



Intercohort competition causes spatial segregation in brown trout in artificial streams

T. VEHANEN*§, A. MÄKI-PETÄYS*, J. ASPI† AND T. MUOTKA‡

*Finnish Game and Fisheries Research Institute, Kainuu Fisheries Research and Aquaculture, Manamansalontie 90, FIN-88 300 Paltamo, Finland; †Department of Biology, University of Oulu, P.O. Box 333, FIN-90571 Oulu, Finland and ‡Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland

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When together in a flume, 13-cm L_S (age-1) trout appeared to increase their activity and behaved more aggressively, whereas 10-cm L_S (age-0) trout tended to move less and were rarely aggressive in the presence of the larger size class. Both size classes were less mobile and preferred lower water velocities in winter than in summer, and increased their use of instream cover in winter. When both size classes were present, only small trout decreased their use of low water velocities and cover. The results indicate that intercohort competition may cause spatial segregation among size groups of brown trout, especially in winter when trout attempt to minimize their maintenance costs.

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INTRODUCTION

Body size has a large influence on interspecific interactions among fishes (Werner & Gilliam, 1984; Schlosser, 1987). For example, size is known to be a decisive factor in competitive interactions between brown trout *Salmo trutta* L., and other stream salmonids (Fausch & White, 1986; Glove & Field-Dodgson, 1995; Kocik & Taylor, 1995). Size is also an important element in intraspecific interactions: the dominance hierarchy among trout individuals is determined largely by the body size of the fish (Bachman, 1984).

Different size classes of brown trout are often segregated spatially in the wild: small trout occur in shallow riffle areas, whereas larger fish occupy deeper habitats with coarser substrates (Bohlin, 1977; Heggenes, 1988, 1996; Mäki-Petäys *et al.*, 1997). This bigger fish–deeper habitat relationship is relatively common among stream fishes, and has usually been interpreted as an anti-predator tactic to avoid encounters with size-selective predators (Schlosser, 1987; Harvey & Stewart, 1991). Another potential mechanism suggested to explain spatial segregation among differently sized brown trout is intercohort competition (Bohlin, 1977). An obvious question is then: do small trout occupy low-velocity microhabitats along stream margins because they actively prefer these areas, or because they do not have access to more preferred habitats due to intercohort competition from larger trout?

§Author to whom correspondence should be addressed. Tel.: +358 0205751661; fax: +358 0205751649; email: vehanen@tp.rktl.fi

Habitat selection by trout also exhibits distinct seasonal and diel variation (Heggenes & Saltveit, 1990; Heggenes *et al.*, 1993; Cunjak, 1996; Mäki-Petäys *et al.*, 1997). In general, trout are predominantly diurnal in summer, but shift to nocturnal activity in winter. In winter, trout also prefer habitats with lower water velocities and more instream cover than in summer.

The objectives of this study were to investigate whether habitat use by juvenile brown trout in experimental flumes is modified by intercohort competition, and whether the importance of competition, if any, varies on a diel and seasonal basis. Therefore the experiments were conducted in two seasons (summer *v.* winter), making direct observations of fish behaviour during both the day and night.

MATERIALS AND METHODS

The experiment was conducted in three indoor flumes at Kainuu Fisheries Research and Aquaculture, Paltamo, northern Finland. The flumes were 6 m long and 37 cm wide, with a maximum depth of 30 cm. Each flume contained a 1.3-m head box at the upper end of the flume, where a baffle was placed to reduce water turbulence. Water from the hatchery main storage was supplied into two large containers (2000 l) by two submersible pumps. Both containers had similar valves providing water into flumes at a rate of 5 l s^{-1} . Water depth during the experiments varied between 10 and 11.5 cm. The flumes were subdivided with wire mesh (5-mm mesh size) into 1 m sections, three in each flume, resulting in a total of nine experimental units. Each flume was bordered on both sides by a 12-cm wide row of bricks. Two velocity shelters, 12 cm wide and 23 cm long, were provided at both sides of each experimental unit by leaving an empty space between the bricks (Fig. 1). One of the shelters (determined randomly) was supplied with a wooden plate, placed 25 cm above the water surface, to provide overhead cover for sheltering fish. The cover reduced light intensity by 45%. Each experimental unit was divided into 5×4.2 -cm grid cells, and mean water velocities were measured at $0.6 \text{ m} \times \text{depth}$ in each cell with a Schiltknecht Mini Water type 642 w-m/l flowmeter fitted with a 20-mm propeller. The mean water velocity (mean \pm s.e.) in the flumes was $20.5 \pm 1.1 \text{ cm s}^{-1}$, ranging from 1.0 to 36.0 cm s^{-1} . The slope of the flumes was 1.5%.

