

Spatial and temporal effects of interspecific competition between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in winter

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

Abstract: Previous work has shown that juvenile stream-dwelling salmonids become predominantly nocturnal during winter by emerging from daytime refuges to feed, with several species having been shown to prefer slow-flowing water while active at night. We used seminatural stream channels, landscaped to provide a choice of water depths, and hence velocities, to test whether Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, show similar habitat preferences during winter. We also tested whether there was any spatial or temporal displacement of Atlantic salmon when in sympatry with brown trout. Nighttime observations revealed that Atlantic salmon did have a preference for slow-flowing water. However, when in direct competition with trout, salmon either remained predominantly nocturnal but occupied shallower water, or became significantly less nocturnal, spending more time active during the day than when in allopatry. These results, which were especially marked in relatively larger fish, indicate that competition between the two species for food and resources is not restricted to the summer months and may affect both the short- and long-term growth and survival of overwintering wild Atlantic salmon.

Résumé : Des travaux antérieurs ont démontré que de jeunes salmonidés habitant les eaux courantes en hiver deviennent surtout nocturnes et qu'ils quittent leurs refuges de jour pour s'alimenter la nuit; plusieurs espèces montrent alors une préférence pour les eaux plus calmes durant cette activité nocturne. Des ruisseaux artificiels, aménagés de façon à offrir un choix de profondeurs et, par conséquent, de vitesses de courant, ont servi à vérifier si des Saumons de l'Atlantique, *Salmo salar*, et des Truites brunes, *Salmo trutta*, ont des préférences d'habitat similaires en hiver. Il a aussi été possible de tester s'il s'opère un déplacement temporel ou spatial du Saumon de l'Atlantique lorsqu'il cohabite avec la Truite brune. Des observations de nuit ont révélé que le Saumon de l'Atlantique a une préférence pour les zones à courant lent. Cependant, lorsque le saumon est en compétition directe avec la truite, ou bien il demeure surtout nocturne, mais en occupant les eaux moins profondes, ou alors il passe plus de temps en activité le jour qu'il ne le ferait en l'absence des truites. Ces résultats, qui sont particulièrement nets chez les poissons relativement plus grands, indiquent que la compétition entre les deux espèces pour la nourriture et les ressources ne se limite pas aux mois d'été, mais qu'elle peut affecter la croissance à court et à long termes et la survie des Saumons de l'Atlantique sauvages pendant l'hiver.

[Traduit par la Rédaction]

Introduction

Diel activity patterns of organisms result from the need to concentrate activity at a time that optimises the balance between competition, predation risk, and food availability (Helfman 1993). For instance, individual rainbow trout, *Oncorhynchus mykiss*, and Arctic charr, *Salvelinus alpinus*, may adopt contrasting diel activity patterns, possibly as a result of subordinates attempting to attain adequate growth while avoiding high levels of aggression from more dominant fish (Alanärä and Brännäs 1997). A grazing mayfly,

Baetis sp., was aperiodic or weakly nocturnal in a fishless stream but became more nocturnal when transferred to a trout-inhabited stream, illustrating the influence of predation risk on diel feeding (Cowan and Peckarsky 1994).

Both experimental and field studies have shown that juvenile Atlantic salmon, *Salmo salar*, undergo a temperature-dependent shift from predominantly diurnal activity above 10°C to predominantly nocturnal activity at lower temperatures (Fraser et al. 1993, 1995; Bremset 2000). Such a switch may account for seasonal changes in diel activity of not only Atlantic salmon but also brown trout, *Salmo trutta*

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(Heggenes et al. 1993), rainbow trout (Riehle and Griffith 1993), and Arctic charr (Linnér et al. 1990). This change in behaviour may be a response to their increased vulnerability in winter to diurnal endothermic predators (Metcalf et al. 1999) that are not affected by decreased water temperatures, which cause the swimming ability and acceleration of fish to be reduced (Rimmer et al. 1985). Alternatively, the shift to nocturnal activity may be a stratagem for avoiding being trapped by anchor ice (Heggenes et al. 1993; Whalen et al. 1999) or may be a response to the pattern of drifting or benthic invertebrates (e.g., Amundsen et al. 2000).

Since salmonids are sit-and-wait predators that rely on vision, the cost of becoming more nocturnal is a decrease in the efficiency of capturing individual food items. Even on the clearest of nights, feeding efficiency is only approximately 35% of that during the day (Fraser and Metcalfe 1997). However, nocturnal foraging may decrease predation risk (expressed per unit of food intake) and therefore may have fitness benefits (Metcalf et al. 1999). Brown trout prefer slower water currents at night than during the day (Heggenes et al. 1993), presumably to see their prey more easily. Moreover, juvenile Atlantic salmon prefer slower water currents on dark nights than on clear nights, to facilitate prey capture (Metcalf et al. 1997). As expected, the preference of salmon to use deep slow water actively on winter nights was observed in the wild by Whalen and Parrish (1999).

