Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids

A.J. Harwood, N.B. Metcalfe, S.W. Griffiths, and J.C. Armstrong

Abstract: The availability of streambed refuges has previously been shown to be of critical importance to the survival of overwintering juvenile salmonids. We used semi-natural stream channels to quantify intra- and inter-specific competition for daytime refuges and the willingness of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) to share available shelter. Refuge use was frequently associated with aggressive behaviour when two fish were provided with only one shelter, with intra- and inter-specific competition being similar in intensity. Resident individuals were less likely to leave the refuge than were intruders, and sharing of refuges was uncommon, both when competing for one shelter (experiment I) and when these were provided in excess (experiment II). Fish showed greater preferences for foraging habitat during the night than for the location of daytime shelters and were therefore willing to shift habitats to find adequate shelter. Overall, these results suggest that winter competition for refuges, both within and between species of salmonid, is likely to be intense if refuge availability is limited in the wild.

Résumé : Il a été démontré que la disponibilité de refuges dans le lit du cours d'eau est un facteur critique pour la survie des jeunes saumons en hiver. Des ruisseaux semi-naturels nous ont servi à quantifier la compétition intra- et inter-spécifique pour des refuges de jour et d'évaluer dans quelle mesure des saumons de l'Atlantique (*Salmo salar*) et des truites brunes (*Salmo trutta*) sont disposés à partager les refuges disponibles. Lorsque deux poissons sont en présence d'un seul refuge, son utilisation génère souvent des comportements agressifs d'intensité semblable, qu'il s'agisse de compétition intra- ou inter-spécifique. Les résidents sont moins susceptibles d'abandonner le refuge que les intrus et le partage d'un refuge reste rare, qu'il y ait compétition pour un même refuge (expérience I) ou qu'il y ait un surplus de refuges (expérience II). Les poissons montrent plus d'intérêt pour les substrats de nuit de quête de nourriture que pour les refuges de jour et ils sont donc disposés à changer d'habitat pour trouver un refuge adéquat. Généralement, nos résultats laissent croire qu'en nature, la compétition pour les refuges en hiver est probablement intense lorsque la disponibilité des refuges est limitée, tant au sein d'une espèce qu'entre les espèces de salmonidés.

[Traduit par la Rédaction]

Introduction

Sheltering behaviour is widespread among both invertebrates and vertebrates and can be used to investigate the trade-off between the cost of lost feeding opportunities and the benefit of predator avoidance during an individual's decision-making processes (Dill and Fraser 1997; Krause et al. 1998). For example, Dill and Fraser (1997) were able to measure the cost of sheltering in terms of lost growth in the polychaete worm, *Serpula vermicularis*, which filter-feeds at the mouth of its calcareous tube but retreats when threatened. Shelter use can influence an individual's chance of survival, particularly through a decreased risk of inter- and intra-specific predation. Predator avoidance has been cited as the primary function of sheltering behaviour in salmonid fishes (Gregory and Griffith 1996*a*; Valdimarsson and Metcalfe 1998). However,

in nature, the ability to find a suitable refuge can also have other benefits. For example, Smith and Griffith (1994) found that rainbow trout (*Oncorhynchus mykiss*) survival in winter was higher in enclosures with cobble substrate than in those without, even though both enclosures excluded predators. The presence of rocks in the enclosures allowed trout to shelter in interstitial spaces that provided them not only with protection against physical damage from dislodged ice moving in the water column, but also with a reduction in daytime energy expenditure. The ability to find adequate shelter can therefore influence survival under natural conditions, independent of predation.

Winter can be a bottleneck during which density-dependent processes occur in some populations of salmonid fish (Bjornn 1971; Mason 1976), with availability of suitable habitat being cited as one of the main limiting factors (Rimmer et al. 1985;

A.J. Harwood[1] and N.B. Metcalfe. Fish Biology Group, Graham Kerr Building, Institute of Biomedical and Life Sciences, University of Glasgow, G12 8QQ, U.K.
J.D. Armstrong. Fisheries Research Services Freshwater Laboratory, Faskally, Pitlochry, Perthshire, PH16 5LB, U.K.
S.W. Griffiths. Fisheries Research Services Freshwater Laboratory, Faskally, Pitlochry, Perthshire, PH16 5LB, U.K., and Cardiff School of Biosciences, Main University Building, P.O. Box 915, Cardiff, Wales, CF10 3TL, U.K.

[1]Corresponding author (e-mail: ajharwood@canada.com).

1516

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

Nickelson et al. 1992; Cunjak 1996). There are two types of preferred winter habitat important to the survival of fishes. First, slow-flowing water has been shown to be important for overwintering salmonids (e.g., Heggenes et al. 1993; Whalen and Parrish 1999; Harwood et al. 2001). Secondly, cobble–boulder substrates that provide shelter have been found to be of critical importance for both stream-dwelling salmonids and cyprinids (see Cunjak 1996). Habitat-enhancement programmes have highlighted the importance of both habitats. Solazzi et al. (2000) have shown that the addition of large woody debris to newly created dammed pools provides salmonids with refuge from high-velocity conditions and improves overwintering survival of coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarki*), and rainbow trout, as well as increasing coho salmon smolt production. Similarly, the addition of patches of cobble to a stream in Idaho increased the number of overwintering chinook salmon (*Oncorhynchus tshawytscha*) eightfold over numbers from the previous winter, despite numbers being comparable at the onset of the two winters (Hillman et al. 1987).