The experiment was conducted on 3–7 April (water temperature $2\text{--}3^\circ \text{C}$) and 7–11 June 1997 (water temperature $9.5\text{--}11^\circ \text{C}$). Fish used in the experiments were selected randomly from among 7500 age-0 and 7500 age-1 hatchery brown trout, reared at Kainuu Fisheries Research and Aquaculture. The same population of age-0 and age-1 trout was used in both summer and winter experiments. A new set of fish collected from the hatchery pond was used in each trial. The size (mean \pm s.d., $n=24$ in all cases) of age-0 trout was $9.7 \pm 1.2 \text{ cm}$ (range: 7.1–11.1 cm) and $9.1 \pm 3.4 \text{ g}$ (range: 3–13 g) in the winter experiment, and $10.3 \pm 1.3 \text{ cm}$ (8.0–11.8 cm) and $10.3 \pm 3.5 \text{ g}$ (4–15 g) in the summer experiment. Corresponding figures for age-1 trout were $12.6 \pm 0.6 \text{ cm}$ (11.7–13.7 cm) and $20.1 \pm 3.2 \text{ g}$ (15–27 g) in winter, and $13.3 \pm 0.5 \text{ cm}$ (12.5–14.3 cm) and $22.4 \pm 3.0 \text{ g}$ (18–28 g) in the summer experiments. Artificial light was provided on a 12:12 light:dark photoperiod (room light, 125 lx *v.* red light, 3 lx). Fish were not fed during the experiments. Fish were allowed to acclimate for 48 h in the flumes before a trial.

A design suggested by Underwood (1986) for an unconfounded test of interspecific competition was used. Our design consisted of three competition treatments: (1) two small trout; (2) two small trout and two large trout; and (3) two large trout. Thus, the total fish density in the mixed-cohort treatment was twice that in single-cohort treatments; this is important to make sure that the addition of the putative competitor is not confounded by a concurrent change in density of the target age class (see Underwood, 1986). Thus, there is only one difference between individuals of age-0 trout in treatments 1 and 2 (or of age-1 trout in treatments 2 and 3): the absence or presence of the other age class. A randomized block design was used where each of the three flumes (blocks)