A greater use of deep water in winter is likely to cause increased competition for foraging opportunities between sympatric salmon and brown trout. In summer months, juvenile trout are more aggressive than salmon of similar size (e.g., Kalleberg 1958) and therefore restrict them to less-preferred (i.e., shallower) areas of a stream (Kennedy and Strange 1986). Such interspecific competition is thought to have long-lasting effects on growth, survival, and fitness (Fausch 1998). Nonetheless, winter has been considered to be the most important period for survival of salmon parr (Cunjak et al. 1998), and interspecific interactions may be important at this time of year. However, as yet there is no information on the relative competitive abilities of trout and salmon during winter.

We conducted experiments using artificial stream channels to test three hypotheses: (1) juvenile Atlantic salmon prefer deep water in winter when living in allopatry (cf. Whalen and Parrish 1999), (2) juvenile Atlantic salmon are displaced from their preferred habitat when living in sympatry with brown trout, and (3) interspecific competition for space in winter results in shifts in diel activity patterns and (or) temporal changes in the habitat use of juvenile Atlantic salmon.

Methods

The experiment was conducted in an outdoor artificial stream (previously described in Valdimarsson et al. 1997) at the University Field Station, Rowardennan, Loch Lomondside, Scotland. The stream was 60 cm wide and formed a continuous, approximately oval shaped loop with straight sides. Fish could be observed from within this loop, since the inside walls of the channel were made from glass panels. The straight sides of the channel were each 6 m in length; however, the variable-speed impeller that pumped water around the channel occupied 2.5 m of one side. The remaining straight parts of the channel were partitioned into three 2.5-m

experimental arenas, using mesh, and landscaped with fine gravel (5–25 mm in diameter) to deter fish from hiding in stream bed cavities. The gravel was landscaped to produce a smooth gradient within each arena, with shallow water (10 cm) at the upstream end and relatively deep water (45 cm) at the downstream end. The surface velocity of the water varied continuously from $0.16 \text{ m}\cdot\text{s}^{-1}$ at the upstream end to $0.03 \text{ m}\cdot\text{s}^{-1}$ at the downstream end. A 1 m long section between each experimental arena was landscaped with the contrasting gradient, to decrease turbulence and smooth the flow down the channel. The outer sides of the channel were marked every 15 cm along their length, to define 15 zones per arena (zone 1 being at the upstream end) and allow referencing of the recorded positions of the fish. Fish shelters were made from six 1-L opaque bottles that were cut in half lengthwise and embedded in the gravel at regular intervals in each of the experimental arenas, creating cavities in the gravel measuring $17 \times 8.5 \times 4.25 \text{ cm}$. These bottles were positioned with the open side against the glass wall, to allow any fish within them to be identified, a technique successfully used by Valdimarsson et al. (1997).

Water was pumped constantly from Loch Lomond 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. However, some overhead cover was provided at all water depths by placing wooden planks approximately 15 cm above the water surface, across half the width of the channel. The position of these planks was randomised with respect to the inside and outside walls of the stream channel. This allowed comparison of the amount of time spent under overhead cover and out of cover. Food was provided via a belt feeder, which dropped pelleted food at a trickle rate at the upstream end of each arena. Fish were provided with 0.5% of their total body weight in food per day, an amount chosen so growth would be minimal but fish would not lose condition during the experimental trials. This pelleted food was supplemented by the low level of zooplankton found in the water pumped from Loch Lomond.

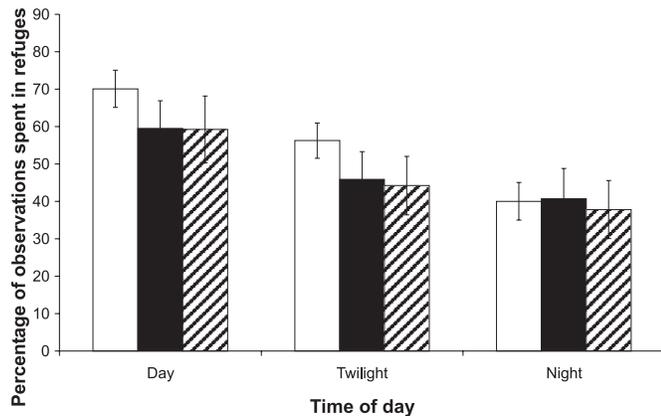
Two treatments were used to test the effects of trout on the behaviour of salmon: allopatric (four salmon) and sympatric (two salmon with two trout). Data collected from the salmon in allopatry would reveal whether salmon prefer areas of deep slow-moving water or areas of shallow fast-flowing water, while the sympatric treatment would reveal whether habitat use changes under conditions of interspecific competition. Fish in both treatments were size-matched to reduce any confounding effects of large size differences. Both treatments were run simultaneously in different arenas of the stream channel, to prevent any confounding effects of temperature or time of year influencing the results.