The importance of shelters in salmonid ecology is not restricted to the winter months, as some species of salmonid also shelter during the day in summer (Rimmer et al. 1984; Gries et al. 1997; Gries and Juanes 1998). Despite the significance of shelters, few studies have examined whether fish actively compete for, or defend, refuges. This is largely because fish are thought to become less aggressive during winter (McMahon and Hartman 1989; Fraser et al. 1993) and studies in summer have concentrated on territorial disputes over food rather than shelter resources (e.g., Fausch 1984). McMahon and Hartman (1989) and Glova (1986) both reported territorial behaviour among cover in juvenile coho salmon and cutthroat trout, respectively; however, only Gregory and Griffith (1996b) have quantified the aggression associated with shelter use.

Here we report more detailed investigations into competition for refuges than have previously been conducted. In our first experiment, where shelter availability was limited, we provide the first quantitative assessment of shelter competition among conspecific and heterospecific pairs of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). We test for asymmetry in the abilities of Atlantic salmon and brown trout to compete for shelter during winter. Aggressive behaviour and shelter sharing were observed at dawn, when movement into shelters is at its peak (Gregory and Griffith 1996b). In experiment II, when shelters were provided in excess, we examined the frequency of shelter sharing among allopatric groups of salmon and sympatric groups of Atlantic salmon and brown trout. The influence of surrounding habitat type on refuge use was also investigated.

Materials and methods

Experiment I

This experiment was carried out in a glass stream-channel system at the University of Glasgow, U.K. The channel consisted of a stack of three glass tanks measuring 180 cm × 25 cm × 20 cm and one glass tank measuring 120 cm × 25 cm × 20 cm, which were interconnected by plastic pipes. These tanks then drained into two 60-L sumps, the water from which was recirculated by pumping it into the top stream tank. The stream-channel system was positioned within a temperature-controlled laboratory. In order to separately control the lighting regime for each glass tank, the system was surrounded by black polythene sheeting to block out any light from the laboratory. An observation hide was also created so that fish could be observed without casting any external light on the tanks. The glass tanks had a 4-cm layer of gravel substrate, a water depth of 11 cm, and a flow rate of approximately 0.03 m·s^{-1}. Partitions placed within the tanks created compartments; the partitions were opaque but had panels of fine mesh to allow a directional current through the tanks. The compartments in which the experiments were conducted, hereafter referred to as experimental arenas, measured 40 cm × 25 cm. Six experimental arenas were used in total, two in each of the longer glass tanks. Although juvenile salmonids are unlikely to occupy such a simplified habitat in nature, refuge availability is a limiting factor for overwintering survival in the wild (e.g., Hillman et al. 1987; Griffith and Smith 1993; Cunjak 1996).

A feeder and a shelter were placed in opposite corners of each arena so that fish could not feed while in the shelter. The feeders consisted of 25-mL transparent plastic tubes, each with a small hole drilled near the top to allow water to circulate and a small hole (1.5 mm in diameter) near the bottom to allow a mixture of live *Daphnia* and chironomid larvae to escape at random after having been placed in the feeder. A plastic mount held each tube so that the exit hole for the larvae was 5.5 cm above the substrate. The shelters were made from 1-L opaque plastic bottles cut lengthwise into quarters and embedded in the gravel, creating cavities in the gravel measuring 15 cm × 4 cm × 4 cm. Fish could enter the shelters through a 4 cm × 4 cm vertical hole that was cut into the top corner of each shelter and was positioned flush with the surrounding gravel. These shelters were placed at the downstream end of each section with the open side against the glass wall of the tank, allowing any fish within them to be identified (see Valdimarsson et al. 1997).

The fish used were wild-caught age-0+ Atlantic salmon (fork length = 65.5 ± 1.07 mm (mean ± standard error (SE)); weight = 2.64 ± 0.13 g) and brown trout (fork length = 76.7 ± 1.62 mm; weight = 4.28 ± 0.28 g) from the River Endrick, which flows into Loch Lomond, west Scotland. Fish were captured during a single day less than 1 week before experiments began and were kept in tangential-flow holding tanks, except when being tested. These fish were used in one of three treatments. Allopatric trials (either two salmon or two trout) were used to examine intra-specific competition for shelters in each species, while sympatric trials (one salmon and one trout) were used to study interspecific competition for shelters. Fish in all three treatments were approximately size-matched (size differential < 20%) to ensure that they had similar habitat preferences and so would compete for the refuge. After anaesthetization using benzocaine, fish were individually marked on their caudal fins using small injections of Alcian Blue dye. They were then placed in experimental arenas on the evening before observations began, and light intensity was reduced to nighttime levels (0.01 lx) 30 min later. To ensure that aggressive interactions during initial shelter acquisition were noted, observations began the following day. Light intensity was recorded using a photometer (SKL 300, range 0.01–2000 lx

(Skye Instruments Ltd., Powys, U.K.)), placed alongside the experimental arena.

Light intensity was controlled by the use of three dimmer switches, each of which controlled two bulbs that were situated above the two experimental arenas located on each shelf. To simulate natural dawn conditions, light levels were gradually increased by 33 lx every 5 min for 45 min, reaching a maximum of approximately 300 lx. The position of each fish (either in or out of shelter) was recorded immediately before the dawn light manipulation and then every 5 min over the 45-min dawn observation period. During this same period, continuous observations of feeding attempts, aggressive behaviour, and movement in and out of the shelter were made. For each aggressive interaction, the location and identity of aggressor and recipient was noted (see Kalleberg (1958) for a description of aggressive behaviour among juvenile salmonids). Any movement by the recipient between habitats was also noted (fish were defined as being forced to move habitats if they moved in or out of shelter within 5 s of having been attacked).

Because only two arenas could be monitored simultaneously, it was necessary to stagger the timing of the simulated dawn so that data could be obtained from all six arenas each day. Fish experienced dawn a maximum of 90 min after natural dawn, and the sequence in which treatments were observed was randomized to minimize any effects that shifting photoperiod may have had on the fish. After the dawn period, light levels were kept constant at approximately 300 lx for 8 h in each tank, after which light levels were reduced directly to 0.01 lx until "dawn" the next morning. The fish were fed 1% of their body weight per day, with the feeders being replenished with *Daphnia* and chironomids immediately before light levels were reduced in the evening and immediately after all observations had been carried out in the morning. Equal amounts of food were given in the morning and in the evening.