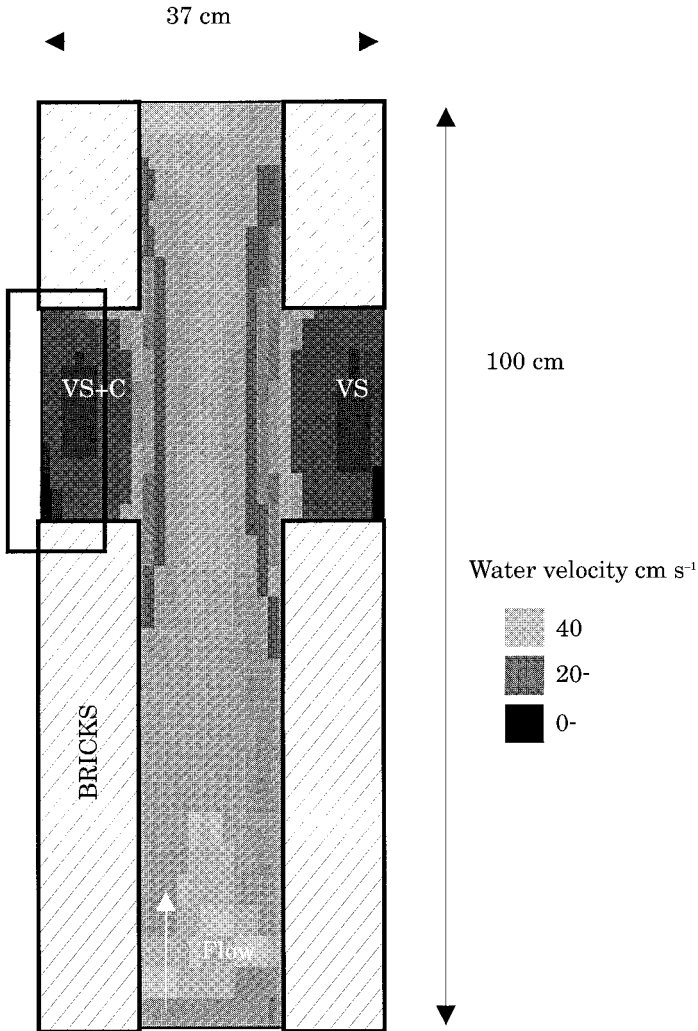


FIG. 1. Schematic presentation of an experimental unit. Each unit consists of an open-stream section, a velocity shelter (VS), and a velocity shelter with overhead cover (VS+C). Spatial variation of current velocity within a unit is represented by different halftones.

contained all three competition treatments in a randomized order. The whole set-up was replicated once in time; thus, six replicates were run for each treatment in both the winter and summer experiments. The null hypothesis was that the presence of large trout had no effect on the behaviour or habitat use of age-0 trout (and vice versa).

Observations of fish behaviour were made from an adjacent room using video monitors. A video camera was located 1 m above each experimental unit. The focal point of each fish was located and marked on outline maps of the units twice during the day (1000 and 1600 hours) and twice at night (2200 and 0400 hours). Fish were considered to be using a velocity shelter, or shelter with cover, when its focal point was within the area delineated by an imaginary line from the upper to the lower corner of the shelter. Within this area, water velocities were considerably lower than in the open stream sections (Fig. 1).

Data on fish behaviour were recorded on video tapes. Four 50-s periods were recorded for each unit, starting at 1100 and 1500 hours during the day, and at 2300 and 0300 hours

at night. The sequence in which the nine units were recorded was determined randomly for each observation period. In total, this resulted in 40 min of observations for each competition treatment. Number of agonistic interactions (chases, bites, displaces, supplants) were counted from the video recordings. In treatments where both size classes were present, agonistic acts were separated into those started by a large or a small fish. Non-agonistic swimming movements by trout were also measured. One swimming movement was recorded when trout moved a distance equal to or longer than its own body length.

A randomized block analysis of variance (ANOVA), with blocking by the flume, was used to analyse the data. Block effect was non-significant for both swimming movements (all $P > 0.42$) and intercohort aggressions (all $P > 0.18$). Differences in swimming movements and aggressions were then analysed separately for age-0 and age-1 fish using repeated-measures ANOVA. Time of day was a within-subject factor, and season and competition between-subject factors. Similarly, water velocities used by brown trout during the day (1600 hours) and at night (0400 hours) were analysed. No block effects were found for either large ($P = 0.395$) or small brown trout ($P = 0.614$); thus, all subsequent analysis omitted blocks as a factor.

Differences in microhabitat use among trout size classes were tested by a logit analysis (Christensen, 1990), where the proportion of a habitat type (velocity shelter, shelter with cover, open stream) used by fish was the response variable, and competition treatment (1, 2, 3), season (summer v. winter), time of day (day v. night), and fish size (small v. large) were the explanatory variables. The GLIM statistical package (Aitkin *et al.*, 1990) was used to determine the parameters of the logit models. Akaike's information criterion (AIC) was also estimated for each logit model to select the model with the highest information content. For logit models, this means choosing a model that minimizes Akaike's information criterion:

$$\text{AIC} = G^2(X) - [q - 2r],$$

where $G^2(X)$ is the likelihood ratio test statistic for testing the X model and its q degrees of freedom for the saturated model (Christensen, 1990).

RESULTS

SWIMMING MOVEMENTS

Measured by swimming movements, both size classes of brown trout were more active in summer than in winter [Table I, Fig. 2(a)]. Movement rate tended to be related to competition treatment in both size classes, but this was not significant. However, the power of these tests was relatively low, 0.43 for small and 0.48 for large trout, respectively, thus leaving a relatively high probability of a type II error. When together with a large trout, small trout appeared to reduce their swimming movements in both summer and winter. By contrast, large trout tended to increase their activity when small trout were present [Table I, Fig. 2(a)]. Time of day had no effect on movement activity in either of the size classes, and all interaction terms were also non-significant (Table I).

