes comparisons difficult. These problems can influence the results of such an experiment. The use of a stream tank with a variety of flow and depth microhabitats would certainly have been better and would have eliminated some of the problems inherent to the present design. The use of a more natural diet or a 'pre-conditioning period' for experimental fish where only those that had adapted to a particular food type would be used - would have standardized conditions between species better.

Dominance hierarchies were the usual form of social organization observed in these experiments. In those groups where no hierarchy was recognized, it was assumed that such would eventually result, but that during the limit of five observations, it had not yet been firmly established, according to my criteria. No evidence of territoriality was observed such that each fish in a pair defended a prescribed segment of the tank space. Only dominants showed a type of despotic territoriality which included the entire tank space. The tank bottom area (approximately 6600 square cm) was smaller than that defined for territories of overyearling salmonids (see review in Allen, 1969). This may explain why a pair of overyearlings, used in any of these experiments, could not hold simultaneous territories. Yamagishi (1962) found the maximum territory size for rainbow trout fry in tanks was only 3500-4000 square cm, smaller than the tank bottom area in these experiments. However, no experimental pair of fry (char or trout) were observed to hold separate territories in any of the observations of this study.

The distinction between territoriality and social hierarchy is difficult in situations such as laboratory aquaria (Payne, 1975 ; Noakes, 1978). The problem is further complicated since territoriality can be modified by density (Keenleyside and Yamamoto, 1962), water velocity (Kalleberg, 1958 ; Hartman, 1963), size of fish (Stringer and Hoar, 1955), food supply (Symons, 1968), bottom topography (Kalleberg, 1958 ; Yamagishi, 1962), temperature (Gibson, 1966), and even species differences (Newman, 1956). Therefore, although dominance hierarchies were the rule in my experiments, on the basis of the above references, such results are not necessarily applicable to different situations, especially the natural environment.

Despite the problems, the experiments indicate a relationship between species' competitive capabilities (in terms of ability to dominate in a hierarchy) and those water temperatures at which each species is best adapted or optimally suited. A similar suggestion was offered by Hartman (1966) in his temperature experiments where he noted it "...quite possible that animals such as young coho salmon and steelhead trout may have temperature optima for the expression of behaviour, particularly as it applies to situations of competition and species interaction ".

The data and results presented here are not conclusive enough to permit acceptance of the hypothesis for extrapolation to the natural environment. However, for the conditions realized here, brook char did show an ability to dominate rainbow trout at 8°C and 13°C whereas rainbow trout were metabolically favoured (weight change estimates) at 19 °C.

GENERAL DISCUSSION

Brian (1956) was the first to introduce the concepts of 'selective segregation' (strictly differential habitat selection) and 'interactive segregation' (species segregation due to competition and/or predation). He concluded that the habitat partitioning observed between ants (*Myrmica* spp.) was due to interactive segregation, and although one species dominated over the other, the latter was still more superiorly adapted to certain conditions thus preventing its complete replacement. Nilsson (1965, 1967) applied these concepts to fish species and determined that habitat partitioning between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in north Swedish lakes was a result of interactive segregation. Other evidence for interactive segregation between fish species include studies between Atlantic salmon and brook char (Gibson, 1973), cutthroat trout and coho salmon (Glova and Mason, 1977a), sculpin species, *Cottus asper* and *C. aleuticus* (Ringstad, 1974), coho salmon and steelhead trout (Hartman, 1965 ; Allee, 1974), rainbow trout and cutthroat trout (Nilsson and Northcote, 1981), brook char and brown trout (Fausch and White, 1981). There are no studies which have demonstrated the existence of selective segregetion for closely related groups of fish in temperate freshwater ecosystems, as it pertains to food and habitat resources. Bartnik (1970) found that two species of sympatric dace were reproductively isolated in Manitoba streams. _Rhinicthys cataractae cataractae_ preferred a large stone substrate with water velocities > 45 cm/sec whereas _R. atratulus meleagris_ spawned over gravel bottoms in slower water velocities. However, habitat overlap did occur at other times of the year.

This lack of examples of selective segregation among closely related species in temperate freshwater fish communities is undoubtedly a consequence of the ecosystem. Such an environment offers comparatively few opportunities for specialization (Larkin, 1956). In addition, the 'young' impoverished fauna of temperate systems have not yet had time to diversify within their given habitats (Pianka, 1978). Selective segregation theory presupposes such evolution since it is the hypothetical end point of the interactive segregation process (Nilsson, 1967). It is however doubtful that such an extreme specialization could realistically evolve in a temperate system. The unpredictability of the environment would presumably select for some degree of plasticity to maintain a minimum level of fitness. In fact, Brian (1956), in describing a feeding segregation in British titmice which he believed was largely selective, readily observed interspecies interference as food became limiting.

The results of the present study indicate different specific preferences for stream habitat with respect to cover association and water velocity. Rainbow trout of all age groups tested were most often observed in open main flow stations at both Piccos Brook sites. These preferences were substantiated in allopatric and sympatric experiments at the Benthobservatory (1981). Brook char were primarily found in pool-type stream habitats and were often associated with cover. This was true at both streams. Similar results were obtained during the Benthobservatory experiments where brook char displayed a distinct ability to dominate rainbow trout in a slow flow situation.

Depth differences between the species were not as pronounced. Rather, the importance of this variable was its synergistic effect with cover and velocity. In a recent study, Kennedy and Strange (1982) found depth and gradient differences between sympatric Atlantic salmon and brown trout in northern Ireland but concluded it was '...unlikely that depth alone is the major limiting factor in any habitat choice.' Generally, my field observations showed that brook char preferred deeper water than similar sized rainbow trout, and fry were always in shallower stream margins than overyearlings of both species.

Despite these species specific habitat preferenda, resource overlap did occur for each variable measured in this study. That is, no quantifiable boundaries could be identified which separated adjacent species niches. The greatest species overlap for cover, depth, and velocity occurred at the upstream Piccos Brook site and was attributed to habitat type, specifically its smaller size and lack of diversity compared to the downstream site. Allee (1974) found similar species overlap for coho salmon and steelhead trout in the 'transitional areas' between riffles and pools. He suggests that such overlap would still be expected, by variants in the population even where there is strong selection for habitat segregation, and that this interaction would be most obvious in the intermediate zones between riffles and pools (i.e. runs). In the 1981 experiments at the Benthobservatory, it appeared that those rainbow trout unable to establish territories in the riffle areas or in the shallows at the head of the Downstream Pool, were forced to occupy marginal habitats where they would be more likely to interact with char. The aggregations seen in the field and at the Benthobservatory were occasionally mixed species assemblages and may have been groupings of subordinate individuals unable to compete for more favoured stream positions, especially during adverse environmental conditions (such as high water temperatures).