Observations were made on four successive mornings, after which time the fish were removed and replaced by new groups. All three treatments were replicated eight times, with all fish being used only once. Water temperature was continuously measured using a digital thermometer placed in the stream tank and varied between 6.9°C and 10.3°C during the course of the experiment, which ran between 7 February and 8 March 2001. We were unable to conduct experiments I and II under the same temperature regime; however, both experiments were conducted within the range of naturally occurring winter temperatures in Scotland and below the critical value of 10°C at which juvenile salmonids switch from diurnal to nocturnal behaviour (Fraser et al. 1993). We therefore have no reason to believe that differences in temperature regimes influenced the direction of our results.

Experiment II

A full description of the materials and methods for this experiment is given in Harwood et al. (2001), and only details relevant to shelter use are presented here. A comparison of the experimental procedure of experiments I and II can be seen in Table 1. Experiment II consisted of monitoring habitat and shelter use by salmon and trout in a semi-natural outdoor stream channel at the University Field Station, Rowardennan, Scotland. In a series of replicated trials, groups of four salmon

Table 1. Summary of the experimental design for the two experiments.

	Experiment I	Experiment II
Number of individuals/replicate	2	4
Number of shelters/replicate	1	6
Habitat	Simple	Varied
Settling time	None	72 h
Number of days observed	4	4
Treatments		
Salmon in allopatry	Y (8)	Y (8)
Trout in allopatry	Y (8)	N
Salmon and trout in sympatry	Y (8)	Y (8)

Note: Numbers in parentheses represent the number of replicates.

(allopatric treatment) and two salmon with two trout (sympatric treatment) were observed in identical experimental arenas, each of which had a gradual increase in water depth from 10 cm at the upstream end to 45 cm at the downstream end. Accordingly, the surface velocity of the water varied continuously from 0.16 m·s^{-1} at the upstream end to 0.03 ms^{-1} at the downstream end. Each experimental arena was 225 cm × 60 cm, and the outer side of the channel was marked every 15 cm to define 15 zones per arena (with zone 1 being at the upstream end) and allow referencing of the recorded positions of each fish. The arenas were landscaped with fine gravel (5–25 mm diameter) to prevent fish from hiding in streambed cavities. Six shelters were placed at regular intervals in each of the experimental arenas with the open side against the glass wall to allow any fish within them to be identified by their Alcian Blue marks (see below). The shelters were made from 1-L opaque bottles that were cut in half lengthwise, creating cavities in the gravel measuring 17 cm × 8.5 cm × 4.25 cm. Hence, in this experiment, streambed shelters were provided in excess.

Water was pumped constantly from Loch Lomond into the stream channel and ranged in temperature from 4.3 to 6.1°C. Light conditions and photoperiod for the outdoor stream channel were the same as the ambient conditions of Loch Lomond. Fish were provided with 0.5% of their total body weight in food per day. The food was delivered via a belt feeder that dropped pelleted food at a trickle rate at the upstream end of each arena. The fish used were wild-caught age-1+ Atlantic salmon (fork length = 109.4 ± 1.83 mm (mean ± (SE)); weight = 13.42 ± 0.65 g) and brown trout (fork length = 100.7 ± 2.77 mm; weight = 9.87 ± 0.90 g) from the River Blane, a tributary of the River Endrick. Fish were captured during a single day 1 week before the start of the experiments and were kept in tangential-flow holding tanks, except when being tested. The fish were approximately size-matched (size differential < 20%) and individually marked as in Experiment I. Fish were then allowed to reside in the experimental arenas for a period of 72 h before observations began.

Observations on each group of acclimated fish were made on four consecutive dates. Each observation period lasted 7 h and covered the day–night transition at either dusk or dawn. During each observation period, the position of each fish was recorded every 30 min by scanning briefly with a flashlight, a method chosen to minimize the disturbance of the fish (see Heggenes et al. 1993). Data collected during each scan observation included the zone number in which each fish was located (1–15) or the shelter in which the fish

1518

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

was hiding (1–6, with shelter 1 being at the upstream end). Light intensity and water temperature were also noted. Light intensity was measured using a SKL 300 photometer (range 0.01–2000 lx, Skye Instruments) and recorded as the mean of two measurements made just above the water surface. Water temperature was measured using a digital thermometer placed permanently in the stream. After the data for each group were collected, the fish were removed and different fish were placed in the test arena. Both treatments were replicated eight times; all fish were used only once. The experiments were carried out between 16 January and 4 March 1999.

Data analysis and statistical treatment

Experiment I

To determine whether fish increased their use of shelter as the simulated dawn period progressed, we calculated the mean percentage of observations in which each individual fish was in shelter over the 4 days at the start point (dimmest) and end point (brightest) of each observation period. The mean for each replicate was then calculated and used in a paired-sample t test. To examine the occurrence of shelter sharing in the different treatments, we calculated the percentage of all observations in which both fish were found occupying the shelter. We used one-way analysis of variance (ANOVA) using replicate mean values as data points to determine whether there were any species or treatment effects on the percentage of time that fish spent sharing shelters. Analysis of covariance (ANCOVA) was used to determine whether absolute size (averaged for the two fish within a replicate), or the size difference between the two fish in a replicate, had any effect on the amount of time that fish spent sharing shelters.