The fish used were wild-caught salmon (fork length = $109.4 \pm 1.83 \text{ mm}$ (mean \pm standard error (SE)); weight = $13.42 \pm 0.65 \text{ g}$) and trout (fork length = $100.7 \pm 2.77 \text{ mm}$; weight = $9.87 \pm 0.90 \text{ g}$) from the River Blane, a tributary of the River Endrick that flows into Loch Lomond. Fish were individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Fish were then allowed to reside in the experimental arenas for a period of 72 h before observations began.

The observations of each group of fish were made on four consecutive dates. Each night of observation lasted 7 h and covered the day–night transition at either dusk or dawn. During this observation period, the position of each fish was recorded every 30 min by scanning briefly with a flashlight, a method thought to minimise disturbance of the fish (see Heggenes et al. 1993). Data collected during each scan observation consisted of the position of each fish in the water column (either resting on the bottom or swimming in the water column), the number of the zone in which the fish was located (1–15, which was a relative measure of water depth, and hence velocity), and whether or not the fish was under overhead cover. The use of shelters was also recorded, to determine the

Table 1. Summary of results from a repeated measures ANOVA for the effect of time of day on behavioural responses; in all cases, multivariate significance tests were used, as Mauchly's test of sphericity was significant.

Source of variation	Proportion of time spent in refuges			Proportion of time spent on substrate while not in refuges			Proportion of time spent under overhead cover while not in refuges		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Within subjects									
Time of day	2	16.70	<0.001	2	3.70	0.038	2	0.38	0.688
Error	60			27			27		
Between subjects									
Category of fish	2	0.74	0.481	2	8.01	0.002	2	0.60	0.558
Error	61			28			28		
Time of day × category of fish	4	0.60	0.662	4	1.93	0.119	4	0.30	0.874
Error	122			56			56		

Fig. 1. Graph of the percentage (\pm SEM) of observations spent in refuges at various times during a 24-h period for salmon in allopatry (open bars), salmon in sympatry (filled bars), and trout in sympatry (shaded bars). Percentages are arcsine transformed, thus fish with a value of 90.0% never left the refuges.

frequency with which fish sought refuge; light intensity and water temperature were also noted. Light intensity was measured using a Skye Instruments SKL 300 photometer (range 0.01–2000 lx) and recorded as the mean of two measurements made just above the overhead cover provided in the middle of the straight section on either side of the channel. Light intensity readings were used to split observations into three categories, day (≥ 100 lx), twilight (between 0.02 and 100 lx), and night (≤ 0.02 lx). Water temperature was measured using a digital thermometer (Oregon Scientific EM913, resolution 1°C) placed permanently in the stream. After the data for each group were collected, the fish were removed and different fish 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

For the purpose of comparing treatments, the data were split into three categories: salmon in allopatry, salmon in sympatry (with trout), and trout in sympatry (with salmon), with data for the latter two categories coming from the one sympatric treatment. To evaluate the effect of body size on behaviour while standardising for size differences between trials, the relative body length (body length as a proportion of the body length of the largest fish in each group of four fish) was calculated for each fish. All percent data were normalised by arcsine transformation prior to use in paramet-

ric tests, and all quoted probabilities are for two-tailed tests of significance.

Repeated measures analysis of variance (ANOVA) was used to test the null hypotheses that time of day (within-subject effect) and category of fish (between-subject effect) had no effect on response variables (proportion of observations when in refuges or on substrate or under overhead cover while not in refuges).

To compare the timing of activity between treatments, the percentage of activity (i.e., time out of shelters) that occurred by night was determined for each fish. This was calculated using the formula:

$$100 \times E_n / (E_n + E_d)$$

where E_n is the percentage of nighttime and twilight observations during which a fish was out of shelter and E_d is the percentage of daytime observations during which a fish was out of shelter (Fraser et al. 1995). This was termed the nocturnal index and ranged from 0% (the fish was only observed out of shelter during the day) to 100% (the fish was only observed out at night). To compare between treatments, a mean value for each category of fish was calculated for each replicate group.