AGGRESSION

Aggressive behaviours were clearly related to competition treatment. When size classes were held separately, aggressions between fish were rare in both seasons [Fig. 2(b)]. When both size classes were present, only large trout increased the amount of agonistic acts [Table II, Fig. 2(b)]. No seasonal effects were found: large trout increased their aggressiveness in both warm and cold

TABLE I. Summary of the results from repeated-measures ANOVA for the effects of time of day (day *v.* night), season (summer *v.* winter) and competition treatment (size group alone *v.* both size groups together) on the amount of swimming movements by large (age-1) and small brown trout (age-0)

Source of variation	d.f.	SS	<i>F</i>	<i>P</i>
Large brown trout				
Within subjects				
Time of day	1	1.470	0.942	0.343
Time of day*season	1	0.030	0.019	0.891
Time of day*competition	1	0.030	0.019	0.891
Time of day*season*competition	1	1.470	0.942	0.343
Error	20	31.200		
Between subjects				
Season	1	45.630	27.356	0.000
Competition	1	6.750	4.047	0.058
Season*competition	1	3.630	2.176	0.156
Error	20	33.360		
Small brown trout				
Within subjects				
Time of day	1	0.480	0.322	0.577
Time of day*season	1	2.430	1.630	0.216
Time of day*competition	1	1.080	0.724	0.405
Time of day*season*competition	1	0.750	0.503	0.486
Error	20	29.820		
Between subjects				
Season	1	12.000	34.636	0.000
Competition	1	8.670	3.564	0.074
Season*competition	1	0.480	0.197	0.662
Error	20	2.433		

water. Finally, no differences were found in the number of agonistic acts between day and night, either in summer or in winter (Table II).

SITE SELECTION

Water velocities used by brown trout in winter were lower than in summer for both size classes and in all competition treatments (Table III, Fig. 3). Large trout did not alter their flow preference in the presence of small trout, which, in turn, used higher water velocities in the presence than absence of large fish on both seasons. Time of day had no effect on water velocities used by brown trout, and none of the interaction terms were significant (Table III).

The logit analysis indicated that competition (*C*), season (*S*) and size of fish (*F*) affected the selection of cover type (i.e. velocity shelter *v.* shelter with cover *v.* open stream) by trout ($P < 0.001$ in each case), whereas time of day had no effect ($G_{(3)} = 2.68$; $P = 0.444$, Fig. 4). None of the models including the main effect of only one explanatory variable ($\{C\}$, $\{F\}$, or $\{S\}$) was an adequate representation of the data ($P < 0.05$ in each case).

The models including either the main effects of competition and fish size ($\{C\}\{F\}$), or season and fish size ($\{S\}\{F\}$), both fitted the data well ($G_{(41)} = 48.37$, $P = 0.200$, and $G_{(36)} = 43.64$, $P = 0.179$, respectively), whereas the model