The analyses described above were used to investigate overall trends in shelter use; therefore, when calculating the replicate means in the sympatric treatment, the two species were not treated separately. However, when calculating replicate means for all subsequent analyses, salmon and trout in sympatry were treated separately in order that the behaviour of each species under allopatric and sympatric conditions could be compared. Fish were therefore divided into the following categories: salmon in allopatry, trout in allopatry, salmon in sympatry (with trout), and trout in sympatry (with salmon). Two-way ANOVA was used to determine which species (trout or salmon) spent most time in shelter under allopatric conditions and to ascertain whether the larger fish of a pair was able to monopolize shelter. The percentage of observations in shelter over the whole trial was the dependent variable and size (larger or smaller of a pair) and species (salmon or trout) were the fixed factors. Paired-sample t tests were used to test for similar relationships in the sympatric trials.

Data on aggression were analyzed by calculating the rate of aggression per minute for each individual and then calculating replicate means, while maintaining the integrity of species data in the sympatric trials. The rate of aggression both in and out of the shelter was also calculated, controlling for the time that fish spent in different habitats by using only observation periods in which both fish started in the same habitat (either in or out of shelter). Separate two-way ANO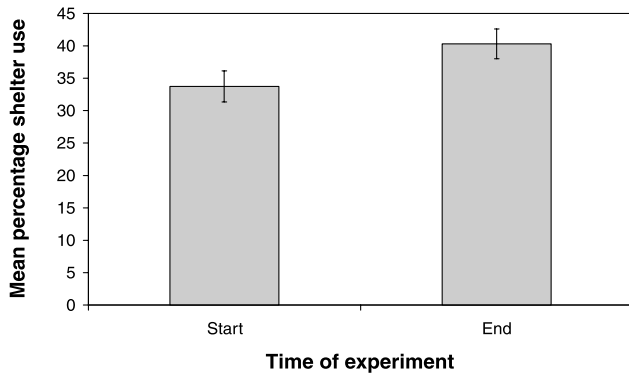VAs were used to determine whether there was any difference between allopatry and sympatry in the percentage of aggressive interactions that forced a habitat switch in salmon and trout. The percentage of aggressive interactions that forced a habitat switch was the dependent factor with category of fish (allopatry or sympatry) and the direction of enforced change (into or out of shelter) as the fixed factors. To determine whether there was a prior residence effect on shelter use, the number of occasions when a fish entered an already occupied shelter was counted along with the percentage of such times when the intruder left before the resident, and vice versa. The relationship between the percentage of times that the intruder left before the resident and the relative length of the intruder (its body length as a percentage of that of the resident) was investigated using linear regression. Finally, as a result of the temperature fluctuations that occurred over the course of the experiment, regressions were carried out to determine whether temperature had an effect on the rate of aggression or the percentage of time that fish spent sharing shelters.

Experiment II

A comparison of the overall percentage of time that fish spent sharing in allopatry and sympatry was undertaken in a manner identical with that of Experiment I, by calculating overall replicate means. The percentage of time spent sharing with the same or different species during the sympatric trials was calculated by taking a mean for the two salmon in a replicate and a mean for the two trout, thus preserving the integrity of the species data. When determining whether fish preferred to share with the same or different species in sympatry, it was necessary to control for the number of fish of each species type. Because there were four fish in each replicate trial, each fish had a one in three chance of sharing with a conspecific shelter-mate and a two in three chance of sheltering with a heterospecific shelter-mate. Therefore, the percentage of time spent sharing with conspecifics was multiplied by one-third, whereas the percentage of time spent sharing with the heterospecifics was multiplied by two-thirds. These values were then compared using a Mann–Whitney U test. A Wilcoxon's signed-rank test was used to determine whether salmon shared with other salmon more frequently than trout shared with other trout.

For the purpose of comparing the relative use of different habitats for foraging and for shelter, zones were divided into those in deep water (zones 11–15), shallow water (zones 1–5), and water of intermediate depth (zones 6–10). The six shelters were categorized in a similar manner with shelters in deep (5 and 6), intermediate (3 and 4), and shallow (1 and 2) water. Analysis of covariance was then used to examine the relationship between the percentage of time in deep shelters (dependent factor) and the percentage of foraging (i.e., nonsheltering) time in deep zones (covariate), with category of fish (salmon in allopatry; salmon in sympatry; trout in sympatry) as the fixed factor. To determine the relative importance of using shelters located in deep water and the use of deep water for foraging, we used a Wilcoxon's signed-rank test to compare the percentage of observations of sheltering in which an individual was in deep shelters with the percentage of foraging observations in which an individual was recorded in deep zones.

Fig. 1. Mean percentage of observations (± standard error) spent in shelters for individuals from all treatments at the start and end of daily dawn observation periods in Experiment I. Percentages are arcsine-transformed, thus a value of 45 corresponds to equal amounts of time spent in and out of shelter.

Fig. 2. Shelter use in Experiment I in relation to relative body size. Mean percentage of time (± standard error) spent in shelters for the larger and smaller fish in a pair for (*a*) allopatric salmon (*Salmo salar,* open bars) and trout (*Salmo trutta,* shaded bars) and (*b*) sympatric salmon (open bars) and trout (shaded bars). Percentages are arcsine-transformed.

For both experiments, all percentage data were normalized by arcsine transformation before use in parametric tests. On the occasions when transformation did not normalize the data, nonparametric tests were used. All quoted probabilities are for two-tailed tests of significance.