Results

Time of day effects on the use of cover

As expected, there was a significant difference in the proportion of time that both salmon and trout were observed to spend in refuges during day, twilight, and night (Table 1; Fig. 1). This difference represented a significant decrease in the use of shelters from daytime through twilight to night (linear term of polynomial contrasts: $F_{1,61} = 28.63$, $P < 0.001$). However, there was no significant difference in this time effect between categories of fish (Table 1; Fig. 1), indicating that both salmon and trout became more active at night. There was a significant difference in the proportion of time that both salmon and trout were observed to spend on the substrate while not sheltering during all three time periods (Table 1; Fig. 2). This difference represented a significant increase in the amount of time spent on the substrate from daytime through twilight to night (linear term of polynomial contrasts: $F_{1,28} = 7.20$, $P = 0.012$). There was also a significant difference between the species, with salmon observed on the substrate more often than trout (Table 1; Fig. 2). There was no time of day or species effect on the proportion of time observed under overhead cover (Table 1).

Fig. 2. Graph of the percentage (\pm SEM) of observations spent holding position on the substrate while not in refuges for salmon in allopatry (open bars), salmon in sympatry (filled bars), and trout in sympatry (shaded bars). Percentages are arcsine transformed, thus fish with a value of 90.0% were always found resting on the substrate.

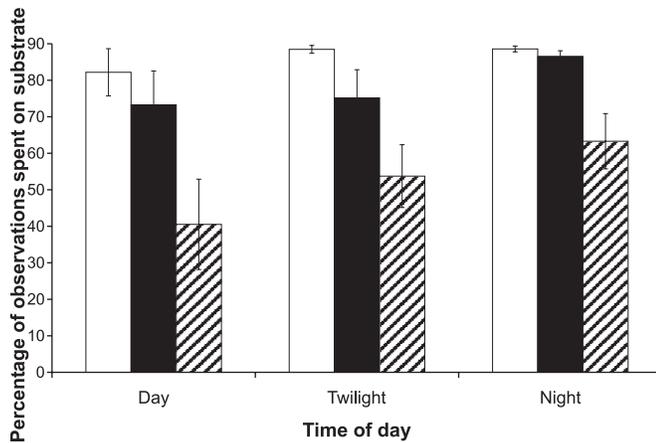


Table 2. Summary of the results from a stepwise multiple regression for the relative influence of light intensity, time of year (Julian date), and temperature on the use of refuges.

Variable	Order in which entered	<i>t</i>	<i>P</i>
Light	1	8.26	<0.001
Temperature	2	9.62	<0.001
Day	3	7.16	<0.001

Note: Overall, $r^2 = 0.333$, $F_{3,345} = 58.91$, $P < 0.001$.

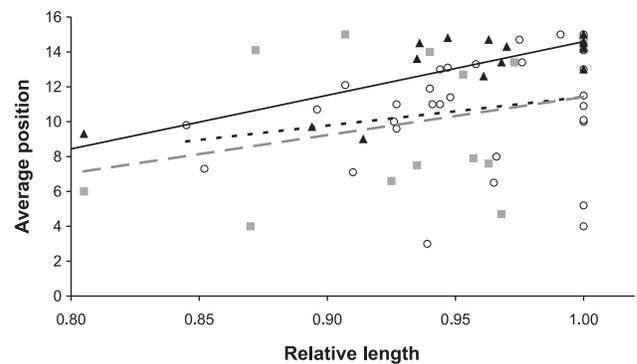
Influence of light intensity, temperature, and time of year on refuge use

To test for the relative influence of light intensity, time of year (Julian date), and temperature on the use of refuges, a stepwise multiple regression was performed on the (arcsine-transformed) percentage of fish hiding at each observation. Owing to the fact that no significant difference was found in the proportion of time spent in shelter between categories of fish (Table 1), this analysis was carried out on the overall percentages of both species combined that were observed in the refuges. It revealed that light intensity was the most important single explanatory variable, and its effect was independent of that of date and temperature (see Table 2).

Effect of body size and treatment on the depth of water used

To compare the influence of absolute and relative body size on the position adopted by fish, a stepwise multiple regression was carried out on the mean zone in which a given fish was observed when out of shelter, irrespective of time of day or species. This illustrated that relative length was more important in predicting the position of fish than absolute length (stepwise multiple regression: absolute length not included in model: model, $r^2 = 0.117$, $F_{1,142} = 19.94$, $P < 0.001$). Therefore, relative length was used as the measure of body size in all subsequent analyses.

