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 sympathy 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 les 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.

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 char, *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*.
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 (Metcalfe 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 (Metcalfe 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 nile 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 sympathy 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 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 17.5 × 8.5 × 4.25 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 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 ± 1.83 mm (mean ± standard error (SE)); weight = 13.42 ± 0.65 g) and trout (fork length = 100.7 ± 2.77 mm; weight = 9.87 ± 0.90 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 alcan 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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time of day</td>
<td>2</td>
<td>16.70</td>
<td>&lt;0.001</td>
<td>2</td>
<td>3.70</td>
<td>0.038</td>
<td>2</td>
<td>0.38</td>
<td>0.688</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td></td>
<td></td>
<td>27</td>
<td></td>
<td></td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Category of fish</td>
<td>2</td>
<td>0.74</td>
<td>0.481</td>
<td>2</td>
<td>8.01</td>
<td>0.002</td>
<td>2</td>
<td>0.60</td>
<td>0.558</td>
</tr>
<tr>
<td>Error</td>
<td>61</td>
<td></td>
<td></td>
<td>28</td>
<td></td>
<td></td>
<td>28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time of day × category of fish</td>
<td>4</td>
<td>0.60</td>
<td>0.662</td>
<td>4</td>
<td>1.93</td>
<td>0.119</td>
<td>4</td>
<td>0.30</td>
<td>0.874</td>
</tr>
<tr>
<td>Error</td>
<td>122</td>
<td></td>
<td></td>
<td>56</td>
<td></td>
<td></td>
<td>56</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

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).
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 sympathy (see Fig. 3). There was, however, no significant difference in the depth of water used by salmon in allopatry and salmon in sympathy, 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 (arc sine-transformed) between salmon and trout when...
the two species were in sympatry (paired 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). 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.

**Discussion**

Habitat preferences and activity patterns

Our first hypothesis, that juvenile salmon in winter prefer 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 sympathy, 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

**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.
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 nutrition requirements were increased (see Metcalfe et al. 1998, 1999). This result is also analogous to that found by Alánarå and Brännås (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 (Bremsete 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 decrease 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 sympathy 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. Bremsete 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 sympathy 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.

Acknowledgements

We thank Matt Stewart and Angus McRitchie for permission to fish in the Loch Lomond catchment; Matt Stewart, David Stewart, and Christopher West for help with electro-fishing; Vivien Cameron and Peter Wilmott for fish husbandry; and Gunnbjorn Bremset and an anonymous reviewer for helpful comments on the manuscript. Andrew Harwood was funded by a Natural Environment Research Council, Cooperative Awards in Science and Engineering studentship supported by the Fisheries Research Services Freshwater Laboratory.

References


© 2001 NRC Canada