Results

Experiment I

There was a significant increase in the use of shelters from the start to the end of the simulated dawn period when considering all replicates of the three treatments (paired-sample t test: $t_{23} = 2.56$, $P = 0.018$; Fig. 1), indicating that the increase in light intensity at dawn prompted fish to seek shelter. There were no significant differences between species or treatments in the percentage of time over the dawn observation period that fish spent sharing shelters (one-way ANOVA: $F_{2,23} = 1.06$, $P = 0.364$; salmon in allopatry, 21.7 ± 5.27% (mean ± SE); trout in allopatry, 18.9 ± 6.39%; sympatry, 10.4 ± 5.30%). There was a significant trend for larger salmon in allopatry and trout in allopatry to share more often than smaller salmon and trout. However, when the two species occurred together in sympatry, larger fish shared less often than smaller fish (ANCOVA, comparison of regression slopes: $F_{2,18} = 4.86$, $P = 0.020$). There was, however, a lot of noise in the regression equations with the relationship for trout in allopatry in particular being driven by one outlier. There was no significant relationship between the percentage of time that the shelter was shared and the weight difference between the two fish in a replicate (ANCOVA: comparison of regression slopes, $F_{2,18} = 2.97$, $P = 0.077$; effect of weight difference, $F_{1,20} = 0.14$, $P = 0.715$; comparison of regression elevations (effect of treatment), $F_{2,20} = 1.01$, $P = 0.384$).

There was no significant difference between categories of fish in the rate at which fish were observed to enter the shelter (one-way ANOVA: $F_{3,31} = 0.37$, $P = 0.773$). There was no effect of an individual's body size (two-way ANOVA: effect of size, $F_{1,29} = 0.20$, $P = 0.657$) or species (effect of species, $F_{1,29} = 0.11$, $P = 0.747$) on the percentage of observations that fish in allopatry were found in shelter (Fig. 2*a*). However, in sympatry, there was a significant effect of rela-
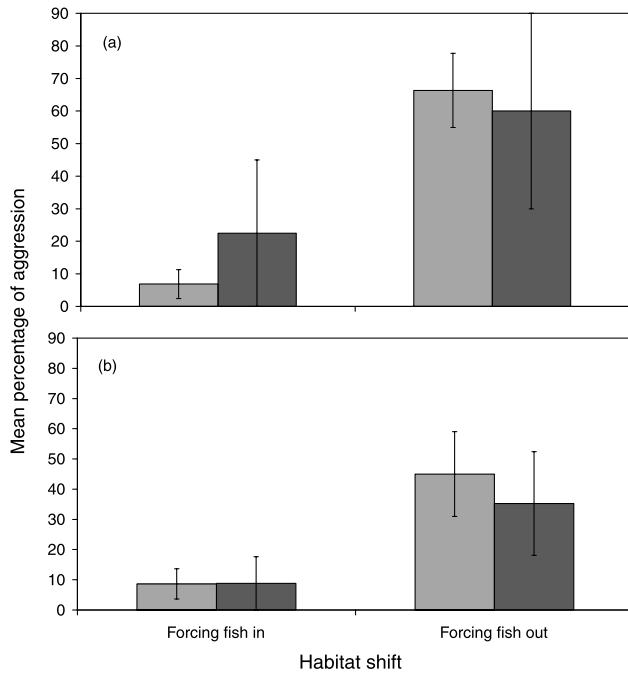
tive body size (paired-sample t test: $t_7 = 4.47$, $P = 0.003$), with the larger fish in a pair spending more time in the shelter over the dawn period than the smaller fish, although there was no difference between the two species (paired-sample t test: $t_7 = 0.68$, $P = 0.518$; Fig. 2*b*).

There was no significant difference in the rate of aggression by salmon and trout, either in allopatry or sympatry (one-way ANOVA: $F_{3,31} = 1.84$, $P = 0.163$). There was also no significant difference in the amount of aggression that was initiated in, vs. out of, shelter (nonparametric two-way ANOVA, Scheirer–Ray–Hare test (Dytham 1999): effect of being in or out of shelter, $\chi^2 = 0.93$, df = 1, $P = 0.761$; effect of category of fish, $\chi^2 = 1.58$, df = 3, $P = 0.663$; interaction between category and position, $\chi^2 = 0.41$, df = 1, $P = 0.998$). For both salmon in allopatry and salmon in sympatry, a higher percentage of aggressive interactions forced fish out of shelters than forced fish into shelter (two-way ANOVA: effect of category of fish, $F_{1,17} = 0.12$, $P = 0.731$; effect of context of aggression, $F_{1,17} = 12.53$, $P = 0.003$; Fig. 3*a*). A similar result was found for trout in both allopatry and sympatry (two-way ANOVA: effect of category of fish, $F_{1,20} = 0.18$, $P = 0.679$; effect of type of aggression, $F_{1,20} = 7.43$, $P = 0.013$; Fig. 3*b*).

The first fish to enter the shelter during an observation period was recorded on 80 occasions, and in 55 of these cases, this first fish was the larger of the pair, a significantly higher proportion than would be expected by chance ($\chi^2 = 10.51$, df = 1, $P < 0.01$). There was no significant difference between treatments in the percentage of times that the larger

Fig. 3. Consequences of aggression in Experiment I. Mean percentage (± standard error) of the aggressive interactions occurring when both fish were outside of the shelter that led to one fish being forced into shelter and percentage of aggressive interactions that occurred when both fish were inside the shelter that forced one fish out for (*a*) allopatric (shaded bars) and sympatric salmon (*Salmo salar,* solid bars) and (*b*) allopatric (shaded bars) and sympatric trout (*Salmo trutta,* solid bars). Percentages are arcsine-transformed, thus a value of 90% represents a situation where aggression always forced the other fish to shift habitats.