Fig. 3. The average position of each fish while out of shelter during the night plotted against relative length for salmon in allopatry (open circles, dotted line), salmon in sympatry (shaded squares, broken line), and trout in sympatry (filled triangles, solid line). Average position is calculated by averaging zone use during the night. Zone 15 is the deepest and thus has the slowest-flowing water, while zone 1 is the shallowest and thus has the fastest-flowing water. Similar trends were witnessed during daylight and twilight observations, however these are not presented for the sake of clarity.

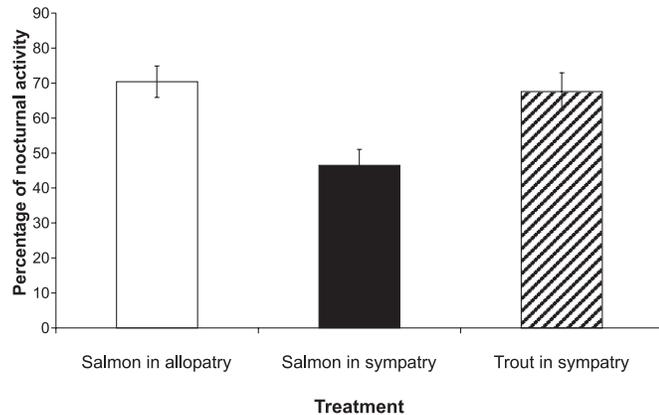


To test both our first hypothesis, that salmon prefer deep water, and our second hypothesis, that they are displaced spatially by trout, we investigated the depth of water used by individual fish. For each fish, an indication of the depth of water used was calculated separately for day, twilight, and night by averaging zone use during each of these periods over the 4 days. The effect of treatment on distribution patterns was then analysed separately for daytime, twilight, and nighttime observations, using analysis of covariance (ANCOVA), with fish category (allopatric salmon, sympatric salmon, or sympatric trout) as the factor and relative body length as the covariate. There was a significant effect of relative body length on average position during the day (ANCOVA: effect of length, $F_{1,30} = 7.98$, $P = 0.008$), during twilight ($F_{1,46} = 6.61$, $P = 0.013$), and during the night ($F_{1,56} = 9.18$, $P = 0.004$), with fish of greater length relative to the other fish in their replicate group being found in deeper water (see Fig. 3). The tendency for salmon to be found mostly in the deeper parts of the stream channels suggests that they, as well as trout, prefer deep water, thus supporting our first hypothesis. During the night there was also a significant effect of category of fish on average position (ANCOVA: comparison of regression slopes, $F_{2,54} = 0.37$, NS; comparison of regression elevations, $F_{2,56} = 4.07$, $P = 0.022$), with trout being found in deeper water than salmon of equivalent size in both allopatry and sympatry (see Fig. 3). There was, however, no significant difference in the depth of water used by salmon in allopatry and salmon in sympatry, thus providing no support for our second hypothesis.

Nocturnal versus diurnal activity

We used the calculated nocturnal index to test our third hypothesis, that interspecific competition results in a shift in diel activity and (or) temporal changes in habitat use by salmon. There was no significant difference in the nocturnal index (arcsine-transformed) between salmon and trout when

Fig. 4. Percentage (\pm SEM) of nocturnal activity (where nocturnal activity is nocturnal activity/overall activity) for each treatment. Percentages are arcsine transformed, therefore 90% nocturnal activity represents fish only active at night, whereas 0% nocturnal activity represents fish active only during the day.



the two species were in sympatry (paired sample t test, $t_7 = 1.50$, NS; see Fig. 4). However, there was a significant difference in the nocturnal index between salmon in allopatry and salmon in sympatry (independent sample t test, $t_{14} = 2.39$, $P = 0.031$), with salmon in allopatry being more nocturnal (see Fig. 4). This supports our hypothesis that salmon undergo a shift in diel activity when they switch from allopatric to sympatric conditions. To determine the influence of body size on nocturnal versus diurnal activity for salmon in the two treatments, ANCOVA was performed on the nocturnal index with treatment (allopatry or sympatry) as the factor and relative size as the covariate. This revealed a significant difference in the diel activity pattern of salmon of different lengths in the two treatments, with the largest salmon in a replicate group being the most nocturnal in allopatry but the least nocturnal in sympatry (ANCOVA: comparison of regression slopes, $F_{1,40} = 11.96$, $P = 0.001$; see Fig. 5).