This is not to say broad habitat use is a subordinate trait. As already discussed, it may reflect the evolutionary state of the fauna (Nilsson, 1967) and the species' plasticity enabling them to display a wide tolerance of habitat variation - often a valuable characteristic in a temperate environment. McNaughton and Wolf (1970) described the phenomenon in terms of 'niche breadth' and suggested that substantial species overlap would be preserved even though the centres of exploitation were not identical.

In Piccos Brook, both salmonid species were observed occupying all habitat types but with the majority of each species distributing themselves into those microhabitats where they were more likely to dominate. Rainbow trout displayed the greatest habitat range as they were able to occupy positions in the fastest water velocities as well as in pools where flow was negligible. Brook char were never observed in the fastest riffles, either in sympatry or in allopatry (Pouch Cove Brook and the Benthobservatory experiments). Gibson (1973) found that where brook char occurred alone, above a waterfalls in a Quebec river, they were found in faster water velocities than where they were sympatric with Atlantic salmon downstream. When in the rapids, the char were less mobile and '...usually in the slower pockets of water near rocks or in the slower water below a fast current.' Kennedy and Strange (1982) found that brown trout were unable to occupy all of the available stream habitat as they were absent from the fastest riffle sections whereas the coexisting salmon parr were equally abundant in all stream habitats. A similar situation is indicated for the species in this study based on the Benthobservatory experiments. This adaptation to faster water velocities and open water stations by rainbow trout (together with their comparable aggressiveness in these habitats)and the preference for (and dominance in) areas of slow flow and cover by brook char appear to be the compensatory mechanisms allowing these species to coexist. MacArthur and Levins (1964) speculated that '...species which specialize on a particular proportion of two or more particular resources will be found only where their favoured proportion is found and will be replaced by other species in other habitats where the proportion of the mixture changes to one on which the new species are more effective'. This proportionality theory may explain the greater abundance of rainbow trout observed at the downstream Piccos Brook site where the ratio of riffles : pools and the discharge were much greater than at the upstream site.

The evidence presented here suggests that interactive segregation is occurring between these two species (and even between age groups), at least during the spring to fall period. Neither species was observed to be socially dominant over the other to the extent of competitive exclusion. Species dominance was however evidenced as relative abundance within preferred microhabitats of stream sections. These preferences were demonstrated by the Benthobservatory experiments and substantiated in the field according to relative species representation between upstream and downstream sites at Piccos Brook.

When sympatric (Piccos Brook), both species appeared to decrease their niche breadth as compared to allopatric char in Pouch Cove Brook and trout (intra-specific experiments at the Benthobservatory in 1981) but neither species noticeably shifted its activities to a previously unused area. Instead, each species concentrated in that part of its fundamental niche where it was best adapted.

Nilsson (1967) stated that the phenomenon of interaction would be most severe if competition was at work. According to Larkin (1956), competition can only exist if some common resource is in short supply. None of the resource variables used in this study (i.e. cover, depth, velocity, food) were definitely quantified to meet this criterion. However, estimation was attempted in several cases. At Pouch Cove Brook, the apparent paucity of suitable cover in the form of riparian overhang and aquatic macrophytes strongly suggested interactive segregation may be occurring between fry and overyearling brook char, resulting in the displacement of the former to unfavourable areas of open water. At the upstream Piccos Brook site, stream morphology was such that open water riffles were scarce and this was taken to infer a spatial competition for the remaining pool-type habitat. The consequence was a higher proportion of brook char than that found downstream where no such limitation was identified.

Food resource partitioning between species could not be demonstrated on the basis of the stomach analyses. Both species fed on much the same food items. The myriad of complexities of diel feeding responses and food availability, habitat overlap of the fish species, and the opportunistic foraging strategies displayed by both species precluded any attempt at generalization in this regard. Differences were identified which reflected the respective habitat preferences of each species. Brook char appeared to rely more on aquatic annelids (and large non-winged terrestrials of similar shapes) which were common in lentic environments. Rainbow trout fed substantially more on surface drift items, winged terrestrials, and riffle dwelling ephemeroptera than did char. Competition for food was expected to be greatest in mid-summer when invertebrate biomass would be lowest and metabolic demands highest. This inference was based on estimations of stomach fullness values which were lowest at this time. Such a limitation might be expected to intensify inter-specific competition (Brian, 1956 ; Gibson, 1973) and consequently habitat segregation, possibly due to increased aggression (Symons, 1968). The result might tend to shift each species into their respective preferred habitats (spatial niches). This niche compression phenomenon, in sympatry, was also demonstrated for congeneric centrarchids by Werner and Hall

(1976, 1979). Their experiments indicated that the ecological flexibility exhibited by the sunfish was a dynamic process determined by the relation between resource levels and differences in foraging efficiencies among species.

The results of the MSRL experiments suggest that thermal regimes realized in the stream environment might have important implications for habitat partitioning. As char and trout have different temperature preferenda (Fry, 1948 ; Peterson et al., 1979), competitive ability might be maximized at each species' optimal temperature (Hartman, 1966). The experimental evidence from this study showed that brook char were best able to dominate rainbow trout (and show their greatest weight change) at 13° C, the presumed optimal temperature for this species. The results for rainbow trout were less conclusive but suggest that this species was metabolically favoured at 19°C (the presumed optimal temperature for rainbow trout) when char showed their greatest weight loss. The implication is that rainbow trout might enjoy an advantage for exploiting resources, especially food, at high stream temperatures. Indications of such a relationship were evident at Piccos Brook as stream temperatures rose above 20°C. At these times, brook char decreased their activity, formed aggregations, and/or became secretive in habit whereas trout remained in mid-stream stations and continued feeding. If excessively high temperatures were to continue, brook char might be expected to emigrate from localized areas in search of cooler temperatures (Elson, 1942 ; Fry, 1951). Such movements could result in habitat partitioning on a larger scale than simply between riffles and pools. Burton and Odum (1945) suggested that longitudinal distribution of brook char in streams was due partly to temperature where 19°C was estimated as the 'thermal limit' of this species. Other researchers have noted similar indications of thermal habitat partitioning in fish species (Wurtsbaugh et al 1975 ; Brandt et al., 1980, Crowder et al., 1981) but Shrode et al., (1982) cautions that fish distribution is a complex phenomenon subject to the control and modification by many variables, other than simply water temperature. It is doubtful that cooler stream temperatures (approaching or below the optimum for brook char) would result in emigration of rainbow trout to warmer stream sections. Rather, it may create conditions more favourable for dominance by char in a localized habitat and lead to the displacement of trout to a narrower niche in order to reduce interaction.