Fig. 4. Percentage of times in Experiment I that the intruding fish, on entering an already occupied shelter, then left before the prior resident. Percentages are plotted with respect to the relative length (expressed as percentage size difference from the resident) for fish in allopatry (solid diamonds, solid regression line, see text for analysis) and fish in sympatry (shaded squares, broken line). Percentages are arcsine-transformed, thus intruders with a value of 90% always left the shelter before the resident.
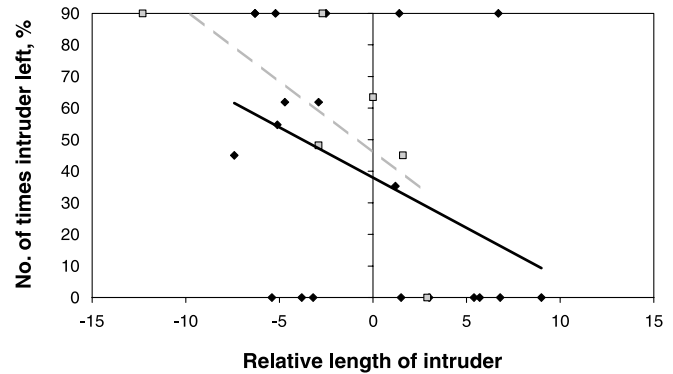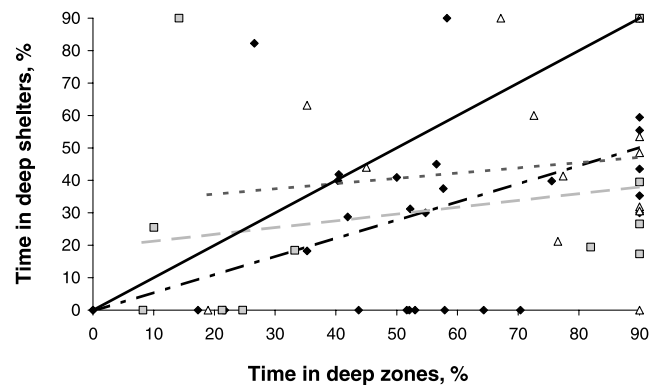

Fig. 5. Percentage of observations of sheltering in Experiment II in which the fish was in deep shelters against percentage of observations of the same fish out of shelter in which it was in deep zones. Data are plotted separately for salmon (*Salmo salar*) in allopatry (solid diamonds; dashed–dotted line), salmon in sympatry (shaded squares; dashed line), and trout (*Salmo trutta*) in sympatry (open triangles; dotted line). Solid black line represents equal percentage of observations in deep shelters and deep zones; percentages are arcsine-transformed.

fish entered first (one-way ANOVA: $F_{2,21} = 2.11$, $P = 0.146$), although there was a trend for the larger fish in sympatry to enter first on more occasions (75.7 ± 7.5%, mean ± SE) than the larger fish in allopatry (salmon in allopatry, 43.8 ± 14.8%; trout in allopatry, 53.7 ± 10.2%). On entering an already occupied shelter, the intruder left first significantly more times than did the resident (percentage of occasions that intruder left first: salmon in allopatry, 76.6%; trout in allopatry, 75.0%; sympatry, 77.8%; $\chi^2 = 21.78$, df = 1, $P < 0.001$). Size was also a factor in predicting which fish left first, with larger intruders less likely to leave before the resident than smaller intruders (regression: $r^2 = 0.23$, $F_{1,24} = 7.34$, $P = 0.012$; Fig. 4).

Temperature had no significant effect on either the rate of aggression (regression: $r^2 = 0.019$, $F_{1,94} = 1.79$, $P = 0.185$) or the percentage of fish sharing shelters (regression: $r^2 = 0.002$, $F_{1,94} = 0.16$, $P = 0.694$), possibly because of the narrow temperature range during the experimental period.

Experiment II

There was no significant difference between the allopatric and sympatric treatments in the percentage of time that fish spent sharing (Mann–Whitney U test: $U = 21.0$, $z = -1.16$, $P = 0.244$). In sympatry, neither salmon nor trout showed a preference for sharing with conspecific over heterospecific shelter-mates (Mann–Whitney U test: $U = 29.0$, $z = -0.38$,

$P = 0.702$). There was also no significant difference in the sympatric treatment between the amount of time salmon spent sharing with salmon and the amount of time trout spent sharing with trout (Wilcoxon's signed-rank test: $z = -0.447$, $P = 0.655$).

There was a significant positive relationship between the percentage of observations where an individual fish was recorded in deep zones when out of refuges (presumed foraging) and the percentage of observations where fish were occupying shelters in deep water, for all categories of fish (ANCOVA: comparison of regression slopes, $F_{2,49} = 0.88$, $P = 0.423$; effect of zone use, $F_{1,51} = 7.46$, $P = 0.009$; comparison of regression elevations, $F_{2,51} = 0.30$, $P = 0.743$; Fig. 5). However, the preference for deep zones when out of shelters was stronger than the preference for deep shelters. Thus the percentage of foraging observations in which an in-

dividual was recorded in deep zones was generally greater than the percentage of observations of sheltering in which it was recorded in deep-water shelters (Wilcoxon's signed-rank test: $z = -4.461$, $P < 0.001$).

Discussion

Our experiments show that Atlantic salmon and brown trout compete for daytime shelters during winter and that intra- and inter-specific competition can be equal in intensity. Experiment I shows that there was a prior residence effect involved in the resolution of contests over shelters, and experiment II suggests that fish were willing to shift habitats to find adequate shelter. These findings and the implications of this competition are discussed below with reference to other relevant work.

Fish of both species increased their use of shelters during dawn as light intensity increased in experiment I, as predicted based on previous work in which salmonids have been found to be active at night but then seek shelter during daylight in winter (e.g., Fraser et al. 1993; Heggenes et al. 1993). The frequency with which fish shared shelters was low in both of our experiments, supporting previous studies on salmonid sheltering behaviour in which the use of refuges was almost exclusively by single fish both in winter (Glova 1986; Cunjak 1988; Gregory and Griffith 1996a) and in summer (Rimmer et al. 1984; Gries and Juanes 1998). Armstrong and Griffiths (2001), using wild fish in a semi-natural stream channel, found that shelter use was density dependent, with the mean number of fish per refuge being ≤1.5 even at densities that would result in five fish per shelter if all fish were sheltering simultaneously. Most previous work therefore shows that salmonids do not share shelters with conspecifics, suggesting that intra-specific competition for shelters would arise if refuges were limited in number.