Nearest-neighbour distances

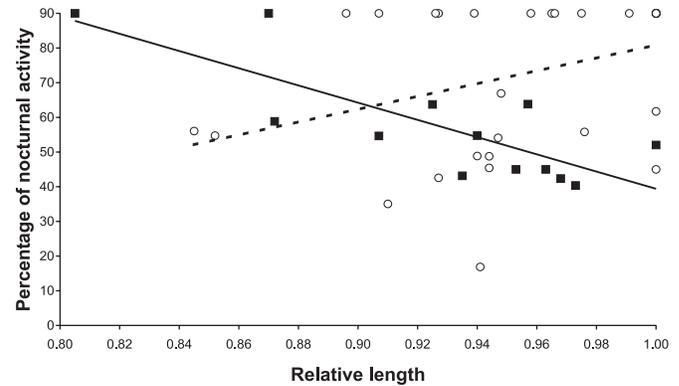
To gain an insight into nearest-neighbour distances, the occasions when fish occurred in the same or adjacent zones were examined. Out of a total of 245 scan samples of the three test arenas at night, fish occurred in the same or adjacent zone on 83 occasions in allopatry and 125 occasions in sympatry. A χ^2 goodness-of-fit test revealed that this represented a significant difference between the treatments ($\chi^2 = 8.48$, $df = 1$, $p < 0.01$), with fish more likely to be in close proximity to each other in sympatry than in allopatry. Interestingly, salmon in allopatry were in close proximity on 83 occasions, whereas in sympatry, salmon only occurred in proximity with other salmon on two occasions, with trout being found in proximity with other trout on 55 occasions. A χ^2 test revealed that this represented a significant difference between the two species ($\chi^2 = 49.28$, $df = 1$, $p < 0.001$).

Discussion

Habitat preferences and activity patterns

Our first hypothesis, that juvenile salmon in winter prefer

Fig. 5. The percentage (\pm SEM) of nocturnal activity plotted against relative length for salmon in allopatry (open circles, dotted line) and salmon in sympatry (filled squares, solid line). Percentages are arcsine-transformed, therefore 90% nocturnal activity represents fish only active at night, whereas 0% nocturnal activity represents fish active only during the day.



deep water, was supported, with salmon preferring the deepest, and thus slowest-flowing water that was available. This preference was supported by our observation of relatively larger fish holding deep-slow positions more frequently than relatively smaller fish, coupled with the fact that, at this stage in the life cycle of both salmon and trout, dominant fish are larger than subordinates (Huntingford et al. 1990). Although this study does not differentiate between selection for water depth and selection for water velocity, previous studies of both Atlantic salmon (Whalen and Parrish 1999) and brown trout (Cunjak and Power 1986; Mäki-Petäys et al. 1997) in the wild have shown a stronger selection for water velocity than for water depth in winter. Therefore, the habitat preferences exhibited by Atlantic salmon could be considered to be a preference for slow-flowing water, occurring in areas of deep water, rather than a selection for deep water. A comparison of the average positions of brown trout in sympatry and Atlantic salmon in allopatry indicates that the trout had a stronger preference for deeper and (or) slow-flowing water, but that their preferred microhabitat overlapped that of the salmon. Rainbow trout (Riehle and Griffith 1993) and coho salmon, *Oncorhynchus kisutch* (Nickelson et al. 1992), also preferred slow-flowing water in winter. Similarly, coho salmon preferred deep pools that offered protection from fast-flowing water and turbulence over deep pools that offered no shelter from high water velocities (Nickelson et al. 1992).

A comparison of the positions adopted by salmon in allopatry and sympatry indicates that salmon were not significantly displaced from this preferred microhabitat by trout, thus providing no support for our second hypothesis. However, there is evidence of competition between the two species, with the data supporting our third hypothesis of a shift in the diel activity of Atlantic salmon caused by the presence of brown trout. The significant shift towards more daytime activity exhibited by salmon in sympatry, as opposed to salmon in allopatry, is evidence of the dominance of brown trout over Atlantic salmon. In allopatry, the largest salmon were the most nocturnal and were found in the deepest water; that they occupied this preferred spatial and temporal

niche suggests that they are the dominant fish. Furthermore, their lack of daytime activity suggests that, under allopatric conditions, dominant salmon obtained enough food during the night to avoid risky daytime feeding. However, the presence of trout may have prevented these largest salmon from effectively feeding in deep water at night, causing them to become more active during the day. This is in accordance with earlier studies in which salmon were shown to become more diurnal when food availability was reduced or nutritional requirements were increased (see Metcalfe et al. 1998, 1999). This result is also analogous to that found by Alanärä and Brännäs (1997), who observed individual rainbow trout and Arctic charr adopting contrasting diel activity patterns, apparently to reduce competition in accessing food. The similarity in the amount of time salmon and trout were observed to spend in refuges suggests that the two species have rather similar time budgets and feeding rates in relation to their nutritional needs.