Evidence of seasonal and temporal partitioning of resources (Sale, 1979) can be important as they relate to this study. Gibson (1966) observed brook char to move away from daytime cover positions to feed in more open areas at dusk whereas Atlantic salmon parr continued to feed in open sunlit areas during the day. Johnson and Johnson (1981) studied diel feeding variation in subyearling steelhead trout and coho salmon and demonstrated the former were primarily diurnal feeders and the latter fed mostly during the night. Such temporal variation would tend to reduce inter-specific competition for food and space. In my study, all underwater observations and Benthobservatory experimentation were performed during the daylight hours and therefore no such diel variation in feeding or habitat choice was seen. However, such behaviour would reduce the amount of food and habitat overlap as a result of drift periodicity (Waters, 1972) and niche shifts (Werner and Hall, 1976, 1979 ; Sale, 1979), respectively.

Seasonal variation in habitat choice and aggression was observed for both species at both streams. As water temperatures decreased from summer to fall, the frequency of aggression showed a similar decline in the Benthobservatory experiments. Both species showed habitat changes indicating a preference for lower water velocity microhabitats as temperatures fell below approximately 7°C and eventually a cryptic behaviour or emigration to suitable overwintering areas when stream temperatures decreased below 4°C. Similar observations have been noted for Atlantic salmon (Gibson, 1978 ; Rimmer, 1980), chinook salmon and steelhead trout (Chapman and Bjornn, 1969), and coho salmon (Hartman, 1965 ; Bustard and Narver, 1975). The lowered aggression may be attributed to seasonal decline in food abundance from spring to fall, reflecting the close association of these two activities (Kalleberg, 1958). Hartman (1965) suggested that such a decline in aggressiveness would be necessary for coexistence in the same overwintering pools. This would also tend to reduce energy expenditure that would otherwise be used up in aggressive interaction at a metabolically critical time of the year.

This utilization of different habitat types by brook char and rainbow trout is not a rigidly defined phenomenon. Species overlap was observed and experimentally demonstrated. Habitat preferences and specific behaviours were continuously affected by factors as site morphology, light intensity, food availability, diel activity patterns, and even fish age.

In conclusion, this study produces evidence that rainbow trout and brook char show specific seasonal habitat partitioning as a consequence of interactive segregation. This segregation is not believed a direct result of their own local interactions since the relatively recent introduction of rainbow trout to Newfoundland precludes this possibility. Instead, it is believed that historic interactions in their indigenous environments resulted in selection for the respective habitat preferences observed here. In its native rivers on the West Coast of Canada, Salmo gairdneri typically coexist with species as cutthroat trout and coho salmon. In these rivers, evolution favoured an adaptation and dominance by rainbow trout in a main stream habitat where water velocities were greater than that preferred by cohabiting species. In eastern North America, Salvelinus fontinalis often occurs sympatrically with Atlantic salmon where interactive segregation has tended to reduce competition by partitioning the two species into pool and riffle habitats, respectively. Therefore, in the present context of this study, the rainbow trout can be regarded as the ecological homologue of the Atlantic salmon. Reinforcement of the Atlantic salmon - brook char interactive segregation is therefore accomplished and believed continuing to evolve, in these streams, presumably towards a situation resembling selective segregation but realistically falling somewhere between.

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APPENDIX

A

Table 1. Chemical characteristics of the study sites at Piccos Brook and Pouch Cove Brook from May - October, 1980. Methodology of specific analyses were as described in Jamieson (1974).

Study Site	Date (1980)	pH	Total Hardness (ppm)	Specific Conductance (micro mhos cm^{-1})	Turbidity (J.T.U.)	Total Alkalinity (ppm)	Calcium Ca^+ (ppm)	Chloride Cl^- (ppm)
Piccos	May 30	6.21	6.0	32.0	0.75	1.5	0.7	13.5
Brook	August 22	6.10	8.0	28.0	1.70	< 1.0	1.0	10.5
Downstream	October 20	5.90	6.0	38.0	0.60	1.8	0.6	12.5
Piccos	May 20	5.75	6.0	44.0	1.00	1.0	0.6	16.0
Brook	August 22	5.44	6.0	26.0	2.10	1.0	1.0	12.0
Upstream	October 20	5.57	7.0	35.0	0.60	1.0	0.6	12.5
Pouch	May 22	6.51	8.0	53.0	1.50	2.0	1.1	18.5
Cove	August 22	6.28	10.0	31.0	2.20	2.0	1.2	13.0
Brook	October 20	6.20	8.0	42.0	0.58	2.5	0.7	16.0

APPENDIX

B

Table 1(a). Data from snorkelling observations at the downstream [illegible] Brook site in 1980-1981. Unless otherwise indicated, numbers of fish observed refer to overyearlings.

* spawning condition. ** aggregation

Date	Start Time of Observations (hrs)	Weather Conditions	Water Level[1] (cm)	Water Temperature (°C)	Numbers of Rainbow Trout Observed	Numbers of Brook Char Observed
02/06/80	1400	Overcast Raining Cool	23.3	12.3	5	0
17/06/80	1200	Sunny Mild	15.3	13.9	5	0
11/07/80	1000	Overcast Mild	10.5	14.6	4 1 fry	2
29/07/80	1230	Sunny Hot	23.9	20.5	5 21 fry	[illegible]
01/08/80	1420	Mainly Sunny Warm	31.0	16.1	2 3 fry	3
19/09/80	1030	Overcast Drizzle Mild	26.8	12.8	3 7 fry	2
23/10/80	1330	Mainly Sunny Cool	31.0	8.0	0	3 8*
28/04/81	1130	Cloudy Mild	—	7.5	5	0
14/05/81	1130	Sunny Warm	42.5	12.0	8	3
11/06/81	1600	Overcast Raining Mild	42.0	13.0	9	4 8 fry
24/06/81	1230	Mainly Sunny Mild	51.0	14.0	11	1
29/06/81	1400	Overcast Raining Mild	47.0	16.0	10 1 fry	4 2 fry
13/07/81	1100	Mainly Cloudy Mild	50.5	14.5	2 8 fry	4 fry
28/07/81	1600	Sunny Hot	43.0	20.5	14 1 fry	3 1 fry
09/08/71	1530	Mainly Sunny Mild	44.5	15.5	6 5 fry	1 6 fry 4 fry**
27/08/81	1230	Mainly Cloudy Mild	47.0	16.0	7 4 fry	1 2 fry

[1] 1980 water levels not comparable with water levels in 1981.

Table 1(b). Data from snorkelling observations at the upstream [illegible] Brook site in 1980-1981. Unless otherwise indicated, numbers of fish observed refer to overyearlings.

