Sympatric association influences within-species dominance relations among juvenile Atlantic salmon and brown trout

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Size and aggressiveness are determinants of social dominance in many vertebrate species, including juvenile stream-dwelling salmonids. We used seminatural stream channels, landscaped to provide a range of depths, to test whether the factors influencing the formation of social hierarchies are similar in single- and mixed-species groups of Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. We also tested whether these species have similar feeding rhythms during the day and whether dominant and subordinate individuals feed at different times, under both allopatric and sympatric conditions. Size appeared to be a good predictor of feeding success of both species in allopatry, but not when they were in direct competition. In contrast, rate of aggression was positively correlated with feeding success in both allopatry and sympatry. However, the timing and rate of feeding of dominants and subordinates differed significantly only in the allopatric trials, with subordinate individuals in the sympatric trials being able to adopt a nonaggressive alternative strategy and continue feeding. These results highlight the behavioural plasticity of juvenile salmonids, which can adapt their feeding behaviour to the social environment, and suggest that the presence of another species with similar, but not identical, ecological requirements may increase the opportunity for the expression of alternative behavioural strategies. We conclude that the advantages of social dominance may to a large extent be specific to the species assemblage.

Dominance hierarchies are widespread in the animal kingdom, being present within groups as diverse as the social, yet primitively organized, paper wasps (*Polistes*) and the socially complex anthropoid apes (Wilson 1975). The advantages gained by dominants are fairly uniform throughout, namely a priority of access to food, shelter and reproductive opportunities. However, the factors that determine dominance vary considerably. For example, dominance is established by the size and age of an individual within rank orders of antelopes, sheep and other ungulates (e.g. Barroso et al. 2000). By contrast, in dominance-structured groups of baboons and macaques, status can depend on the mother's rank, membership in a coalition or the length of time an individual's family has been associated with that troop (see Wilson 1975).

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Numerous studies have been conducted on the dominance relationships formed within groups of salmonid fish, largely because of the implications of social suppression of feeding for the farming of salmonids (e.g. for Arctic charr, *Salvelinus alpinus*, and rainbow trout, *Oncorhynchus mykiss*: Alanärä & Brännäs 1996), or their life history strategies in the wild (e.g. for Atlantic salmon, *Salmo salar*: Metcalfe et al. 1989). These studies have revealed positive relationships between the ability to monopolize a resource and aggressiveness (Adams et al. 1998; Cutts et al. 2001), metabolic rate (Metcalfe et al. 1995; Cutts et al. 2001) and size, although size is sometimes a consequence rather than a cause of dominance (Huntingford et al. 1990; Adams et al. 1998).

Consistency in the abilities of individual fish to monopolize resources within allopatric assemblages has been shown across a range of temperatures (Kolok 1992; Magoulick & Wilzbach 1998; Cutts et al. 2001) and altitudes (Hayes & Chappell 1990). However, temperature may influence the competitive abilities of fish species relative to one another when coexisting in the same stream (Taniguchi et al. 1998; Taniguchi & Nakano 2000).

Many studies on social dominance in fish have concentrated on hierarchies formed between members of the same species, with dominant individuals obtaining the most profitable sites in terms of food availability (Fausch 1984; Hughes 1992). Studies that have investigated competitive abilities in sympatric assemblages have shown that size and aggression are key determinants of dominance (Fausch & White 1986; Nakano 1995a), as they are in allopatric assemblages of the same species (Fausch 1984; Nakano 1995b). We tested by direct comparison whether the factors influencing the formation of social hierarchies are similar under allopatric and sympatric conditions. We studied the formation of hierarchies in Atlantic salmon and brown trout, *Salmo trutta*, which show considerable spatial niche overlap in sympatric populations (reviewed by Heggenes et al. 1999; Armstrong et al., in press) in which trout tend to dominate salmon (Kalleberg 1958; Kennedy & Strange 1986a, b). We tested the following predictions: (1) size correlates positively with feeding success in both single-species (allopatric) and mixed-species (sympatric) groups of Atlantic salmon and brown trout; and (2) a similar positive correlation relates food acquisition to aggressiveness in single- and mixed-species groups.