Aggregations of fish and habitat partitioning

Previous studies of nocturnal activity during winter have witnessed no aggressive interactions between conspecifics of either Atlantic salmon (Whalen and Parrish 1999) or brown trout (Heggenes et al. 1993). Other studies have concluded that aggregations of trout in pools illustrate a cessation of territorial behaviour during the winter (Cunjak and Power 1986). However, the cessation of territorial behaviour in pools has also been witnessed at other times of year (Bremset and Berg 1997) and may not be especially associated with winter. The lack of aggression in winter noted by Heggenes et al. (1993) was interpreted as an indication of a reduction in the need to feed, and hence maintain territorial boundaries. Fraser et al. (1993) also noted that juvenile salmon were less aggressive at night and more tolerant of subordinates. However, this proximity may be due to the fact that an individual will defend a smaller area at night because the range at which prey can be detected decreases (Fraser and Metcalfe 1997) rather than to a total lack of territorial behaviour. Indeed, in a tributary of Lake Superior characterised by low winter flow, salmon were aggressively maintaining positions at temperatures as low as 3°C, with 53% of fish in dominance hierarchies (Healy and Lonzarich 2000). Despite the general consensus that there is a decrease in overt aggression between salmonids in winter, the results of this experiment indicate that competition for habitat and food does still occur.

The results suggest that aggregations and the general proximity of salmonids in winter, as reported by Cunjak and Power (1986) and Whalen and Parrish (1999), may result not only from a reduction in territorial aggression but from the limited availability of preferred habitat. Limited availability of winter habitats may play a pivotal role in the number of salmonids that a stream can support (Nickelson et al. 1992; Cunjak 1996; Whalen and Parrish 1999).

The greater tendency for fish to have been found in close proximity when in sympatry than when in allopatry is likely to be a result of the difference in the use of the water column by salmon and trout. Trout spent the majority of their time in the water column, whereas salmon were more likely to be on the substrate; this partitioning of the habitat may have allowed more fish to occupy the same area when there

was a mixture of the two species. Bremset and Berg (1999) witnessed a similar segregation of salmon and trout, with trout holding position significantly farther from the substrate than salmon. The tendency for trout to spend a higher proportion of their time in the water column may be a result of several factors that are not mutually exclusive. Salmon have larger pectoral fins than trout and are thus better adapted for holding position on the substrate (Arnold et al. 1991). In addition, in artificial-stream environments, where most food is distributed in the water column rather than in the benthos, salmon always appear to move upwards to take food items at night. This is probably because the silhouette of a food item against the sky allows salmon to see and capture food items more easily. Thus salmon will sit on the bottom at night so they can get underneath all potential prey items (Valdimarsson and Metcalfe 1999). The positioning of trout above salmon in the water column when in sympatry will therefore deplete the food supply available to salmon. Thus, the shift to more diurnal activity by salmon may not be caused by overt aggression by trout, but by trout monopolising the available food in the water column. Salmon and trout may both spend less time on the substrate during the day to take advantage of surface drift, which is not visible to them during the night.

Implications

Recent experimental studies have shown that the trade-off between diurnal and nocturnal foraging is complex and may be related to a number of factors, such as food availability, feeding efficiency, life-history strategy, water velocity, and predation risk (Metcalfe et al. 1997, 1998, 1999). The results of this study suggest that interspecific competition can also affect the trade-off between nocturnal and diurnal foraging.

There are also widespread management implications arising from this study. First, the results reinforce previous reports of the importance of slow-flowing water to juvenile salmonids in winter. That this habitat requirement is often limited (Rimmer et al. 1985; Cunjak and Power 1986; Cunjak 1996) may have profound effects on those species known to depend upon it. The susceptibility of these species to habitat limitations may be further increased by the fact that, although during summer different age groups of fish select different habitats (Kennedy and Strange 1982), in winter young-of-the-year and post-young-of-the-year Atlantic salmon have been found to use similar microhabitats (Whalen and Parrish 1999). Secondly, the results indicate that competition between Atlantic salmon and brown trout for resources such as habitat and food is not restricted to the summer months, during which time it has previously been shown to occur (Kennedy and Strange 1986). The most immediate effect of this competition is that salmon mortality due to predation may increase during the winter if they are forced to become more active during the day (Metcalfe et al. 1999). Longer-term survival rates of salmon may also be affected by interspecific competition with trout. Salmon destined to smolt and migrate to the sea in the spring continue to grow during the winter months (Metcalfe et al. 1988). Since the survival of migrating individuals is size dependent (Lundqvist et al. 1994), reduced over-winter growth of salmon due to competition with trout may lead to decreased chance of survival.