* Part of aggregation

Date	Start Time of Observations (hrs)	Weather Conditions	Water Level[1] (cm)	Water Temperature (°C)	Numbers of Rainbow trout Observed	Numbers of Brook Char Observed
01/06/80	1230	Mainly Sunny Mild	20.0	13.9	10	1
11/06/80	1630	Sunny Mild	18.7	16.6	10	0
09/07/80	1300	Overcast Mild	17.0	14.6	2	1
30/07/80	1730	Mainly Sunny Hot	15.4	21.5	2	2
05/08/80	1400	Mainly Sunny Warm	17.6	14.0	3 1 fry	2
23/10/80	1030	Overcast Cool	28.0	6.0	0	0
28/04/81	1000	Overcast Mild	—	7.0	3	2
12/05/71	1015	Sunny Warm	22.6	15.0	3 6*	3 6*
31/05/81	1330	Overcast Warm	21.3	18.5	5 5*	1 4*
11/06/81	1100	Mainly Cloudy Mild	36.0	9.2	0	0
27/06/81	1330	Overcast Warm	26.0	18.0	3	6 1 fry
13/07/81	1330	Mainly Cloudy Warm	26.4	14.9	4	6
24/07/81	1430	Overcast Mild	23.6	18.5	2 1* 1 fry	8 9*
09/08/81	1300	Cloudy Mild	25.0	18.0	4 1* 1 fry	8 9*
31/08/81	1115	Mainly Sunny Mild	27.0	18.5	7 4 fry	7 7* 1 fry

[1] 1980 water levels not comparable with water levels in 1981.

Table 1(d). Data from snorkelling observations at the Pouch Cove Brook site in 1980-1981. Unless otherwise indicated, numbers of fish observed refer to overyearlings.

* Schools of fish, ** aggregations

Date	Time of Observations (hrs)	Weather Conditions	Water Level[1] (cm)	Water Temperature (°C)	Numbers of Brook Char Observed
06/06/80	1200	Overcast Warm	18.0	11.6	3
11/06/80	1530	Overcast Drizzle Mild	—	12.4	1
11/07/80	1130	Overcast Mild	13.5	14.5	3 6* 1 fry
01/08/80	1500	Sunny Hot	17.0	21.2	3 20* 2 fry
22/09/80	1100	Overcast Showers Mild	21.7	12.5	2 4 fry
21/10/80	1100	Mainly Sunny Cool	28.0	9.1	9 12 fry**
28/04/81	1330	Overcast Drizzle Mild	—	6.5	1
21/05/81	0930	Mainly Sunny Mild	20.0	11.3	9 15* 1 fry
18/06/81	1300	Mainly Sunny Hot	24.0	19.5	15 15** 10* 8 fry
14/06/81	1330	Mainly Sunny Warm	33.5	12.0	16 1 fry
01/07/81	1300	Cloudy Warm	32.5	19.0	14 9** 10* 2 fry
13/07/81	1330	Overcast Cool	34.5	16.0	18 2 fry
26/07/81	1215	Sunny Hot	19.0	21.5	7 20* 1 fry
07/08/81	1330	Overcast Drizzle Cool	28.0	14.0	5 2 fry
23/08/81	1400	Mainly Cloudy Warm	25.5	19.0	18 40* 4 fry

[1] 1980 water levels not comparable with water levels in 1981

FIGURE 1. Prey consumed by overyearling rainbow trout (solid bars) and brook char (open bars) at different times of the season (May to October) at the Piccos Brook (downstream site). Only those prey taxa comprising at least 20% of the stomach volume of an individual fish were included in this analysis. T = sample size of rainbow trout, C= sample size of brook char ; CHI = Chironomidae larvae, SIM = Simuliidae larvae, EPH = Ephemeroptera nymphs, TRI = Trichoptera larvae, ODO = Odonata nymphs, ANN = aquatic Annelida, TER = terrestrial invertebrates (includes obligate forms and aerial stages of aquatic species).

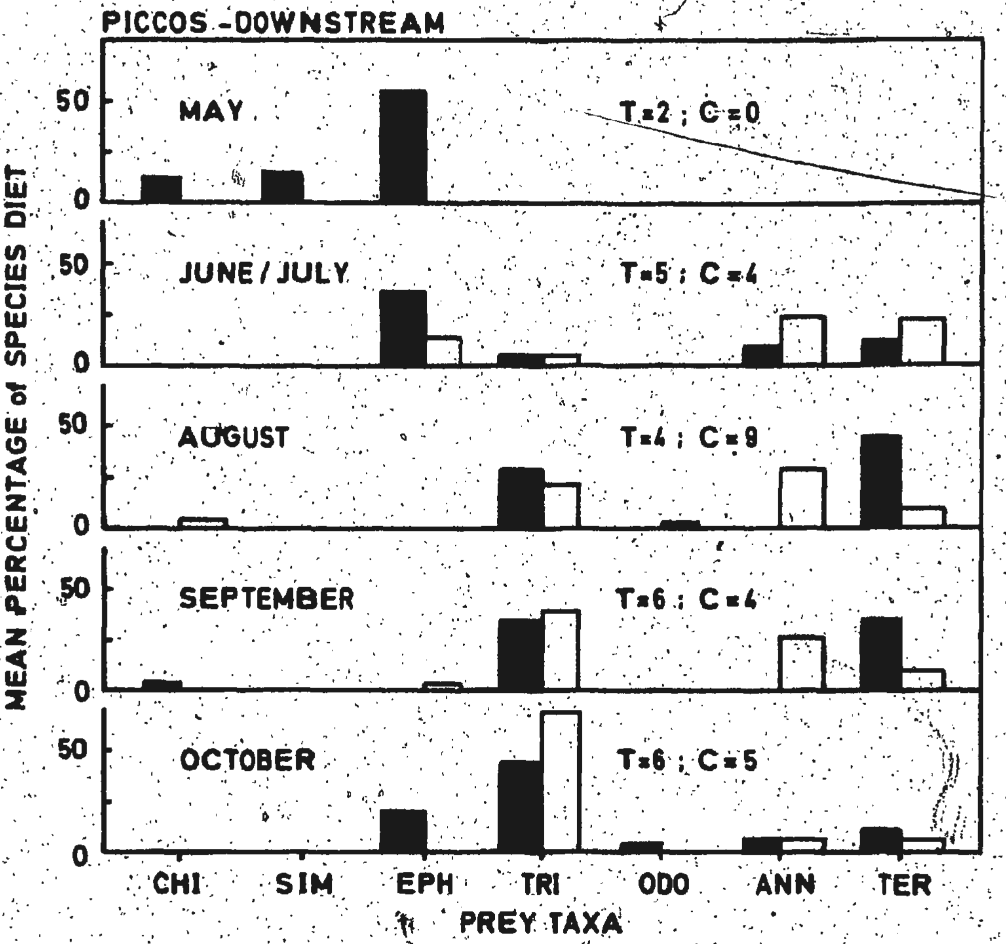

PICCOS - DOWNSTREAM
MAY
T=2 ; C=0
JUNE / JULY
T=5 ; C=4
AUGUST
T=4 ; C=9
SEPTEMBER
T=6 ; C=4
OCTOBER
T=6 ; C=5
50
0
MEAN PERCENTAGE of SPECIES DIET
CHI
SIM
EPH
TRI
ODO
ANN
TER
PREY TAXA