There was no difference in either of our experiments in the frequency with which fish shared shelter with members of the same and different species, suggesting that shelters were of equal importance to both species and that intra- and inter-specific competition for shelters was equivalent in intensity. This is supported by the fact that salmon and trout initiated similar levels of aggression in experiment I, both in allopatry and sympatry. This result is surprising as trout are normally considered to be more aggressive than salmon of a similar size (Kalleberg 1958; Kennedy and Strange 1986) and may reflect the importance of shelter to both species. The rate of aggression witnessed in this study (overall mean of 0.030 interactions per fish per minute in experiment I) was similar to the rate observed between rainbow trout competing for shelters in a laboratory stream (Gregory and Griffith 1996b). Although these rates of aggression are lower than those reported for salmonid populations in summer (e.g., Hartman 1965) and the onset of winter is associated with a reduction in aggressive behaviour associated with feeding territories (Fraser et al. 1993; Heggenes et al. 1993), individuals still compete for shelters. We have recently shown that intra- and inter-specific competition for deep, slow-flowing water also occurs in winter (Harwood et al. 2001), indicating that competition for limited resources occurs throughout the year, not simply during the summer when individuals compete for food (e.g., Fausch 1984).

Aggression inside shelters during experiment I was commonly followed by one fish then moving outside, whereas aggression out of shelters did not usually lead to either fish entering a shelter. This suggests that aggressive attacks within a shelter served to drive a competitor out. Gregory and Griffith (1996b) also provide indirect evidence that the majority of aggression that they observed was related to competition for shelters, because significantly more aggressive acts occurred during the initial concealment period (first 90 min of daylight) than during the rest of the day.

Competition for shelters among underyearling rainbow trout was related to the size of individuals, with one of the larger fish within a group defending a shelter and initiating almost 80% of the aggression (Gregory and Griffith 1996b). In experiment I, individual Atlantic salmon and brown trout did not monopolize shelters or perform aggressive acts in such a manner under allopatric conditions. However, when in sympatry, the largest individual tended to gain a disproportionate share of the shelter, irrespective of its species identity. These contrasting results may be explained by the prior residence effect which dictates that a holder of a territory or shelter has an advantage over intruders and is more likely to win contests for that resource (e.g., Blank and Figler 1996; Tobias 1997). Evidence for a prior residence effect on shelter use was witnessed in all three treatments, with the intruder to an occupied shelter leaving first significantly more often than the resident did. This prior residence effect was related to body size, with relatively larger intruders less likely to leave before the resident than were smaller intruders. Although there was no significant difference in the mean percentage of times that the larger fish of a pair entered first in the different treatments, there was a trend for the larger fish to enter first more often in sympatry than in allopatry. The tendency for the larger fish in sympatry to enter the shelter first (and so obtain an advantage over intruders) may explain why the largest fish in sympatry was able to monopolize shelter use, regardless of species identity. In contrast, in both allopatric treatments, there was a lot of variation in the percentage of times that the large fish entered first, and this may explain why large fish were unable to monopolize shelter use in this situation. Blank and Figler (1996) have previously shown prior residence effects to be important in resolving inter-specific competition for shelters between two sympatric species of crayfish (*Procambarus clarkii* Girard and *Procambarus zonangulus* Hobbs and Hobbs). Further work is needed to determine the importance of prior residency in determining competitive advantage for shelter use in Atlantic salmon and brown trout, as the residency effects witnessed in experiment I were established even though fish were introduced to the arena simultaneously.

Evidence from our second experiment, where fish had a choice of habitats, shows that there was a positive relationship between the relative proportion of foraging time that individual fish spent in their favoured deep, slow-flowing water (see Harwood et al. 2001) and the proportion of sheltering time spent in shelters within that habitat. However, the fact that the relative proportion of foraging time spent in deep water was greater than the equivalent proportion of sheltering time spent in deep-water shelters suggests that fish are willing to move to find shelters or foraging habitat. A certain level of activity and continued movement by

1522

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

salmonids in winter may be adaptive to avoid periodic flooding, freezing, and thaws (Cunjak 1996; Whalen et al. 1999). For instance, Whalen et al. (1999) showed that a period of ice formation led to an extensive alteration in the habitat used by Atlantic salmon parr.

Implications

Intra- and inter-specific competition for shelters (Gregory and Griffith 1996*b*; this study) can lead to density-dependent use of refuge habitat (Armstrong and Griffiths 2001) that could have important implications in terms of the carrying capacity for wild populations of salmonids in streams. In some instances, the availability of instream refuges has been found to be high relative to the number of parr, with disturbed individuals being able to find new shelters easily (Cunjak 1988). Such abundance of shelters relative to the requirements of the population of fish may result in no density-dependent mortality over the winter period (Egglishaw and Shackley 1977; Cunjak et al. 1998). However, in other studies, suitable cobble–boulder substrate has been shown to be both limiting (e.g., in areas where the stream flows over the bedrock) and crucial to salmonid survival (Hillman et al. 1987; Griffith and Smith 1993), with individuals emigrating from areas where adequate cover was not available (Bjornn 1971). Under these circumstances, the number of individuals surviving winter may indeed depend on the availability of refuges.

For stream managers wishing to increase productivity of fish populations by habitat manipulation, it is important to understand competition for habitat among species (e.g., Harwood et al. 2001). Increased production of one species during summer months resulting from the addition of shelter may be lost if that species is excluded by another one during winter. This study suggests that when in sympatry, neither brown trout nor salmon of similar size consistently wins under-gravel shelters during winter and that in some cases an increase in shelters may result in denser populations of both these species. Work is now needed to test the effects of larger ranges of differences in size between the species and to understand how prior residence effects influence competition for shelter among sympatric populations of trout and salmon during natural seasonal changes in their habitat requirements.