The potential of a stream to produce high numbers of good quality salmon smolts does not only depend on the availability of winter habitat, as suggested by Nickelson et al. (1992), but also on the presence of brown trout, which may affect the growth and survival of overwintering salmon. The importance of winter habitat to smolt production has recently been confirmed through a winter habitat modification study in which the over-winter survival and smolt production of coho salmon increased in treatment streams in comparison with unmodified control streams (Solazzi et al. 2000). Similar comparative studies are needed to determine the effects of brown trout on the over-winter survival and size of Atlantic salmon smolts.

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References

- Alanärä, A., and Brännäs, E. 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **54**: 2894–2900.
- Amundsen, P.-A., Gabler, H.-M., Herfindal, T., and Riise, L.S. 2000. Feeding chronology of Atlantic salmon parr in subarctic rivers: consistency of nocturnal feeding. *J. Fish Biol.* **56**: 676–686.
- Arnold, G.P., Webb, P.W., and Holford, B.H. 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *J. Exp. Biol.* **156**: 625–629.
- Bremset, G. 2000. Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Environ. Biol. Fishes*, **59**: 163–179.
- Bremset, G., and Berg, O.K. 1997. Density, size-at-age, and distribution of young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in deep river pools. *Can. J. Fish. Aquat. Sci.* **54**: 2827–2836.
- Bremset, G., and Berg, O.K. 1999. Three-dimensional microhabitat use by young pool-dwelling Atlantic salmon and brown trout. *Anim. Behav.* **58**: 1047–1059.
- Cowan, C.A., and Peckarsky, B.L. 1994. Diel feeding and positioning periodicity of a grazing mayfly in a trout stream and fishless stream. *Can. J. Fish. Aquat. Sci.* **51**: 450–459.
- 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., and Power, G. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* **43**: 1970–1981.
- 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.
- Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. *Can. J. Fish. Aquat. Sci.* **55**: 218–231.
- Fraser, N.H.C., and Metcalfe, N.B. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Funct. Ecol.* **11**: 385–391.
- 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.
- Fraser, N.H.C., Heggenes, J., Metcalfe, N.B., and Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Can. J. Zool.* **73**: 446–451.
- Healy, B.D., and Lonzarich, D.G. 2000. Microhabitat use and behaviour of overwintering juvenile coho salmon in a Lake Superior tributary. *Trans. Am. Fish. Soc.* **129**: 866–872.
- Heggenes, J., Krog, O.M.W., Lindås, O.R., Dokk, J.G., and Bremnes, T. 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *J. Anim. Ecol.* **62**: 295–308.
- Helfman, G.S. 1993. Fish behaviour by day, night, and twilight. *In* Behaviour of teleost fishes. Edited by T.J. Pitcher. Chapman & Hall, London. pp. 479–512.
- Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., Graham, W.D., and Adams, C.E. 1990. Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *J. Fish Biol.* **36**: 877–881.
- 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. Freshw. Res. Drottningholm Rep.* **39**: 55–98.
- Kennedy, G.J.A., and Strange, C.D. 1982. The distribution of salmonids in upland streams in relation to depth and gradient. *J. Fish Biol.* **20**: 579–591.
- 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.
- Linnér, J., Brännäs, E., Wiklund, B.S., and Lundqvist, H. 1990. Diel and seasonal locomotor-activity patterns in Arctic charr, *Salvelinus alpinus* (L.). *J. Fish Biol.* **37**: 675–685.
- Lundqvist, H., McKinnell, S., Fangstam, H., and Berglund, I. 1994. The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. *Aquaculture*, **121**: 245–257.
- Mäki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P., and Kreivi, P. 1997. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Can. J. Fish. Aquat. Sci.* **54**: 520–530.
- Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1988. Feeding intensity, growth-rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* **57**: 463–474.
- Metcalfe, N.B., Valdimarsson, S.K., and Fraser, N.H.C. 1997. Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. *J. Anim. Ecol.* **66**: 866–875.
- Metcalfe, N.B., Fraser, N.H.C., and Burns, M.D. 1998. State dependent shifts between nocturnal and diurnal activity in salmon. *Proc. R. Soc. Lond. Ser. B, Biol. Sci.* **265**: 1503–1507.
- Metcalfe, N.B., Fraser, N.H.C., and Burns, M.D. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J. Anim. Ecol.* **68**: 371–381.
- 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.

- Riehle, M.D., and Griffith, J.S. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. *Can. J. Fish. Aquat. Sci.* **50**: 2119–2128.
- 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.
- 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.
- Valdimarsson, S.K., and Metcalfe, N.B. 1999. Effect of time of day, time of year, and life history strategy on time budgeting in juvenile Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* **56**: 2397–2403.
- 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.