FIGURE 2. Prey consumed by overyearling rainbow trout (solid bars) and brook char (open bars) at different times of the season (May to October) at the Piccos Brook (upstream site). Only those prey taxa comprising at least 20% of the stomach volume of an individual fish were included in this analysis. T = sample size of rainbow trout, C = sample size of brook char ; CHI = Chironomidae larvae, SIM = Simuliidae larvae, EPH = Ephemeroptera nymphs, TRI = Trichoptera larvae, ODO = Odonata nymphs, ANN = aquatic Annelida, TER = terrestrial invertebrates (includes obligate forms and aerial stages of aquatic species).

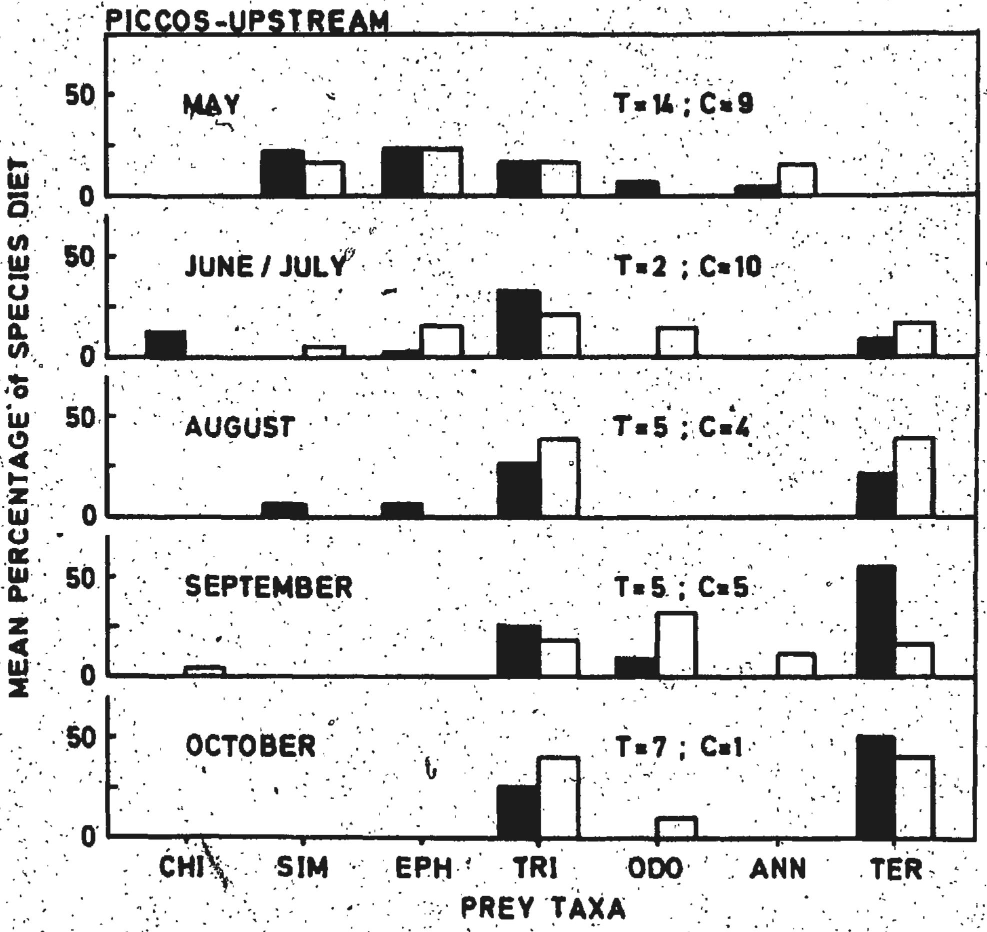
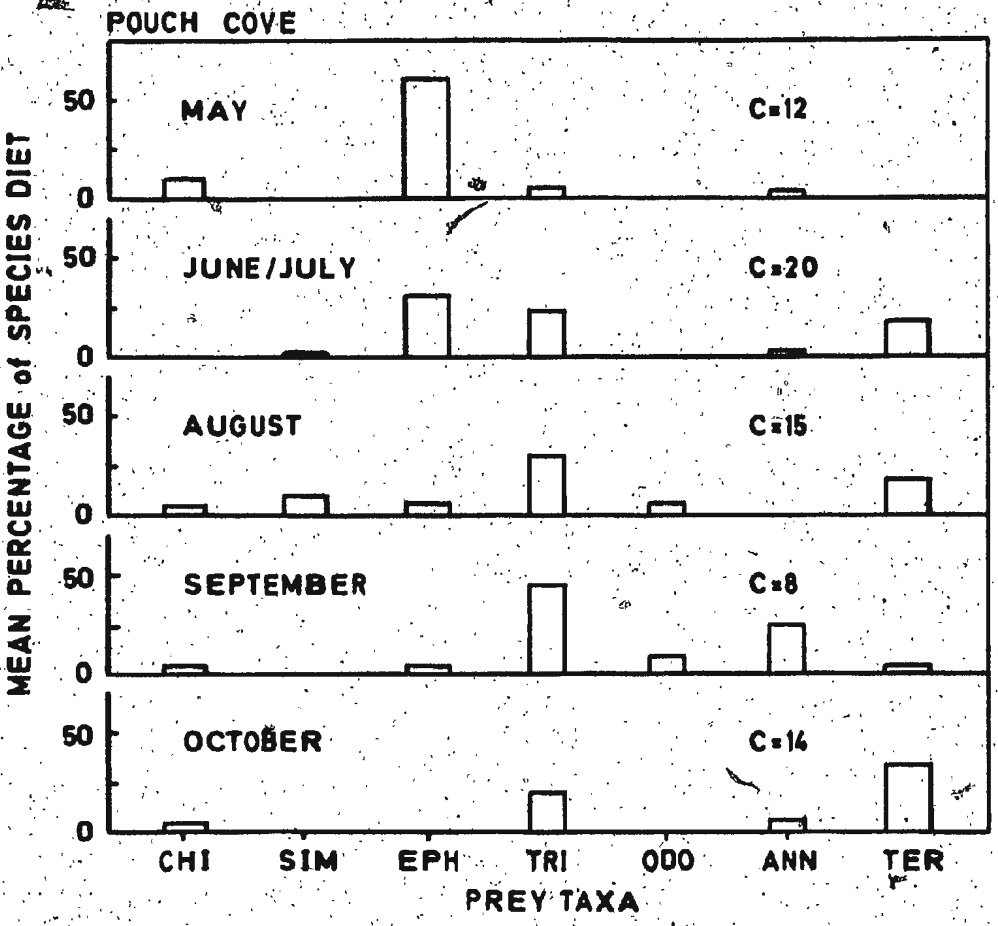