Acknowledgements

References

Armstrong, J.D., and Griffiths, S.W. 2001. Density-dependent ref- uge use among over-wintering wild Atlantic salmon juveniles. J. Fish Biol. **58**: 1524–1530.

Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams related to temperature, food, stream flow, cover and population density. Trans. Am. Fish. Soc. **100**: 423–438.

Blank, G.S., and Figler, M.H. 1996. inter-specific shelter competi- tion between the sympatric crayfish species *Procambarus clarkii* (Girard) and *Procambarus zonangulus* (Hobbs and Hobbs). J. Crustacean Biol. **16**: 300–309.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. **45**: 2156–2160.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Can. J. Fish. Aquat. Sci. **53**: 267–282.

Cunjak, R.A., Prowse, T.D., and Parrish, D.L. 1998. Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent"? Can. J. Fish. Aquat. Sci. **55**: 161–180.

Dill, L.M., and Fraser, A.H.G. 1997. The worm re-turns: hiding be- havior of a tube-dwelling marine polychaete, *Serpula vermicularis*. Behav. Ecol. **8**: 186–193.

Dytham, C. 1999. Choosing and using statistics: a biologist's guide. Blackwell Science, Oxford.

Egglishaw, H.J., and Shackley, P.E. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966–75. J. Fish Biol. **11**: 647–672.

Fausch, K.D. 1984. Profitable stream positions for salmonids: re- lating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

Fraser, N.H.C., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature- dependent switch between diurnal and nocturnal foraging in salmon. Proc. R. Soc. Lond. Ser. B, Biol. Sci. **252**: 135–139.

Glova, G.J. 1986. Interaction for food and space between experimen- tal populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*) in a laboratory stream. Hydrobiologia, **131**: 155–168.

Gregory, J.S., and Griffith, J.S. 1996*a*. Winter concealment by subyearling rainbow trout: space size selection and reduced con- cealment under surface ice and in turbid water conditions. Can. J. Zool. **74**: 451–455.

Gregory, J.S., and Griffith, J.S. 1996*b*. Aggressive behaviour of underyearling rainbow trout in simulated winter concealment habitat. J. Fish Biol. **49**: 237–245.

Gries, G., and Juanes, F. 1998. Microhabitat use by juvenile Atlan- tic salmon (*Salmo salar*) sheltering during the day in summer. Can. J. Zool. **76**: 1441–1449.

Gries, G., Whalen, K.G., Juanes, F., and Parrish, D.L. 1997. Noctur- nal activity of juvenile Atlantic salmon (*Salmo salar*) in late sum- mer: evidence of diel activity partitioning. Can. J. Fish. Aquat. Sci. **54**: 1408–1413.

Griffith, J.S., and Smith, R.W. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. N. Am. J. Fish. Manage. **13**: 823–830.

Hartman, G.F. 1965. The role of behaviour in the ecology and inter- action of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **22**: 1035–1081.

Harwood, A.J., Metcalfe, N.B., Armstrong, J.D., and Griffiths, S.W. 2001. Spatial and temporal effects of inter-specific competition between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in winter. Can. J. Fish. Aquat. Sci. **58**: 1133–1140.

Heggenes, J., Krog, O.M.W., Lindås, O.R., Dokk, J.G., and Bremnes, T. 1993. Homeostatic behavioural responses in a changing environ-

ment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Anim. Ecol. **62**: 295–308.

Hillman, T.W., Griffith, J.S., and Platts, W.S. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Trans. Am. Fish. Soc. **116**: 185–195.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Inst. Freshwater Res. Drottningholm Rep. **39**: 55–98.

Kennedy, G.J.A., and Strange, C.D. 1986. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. J. Fish Biol. **29**: 199–214.

Krause, J., Loader, S.P., McDermott, J., and Ruxton, G.D. 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. Proc. R. Soc. Lond. Ser. B, Biol. Sci. **265**: 2373–2379.

Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. **40**: 775–788.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **46**: 1551–1557.

Nickelson, T.E., Rodgers, J.D., Johnson, S.L., and Solazzi, M.F. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Can. J. Fish. Aquat. Sci. **49**: 783–789.

Rimmer, D.M., Paim, U., and Saunders, R.L. 1984. Changes in the selection of micro-habitat by juvenile Atlantic salmon (*Salmo salar*) at the summer–autumn transition in a small river. Can. J. Fish. Aquat. Sci. **41**: 469–475.

Rimmer, D.M., Saunders, R.L., and Paim, U. 1985. Effects of temperature and season on the position holding performance of juvenile Atlantic salmon (*Salmo salar*). Can. J. Zool. **63**: 92–96.

Smith, R.W., and Griffith, J.S. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. Trans. Am. Fish. Soc. **123**: 747–756.

Solazzi, M.F., Nickelson, T.E., Johnson, S.L., and Rodgers, J.D. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can. J. Fish. Aquat. Sci. **57**: 906–914.

Tobias, J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. Anim. Behav. **54**: 9–21.

Valdimarsson, S.K., and Metcalfe, N.B. 1998. Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? J. Fish Biol. **52**: 42–49.

Valdimarsson, S.K., Metcalfe, N.B., Thorpe, J.E., and Huntingford, F.A. 1997. Seasonal changes in sheltering: effect of light and temperature on diel activity in juvenile salmon. Anim. Behav. **54**: 1405–1412.

Whalen, K.G., and Parrish, D.L. 1999. Nocturnal habitat use of Atlantic salmon parr in winter. Can. J. Fish. Aquat. Sci. **56**: 1543–1550.

Whalen, K.G., Parrish, D.L., and Mather, M.E. 1999. Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic salmon parr. Can. J. Fish. Aquat. Sci. **56**: 87–96.