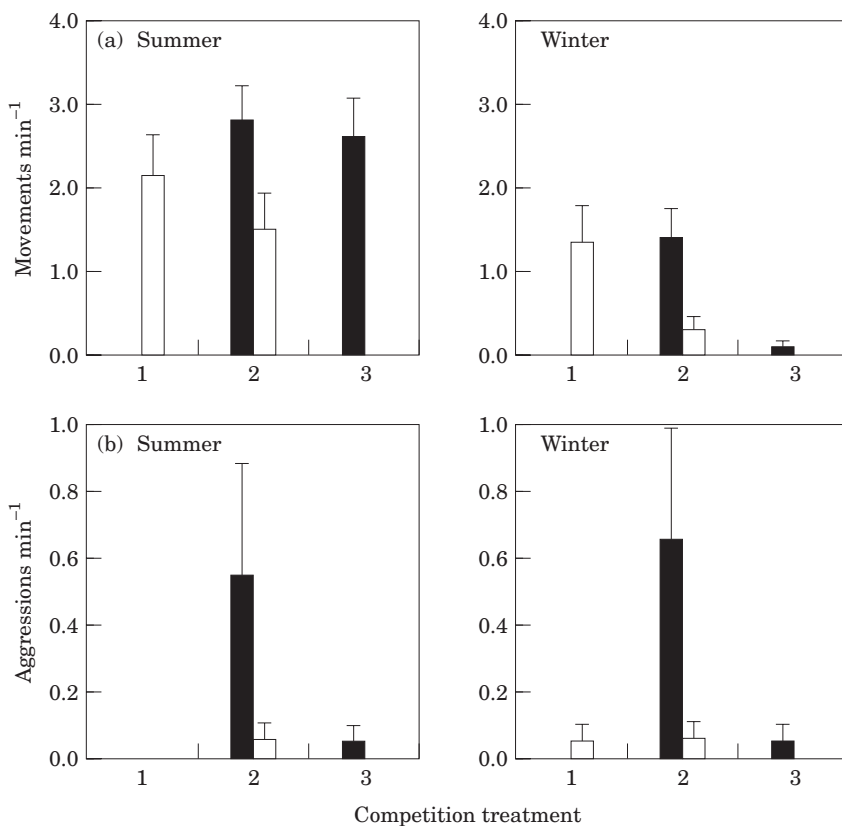


FIG. 2. (a) Movement rates of small (□) and large (■) brown trout in different competition treatments (1, small trout alone; 2, small and large trout together; 3, large trout alone) in summer and in winter. (b) Mean number of antagonistic behaviours per min by small and large trout in different competition treatments. Error bars indicate one standard error of the mean.

incorporating competition and season ($\{C\}\{S\}$) did not ($G_{(36)}=72.79$, $P<0.001$). Nevertheless, including the main effects of all explanatory variables ($\{C\}$, $\{F\}$, $\{S\}$) results in a significantly better model than any of the two factor models ($P<0.001$ in all cases). This model fitted the data very well ($G_{(36)}=20.33$, $P=0.986$), and the information content (based on Akaike's information criterion) of this model was the highest. None of the models including interactions between the three factors fitted the data better ($P<0.05$). Accordingly, the logit analysis suggests that competition, size of fish and season all affected the microhabitat selection by trout, and that there were no interactions between these factors.

DISCUSSION

Social hierarchies in brown trout and other stream salmonids are determined largely by the size of the fish (Bachman, 1984; Elliott, 1994). In these hierarchies, dominant fish have access to the most profitable stream positions, while subordinate individuals are restricted to stream margins and other less

TABLE II. Summary of the results from repeated-measures ANOVA for the effects of time of day (day *v.* night), season (summer *v.* winter) and competition treatment (size group alone *v.* both size groups together) on the amount of aggressions by large (age-1) and small brown trout (age-0)

Source of variation	d.f.	SS	<i>F</i>	<i>P</i>
Large brown trout				
Within subjects				
Time of day	1	0.270	0.336	0.569
Time of day*season	1	0.270	0.336	0.569
Time of day*competition	1	0.750	0.933	0.346
Time of day*season*competition	1	0.270	0.336	0.569
Error	20	16.080		
Between subjects				
Season	1	0.030	0.048	0.829
Competition	1	3.630	5.817	0.026
Season*competition	1	0.030	0.048	0.829
Error	20	12.480		
Small brown trout				
Within subjects				
Time of day	1	0.003	0.145	0.707
Time of day*season	1	0.067	2.945	0.102
Time of day*competition	1	0.013	0.582	0.455
Time of day*season*competition	1	0.008	0.327	0.574
Error	20	0.458		
Between subjects				
Season	1	0.007	0.342	0.565
Competition	1	0.013	0.608	0.445
Season*competition	1	0.007	0.342	0.565
Error	20	0.438		

favourable habitats (Fausch, 1984; Fausch & White, 1986; Hughes & Dill, 1990). Such spatial segregation by body size is common among salmonids (Everest & Chapman, 1972; Heggenes, 1988; Greenberg *et al.*, 1996), but evidence indicating intercohort competition as the underlying mechanism is rare (but see Hughes & Dill, 1990; Hughes, 1998). In the present experiments, large trout behaved more aggressively and tended to increase their activity, while small trout were rarely aggressive and appeared to move less, in the presence of the other size class. These results are thus in accordance with Bohlin's (1977) observation that age-1 trout dominate over age-0 trout when competing for territories they both find suitable. In the experiments of Greenberg *et al.* (1997), the more extensive use of shallow stream areas by 10-cm L_S compared with 12-cm brown trout was not affected by the presence of large trout. The differences between the present results and those of Greenberg *et al.* (1997) may have been caused by dissimilarities in the physical structure of the flumes, for example, differences in habitat availability. Greenberg *et al.* (1997) did, however, observe a reduction in prey consumption rate of small trout in the presence of larger trout.