PICCOS-UPSTREAM
MEAN PERCENTAGE of SPECIES DIET
MAY
T=14 ; C=9
JUNE / JULY
T=2 ; C=10
AUGUST
T=5 ; C=4
SEPTEMBER
T=5 ; C=5
OCTOBER
T=7 ; C=1
50
0
CHI
SIM
EPH
TRI
ODO
ANN
TER
PREY TAXA

FIGURE 3. Prey consumed by overyearling brook char at different times of the season (May to October) at the Pouch Cove Brook site. Only those prey taxa comprising at least 20% of the stomach volume of an individual fish were included in this analysis. C = sample size of brook char ; CHI = Chironomidae larvae, SIM = Simuliidae larvae, EPH = Ephemeroptera nymphs, TRI = Trichoptera larvae, ODO = Odonata nymphs, ANN = aquatic Annelida, TER = terrestrial invertebrates (includes obligate forms and the aerial stages of aquatic species).


POUCH COVE
MEAN PERCENTAGE of SPECIES DIET
MAY
C=12
JUNE/JULY
C=20
AUGUST
C=15
SEPTEMBER
C=8
OCTOBER
C=14
50
0
CHI
SIM
EPH
TRI
ODO
ANN
TER
PREY TAXA

APPENDIX

C

Table 1. Data from the benthobservatory experiments in 1980 on rainbow trout (T) and brook char (C).

F = fast flow; S = slow flow; * fish died or escaped

Experiment (Dates)	Habitat	Species	Initial Weight (g)	Initial Fork Length (cm)	Weight Change at End of Experiment (g)
1	F	T	57.7	16.7	+0.9
(June 5 – 20)		C	35.7	14.3	-3.8
	S	T	15.8	11.1	+3.8
		C	10.9	12.1	+0.3
		C	9.4	9.9	-1.8
2	F	T	23.8	13.7	+0.7
(June 23 – July 3)		C	17.8	11.7	+2.1
	S	T	47.3	16.3	-0.3
		C	52.0	16.7	-1.8
3	F	T	12.0	11.0	+2.0
(July 5 – 14)		C	14.9	11.0	*
	S	T	16.9	11.4	-0.4
		C	11.3	10.4	+1.2
4	F	T	13.2	11.0	-0.2
(July 19 – 28)		C	17.1	12.1	+1.9
	S	T	39.6	17.9	-0.2
		C	61.2	17.3	-1.8
5	F	T	44.6	15.6	+1.9
(July 30 – August 8)		C	34.2	17.0	*
	S	T	17.7	11.8	+1.0
		C	15.8	11.5	-0.7
6	F	T	33.3	13.3	+5.1
(August 20 – 29)		C	26.6	13.4	+4.0
	S	T	29.0	13.3	+2.1
		C	12.6	12.8	+0.2
7	F	T	34.4	16.3	*
(August 30 – September 3)		C	53.0	17.2	*
	S	T	22.6	12.4	*
		C	17.6	12.1	*
8	F	T	24.8	12.9	+1.0
(September 8 – 17)		C	22.0	13.1	+1.3
	S	T	24.2	12.8	-0.7
		C	22.0	12.6	0.0
9	F	T	42.1	16.8	*
(October 9 – 17)		C	58.2	17.3	*
	S	T	35.9	14.9	-0.7
		C	32.1	13.6	+0.8

Table 2(a). Data from the day-long observations of rainbow trout (T) and brook char (C) at the benthobservatory on August 27, 1980. Brook char were dominant in both the slow flow (S) and fast flow (F) habitats for this group.

Start Time of Observations (hrs)	Weather Conditions	Water Temperature (°C)	Experimental Habitat	Number of Feeding Moves T	C	Number of Agonistic Acts Iniatiated
0630	Overcast Cool Foggy	14.0	F	0	16	0
		15.0	S	2	3	11
0930	Overcast	15.0	F	0	16	0
	Mild	16.0	S	1	5	15-20
1230	Partly Sunny	17.0	F	3	22	0
	Mild	18.0	S	0	4	0
1530	Overcast Drizzle Mold	17.0	F	0	22	0
		18.0	S	0	4	0
1830	Overcast Drizzle Mild	16.0	F	4	20	6
		17.0	S	2	7	6

Table 2(b). Data from the day-long observations of rainbow trout (T) and brook char (C) at the benthobservatory on September 15, 1980. The rainbow trout was dominant in the fast flow (F) habitat. No heirarchy was yet identified in the slow flow (S) habitat.

Start Time of Observations (hrs)	Weather Conditions	Water Temperature (°C)	Experimental Habitat	Number of Feeding Moves T	Number of Feeding Moves C	Number of Agonistic Aids
0630	Overcast Cool	14	F	9	2	0
		15	S	0	1	0
0930	Overcast Showers Cool	14	F	3	3	8
		15	S	0	0	0
1230	Overcast Showers Cool	15	F	1	3	0
		16	S	0	0	0
1530	Overcast Raining Cool	15	F	0	0	5
		15	S	0	0	0
1830	Overcast Raining Cool	14	F	6	2	0
		15	S	2	2	9

FIGURE 1. Water velocity profile of the fast flow habitat at the Benthobservatory during the 1980 experiments. All values are mean velocities (cm/sec) for five measurements taken between June 18 and August 29, 1980.

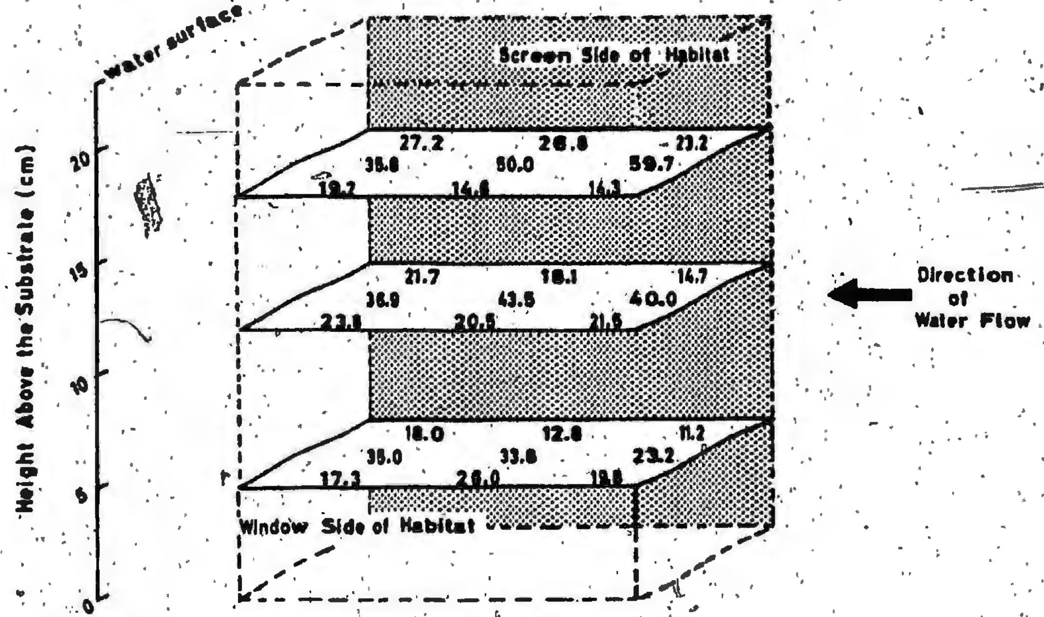
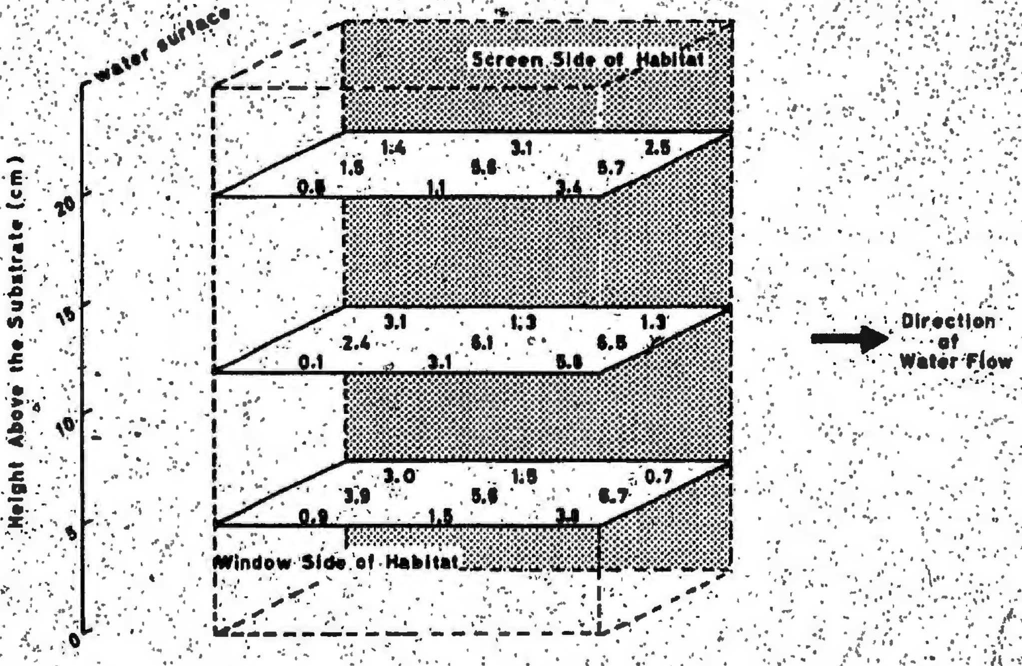

water surface
Height Above the Substrate (cm)
0
5
10
15
20
Screen Side of Habitat
Window Side of Habitat
Direction of Water Flow
27.2
26.8
23.2
35.6
50.0
59.7
19.2
14.6
14.3
21.7
18.1
14.7
36.9
43.5
40.0
23.8
20.5
21.5
18.0
12.8
11.2
35.0
33.8
23.2
17.3
26.0
19.8

FIGURE 2. Water velocity profile of the slow flow habitat at the Benthobservatory during the 1980 experiments. All values are mean velocities (cm/sec) for five measurements taken between June 18 and August 29, 1980.


water surface
Height Above the Substrate (cm)
0
5
10
15
20
Screen Side of Habitat
1.4
3.1
2.5
1.5
5.8
5.7
0.8
1.1
3.4
3.1
1.3
1.3
2.4
6.1
6.5
0.1
3.1
5.8
3.0
1.8
0.7
3.9
5.6
6.7
0.9
1.5
3.8
Window Side of Habitat
Direction of Water Flow

APPENDIX

D

Table 1. Substrate composition within experimental habitats during the 1981 benthobservatory experiments. Values are percentages for each habitat.

Experimental Habitat	Substrate Grain Size (cm)				
	< 1	1-5	5-15	15-25	> 25
Upstream Fast Flow	5	70	15	10	0
Upstream Slow Flow	65	5	10	15	5
Riffle	5	80	15	0	0
Pool	60	10	10	10	5
Downstream Pool	10	20	30	20	20

Table 2. Data from 1981 benthobservatory experiments (May 6 - August 11). Experiments A and C were intraspecific for rainbow trout (T); Experiment B was intra-specific for brook char (C); D-F were inter-specific experiments.

ΔWt - weight change during experiment

Experiment	Mean Water Level (cm)	Mean Water Temperature (°C) (no. hrs. > 20°C)	Species	Number of Fish Introduced	Number of Fish Recaptured	Mean Initial Fork Length (cm)	Mean Initial Weight (g)	Mean ΔWt (g)
A	38.1	14.2 (0)	T	27	8	8.4	8.9	-0.8
B	35.2	13.7 (3)	C	27	22	9.7	11.1	+0.3
C	35.2	13.5 (0)	T	19	9	11.5	17.8	-1.2
D	32.3	18.9 (34)	T	13	8	11.3	17.6	-1.6
			C	13	13	10.7	13.8	-0.6
E	35.5	18.9 (25)	T	13	11	13.3	24.0	-1.3
			C	13	10	12.1	20.8	-2.2
F	31.2	19.2 (48)	T	10	8	13.2	26.1	-0.6
			C	10	4	12.1	19.6	-1.1

APPENDIX

E

Table 1(d). Data from the 8°C experiments at the FBRL between rainbow trout (T) and brook char (C). Tanks A and B represent inter-specific experiments; tanks C and D represent intra-specific experiments. Where no dominance was indicated, a heirarchy was not identified.