Habitat selection by brown trout is also affected by predation risk (Greenberg, 1994; Greenberg *et al.*, 1997), and size-dependent habitat use is probably a

TABLE III. Summary of the results from repeated-measures ANOVA for the effects of time of day (day *v.* night), season (summer *v.* winter) and competition treatment (size group alone *v.* both size groups together) on the water velocities used by large (age-1) and small brown trout (age-0)

Source of variation	d.f.	SS	<i>F</i>	<i>P</i>
Large brown trout				
Within subjects				
Time of day	1	0.052	0.002	0.966
Time of day*season	1	12.420	0.443	0.513
Time of day*competition	1	5.729	0.205	0.656
Time of day*season*competition	1	0.903	0.032	0.859
Error	20	560.232		
Between subjects				
Season	1	357.066	12.352	0.002
Competition	1	8.264	0.286	0.599
Season*competition	1	<0.001	<0.001	0.998
Error	20	578.149		
Small brown trout				
Within subjects				
Time of day	1	8.333	0.273	0.607
Time of day*season	1	0.188	0.006	0.938
Time of day*competition	1	20.021	0.656	0.427
Time of day*season*competition	1	18.750	0.615	0.442
Error	20	609.958		
Between subjects				
Season	1	602.083	26.443	<0.001
Competition	1	252.083	11.071	0.003
Season*competition	1	1.687	0.074	0.788
Error	20	455.375		

trade-off between predation risk, feeding opportunities and social interactions (Hughes, 1998). In summer, drift-feeding salmonids maximize their net energy gain by selecting low-velocity microhabitats adjacent to swift currents (Fausch, 1984; Hill & Grossman, 1993). Daytime foraging by trout in summer would involve an increased risk of predation from visually hunting predators, especially for larger trout. To avoid this, they select deeper habitats, whereas smaller fish can occupy shallower stream areas without any increase in predation risk (the bigger fish–deeper habitat relationship; Schlosser, 1987; Godin, 1997). Thus, size-related differences in vulnerability to predators may also induce spatial segregation among trout size classes. In winter, trout are primarily nocturnal, and selecting deep water would probably incur little, if any, benefits as regards predator avoidance then. Nevertheless, by providing shelter from stream current, depth may still contribute importantly to habitat selection by trout even in winter (Heggenes *et al.*, 1993).

Distinct seasonal variation were found in the behaviour and microhabitat use of juvenile brown trout. Trout generally increased their use of low velocity microhabitats and instream shelter in winter. Such wintertime aggregation to microhabitats with slow currents and abundant instream cover has also been

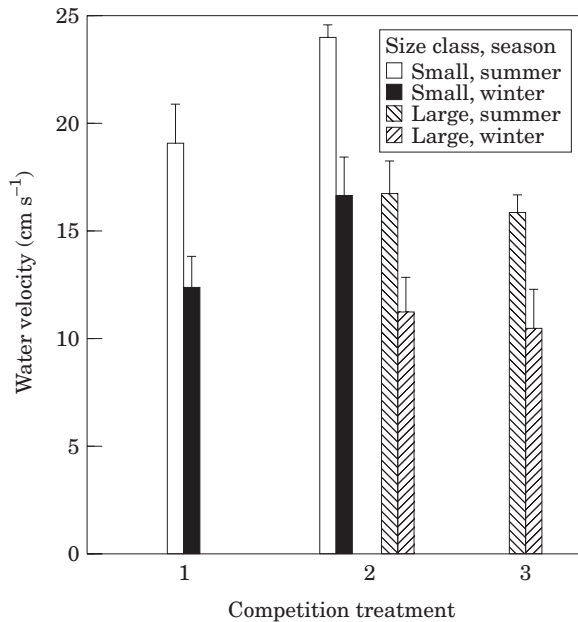


FIG. 3. Mean water velocity used by small and large brown trout in different competition treatments. For other details, see Fig. 2.

observed in natural streams (Cunjak & Power, 1986, 1987; Hillman *et al.*, 1987; Heggenes & Saltveit, 1990; Mäki-Petäys *et al.*, 1997). Heggenes *et al.* (1993) suggested that trout change seasonally their behavioural strategy: in summer, trout attempt to maximize their energy intake, whereas in winter they minimize risk and maintenance costs. Since the feeding rate of trout is relatively low in winter, having access to high-velocity microhabitats is not a prime determinant of microhabitat selection then; instead, they require microhabitats with suitable low-flow refuges. If such refuges are in short supply, overwintering trout may aggregate to the suitable areas available in a stream reach, which may result in increased competition for space. Antagonistic behaviour among trout is usually lower during winter compared to summer (Cunjak & Power, 1986). However, any aggressions at low water temperatures are costly, and extensive overlap in habitat preference among trout size classes in winter (Mäki-Petäys *et al.*, 1997) creates potential for intercohort competition during winter.