* dominant fish; ‡ Δ-weight change at end of group observations

Group and Start Date	Tank	Temperature Range During Observations (°C)	Species	Initial Fork Length (cm)	Initial Weight (g)	‡ Wt (g)
1	A	7.8-8.2	T	8.5	6.1	-0.2
28/12/80			C*	8.5	5.6	-0.5
	B	7.8-8.3	T	7.8	4.4	-0.2
			C	8.3	5.1	-0.5
	C	3.2-6.8	C	5.2	1.2	-0.1
			C	4.8	1.0	-0.1
	D	3.8-6.6	T	6.8	2.9	0
			T	6.8	2.3	-0.1
2	A	7.6-8.8	T	6.9	3.3	-0.3
12/01/81			C	7.2	3.3	0
	B	7.4-8.9	T	7.4	3.3	-0.1
			C*	8.1	4.9	-0.7
	C	4.4-9.2	C	9.5	7.1	-0.4
			C*	9.7	9.8	[illegible]
	D	4.5-6.5	T*	6.8	2.2	-0.1
			T	6.7	2.4	-0.2
3	A	7.0-8.1	T	6.9	3.3	0
27/01/81			C	7.6	3.6	-0.4
	B	7.4-8.0	T	9.6	6.7	-0.2
			C*	9.0	5.4	-0.7
	C	4.2-6.7	C	8.6	6.2	-0.1
			C*	8.8	5.3	-0.2
	D	4.3-6.8	T	6.7	2.8	-0.2
			T	6.8	2.9	-0.1
4	A	7.3-8.5	T	13.4	13.3	-0.1
09/02/81			C	12.3	20.6	-2.4
	B	7.0-8.1	T	8.1	4.8	-0.4
			C	8.2	4.4	0
	C	4.4-8.1	C	12.8	13.3	-0.9
			C*	11.8	13.6	-0.3
	D¹	4.3-8.3	T	6.9	2.6	—
			T	6.3	2.3	—
5	A	7.9-8.1	T	9.0	5.7	-0.1
24/02/81			C*	12.6	9.0	-0.6
	B	7.9-8.6	T*	6.2	2.1	-0.3
			C	5.6	1.2	0
	C	3.6-6.7	C	10.9	10.7	-0.1
			C*	11.3	13.3	-0.7
	D	3.3-5.8	T	6.6	2.6	0
			T	7.0	2.7	-0.1

¹ group observations terminated prematurely due to death of one or both of the fish.

Table 1(b). Data from the 13°C experiments at the WRL between rainbow trout (T) and brook char (C). Tanks A and B represent inter-specific experiments; tanks C and D represent intra-specific experiments. Where no dominance was indicated, a hairarchy was not identified.

* dominant fish; Δ Wt – weight change at end of group observations

Group and Start Date	Tank	Temperature Range During Observations (°C)	Species	Initial Fork Length (cm)	Initial Weight (g)	Δ Wt (g)
1	A[1]	11.2-13.2	T	14.0	28.5	—
11/04/81			C	13.2	23.7	—
	B	12.8-13.4	T	8.1	5.3	-0.2
			C*	8.5	5.6	+0.1
	C	6.6-11.0	C*	13.3	22.4	-1.2
			C	13.3	20.4	-0.9
	D	6.6-11.1	T	5.9	1.7	-0.1
			T	6.3	2.2	-0.1
2	A	12.3-14.1	T	7.3	3.3	-0.1
26/04/81			C*	7.2	3.4	-0.1
	B	13.2-13.7	T	7.2	3.0	-0.1
			C*	7.3	3.4	0
	C	8.0-11.4	T	6.2	2.0	-0.1
			T*	6.9	2.7	0
	D	8.1-11.3	C	7.7	4.0	0
			C*	8.0	4.8	+0.2
3	A	13.8-14.7	T*	7.3	3.0	-0.2
10/05/81			C	7.2	2.9	-0.4
	B	14.0-15.4	T	8.4	5.0	-0.3
			C*	8.4	5.1	+0.1
	C	13.3-15.0	T*	5.8	1.4	+0.1
			T	5.8	1.5	-0.1
	D	13.1-14.9	C*	8.8	6.3	+0.8
			C	7.8	4.7	-0.1
4	A	12.3-13.7	T	7.6	3.7	-0.1
23/05/81			C	7.6	3.8	-0.2
	B[1]	12.0-15.0	T	6.9	2.5	—
			C*	6.8	2.2	—
	C	13.7-16.7	C*	9.1	7.3	+0.9
			C	8.7	6.1	+0.2
	D[1]	13.3-15.0	T	5.8	1.5	—
			T*	6.5	2.1	—

[1] group observations ended prematurely due to death of one or both of the fish

Table 1(c). Data from the 19°C experiments performed at the MSRL between rainbow trout (T) and brook char (C). Tanks A and B represent inter-specific experiments; tanks C and D represent intra-specific experiments. Where no dominance was indicated, a heirarchy was not identified.

* dominant fish; Δ Wt = weight change at end of group observations

Group and Start Date	Tank	Temperature Range During Observations (°C)	Species	Initial Fork Length (cm)	Initial Weight (g)	Δ Wt (g)
1	A¹	19.1–19.9	T	9.1	7.0	—
27/06/81			C	9.9	9.7	—
	B	18.4–21.0	T	11.6	16.6	-1.0
			C*	12.6	23.3	-0.5
	C¹	17.6–19.8	T	9.3	9.1	—
			T	8.0	6.5	—
	D	17.6–20.3	C*	11.8	18.4	-1.1
			C	12.1	19.7	-1.5
2	A	18.0–20.0	T	9.5	8.3	-0.4
11/07/81			C*	9.9	9.7	-0.6
	B	18.0–19.0	T	10.7	12.2	-0.3
			C	10.2	11.2	-0.9
	C	15.2–16.9	C	11.3	15.3	-1.0
			C*	10.1	11.3	-0.4
	D	15.4–16.5	T	11.5	13.9	-1.0
			T	11.2	15.1	-1.2
3	A	18.9–20.0	T	10.0	9.6	-0.7
20/07/81			C	10.2	10.2	-0.6
	B	19.3–20.0	T	9.6	10.6	-1.6
			C*	9.9	9.4	-0.7
	C	16.3–18.7	T	15.3	37.1	-4.3
			T*	16.3	46.8	-3.5
	D	16.1–18.5	C	11.5	14.1	-1.0
			C*	11.3	14.4	-0.6
4	A	18.9–20.3	T*	9.1	7.2	-0.6
30/07/81			C	9.4	6.8	-0.5
	B	18.7–20.2	T*	11.1	14.1	+1.2
			C	10.6	11.6	-0.5
	C	17.7–19.5	C*	10.2	9.7	-0.9
			C	10.0	9.3	-0.1
	D	17.8–19.7	T	11.8	18.6	-1.3
			T*	12.0	18.0	-0.1

¹ group observations terminated prematurely due to death of one or both of the fish