Both brown trout and Atlantic salmon reduce their day activity and become primarily nocturnal at low water temperatures (Heggenes *et al.*, 1993; Fraser *et al.*, 1995), and many recent studies have reported diel variation in the behaviour of salmonid fishes (Hubert *et al.*, 1994; Baxter & McPhail, 1997; Valdimarsson *et al.*, 1997). In the present study there was no effect of time of day on movements, aggressions or microhabitat use by brown trout. An obvious reason for the lack of diel periodicity in the behaviour of brown trout in these experiments was the limited availability of suitable substrates in our flumes. During winter, brown trout typically conceal within the substratum interstices during the day (Griffith & Smith, 1993; Heggenes *et al.*, 1993), which they could not do in the flumes. Another explanation for the lack of diel periodicity in these

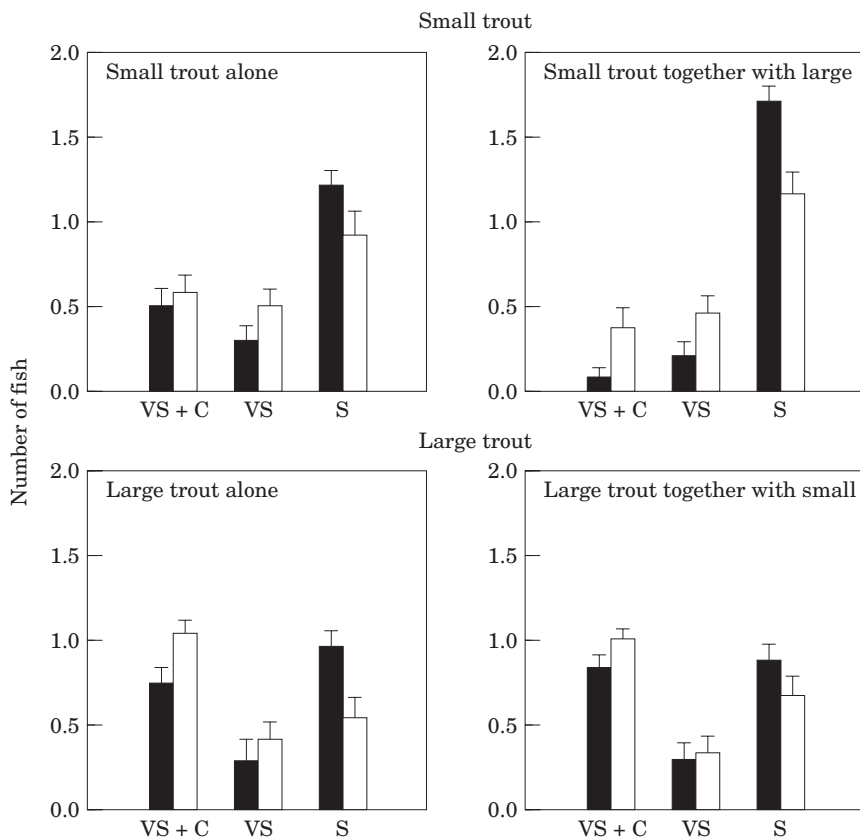


FIG. 4. Use of various cover types (VS+C, velocity shelter with cover; VS, velocity shelter; S, open-stream section) by small and large trout in the summer (■) and the winter (□) experiments. Error bars indicate one standard error of the mean.

experiments could be that hatchery fish were used, which may have been affected by their rearing history and are often reported to be day-active irrespective of water temperature (Pirhonen, 1998). Furthermore, nocturnal behaviour of salmonids is at least partly a means of avoiding diurnal predators (Valdimarsson & Metcalfe, 1998), which hatchery fish are not familiar with. Finally, the activity pattern adopted by individual fish may vary depending on local variation in food supply and the social status of the fish (Alanärä & Brännäs, 1998).

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