We then examined the influence of social dominance on the feeding periodicity of fish in different social contexts. Many studies on groups of juvenile salmonids during the summer have shown that they are day active with a peak in feeding activity at dawn and dusk, leading to the conclusion that for most of the year these fish are crepuscular feeders (e.g. Sagar & Glova 1988; Riehle & Griffith 1993; Kreivi et al. 1999). However, there is growing evidence that dominant and subordinate fish, either of the same (Alanärä et al. 2001) or different species (Alanärä & Brännäs 1997), may adopt different diel activity patterns, with subordinates feeding at a different time of day to avoid aggressive conflict. Therefore, we also tested the following hypotheses: (3) groups of Atlantic salmon and brown trout have the same overall diel pattern of feeding with a peak at dawn and dusk; but (4) within this overall trend, dominants and subordinates will have different temporal patterns of feeding, both in allopatry and sympatry, to partition resources.

METHODS

We used an outdoor artificial stream (previously described in Valdimarsson et al. 1997) at the University Field Station, Rowardennan, near Glasgow, U.K. The 60-cm-wide stream was in the form of a continuous, approximately oval 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 long. 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 2.25-m experimental arenas by mesh, and landscaped with fine gravel (5–25 mm diameter) to deter fish from hiding in streambed cavities. The gravel was landscaped to produce deep and shallow areas. The deep areas were situated in the middle of each arena and had curved sides with water depth at the deepest point being 25 cm. Shallow water areas (10 cm deep) were located on both sides of the deep water in each section. The surface velocity of the water varied continuously from 0.12 m/s in the shallow water to 0.07 m/s in the deeper water. Six large boulders were placed at regular intervals throughout each arena to provide shelter from the current. The sections between the experimental arenas were landscaped to produce a water depth similar to that in the shallow areas (10 cm) to decrease turbulence and smooth the flow through the channel. The outer side of the channel was marked every 15 cm along its length to define 15 zones per arena (zone 1 being at the upstream end) to allow referencing of the recorded positions of the fish.

Water temperatures were approximately ambient (as there was a constant turnover of fresh water pumped from Loch Lomond into the channel) and ranged from 10.9 to 18.1°C during the study. As the channel was outdoors light levels were also ambient. We provided a steady supply of live bloodworms (chironomid larvae) through the day. These were dispensed from small bottle caps filled with water placed on a 24-h belt feeder. In this way a bottle cap would fall from the belt feeder approximately every 2 h, dropping the bloodworms on to a fine net mesh partly submerged in the water. The bloodworms then crawled through this fine mesh and became available for the fish to eat. Fish were prevented from feeding on the bloodworms whilst on the fine mesh by a surrounding coarse metal mesh. Fish were provided with 2% of their total body weight in food per day. This bloodworm supply was supplemented by a low level of zooplankton in the water pumped from Loch Lomond.

To examine the formation of social hierarchies and diel behavioural rhythms of salmon and trout, and to determine whether there was any difference between the two species, we used two single-species (allopatric) experimental treatments in which either six salmon or six trout were placed in separate experimental arenas. In addition, to determine whether interspecific competition affects the formation of a social hierarchy or the behavioural patterns of either species, we had a third experimental treatment in which three salmon and three trout were placed in an experimental arena together (sympatric treatment). Fish in all three treatments were approximately size matched for two main reasons: (1) to reduce any confounding effects of large size differences (size differential >20%), as our primary objective was to investigate species and assemblage differences; and (2) to ensure that we were investigating competition for microhabitats used commonly by both species. There is considerable niche segregation of different age classes in both species (Kennedy & Strange 1982; Heggenes et al. 1999) and therefore fish of widely different size might not compete. We ran replicates of the three treatments simultaneously in different arenas of the stream channel to prevent any confounding effects of temperature or time of year influencing the results.

We used wild-caught salmon ($\bar{X} \pm$ SE; fork length: 68.4 ± 0.62 mm; weight: 3.23 ± 0.09 g) and trout (fork length: 71.1 ± 0.69 mm; weight: 3.69 ± 0.12 g) from the

River Endrick, which flows into Loch Lomond. Fish were housed in two species-specific holding tanks prior to experimentation and were caught less than 1 week before the experiments began. We individually marked fish on their dorsal and caudal fins, using small injections of alcian blue dye, after anaesthetization with benzocaine. We marked the fish in the evening and then placed them individually in separate 0.5-litre opaque plastic containers at the back of the experimental arena in which they were to be observed. The open top was covered with mesh to prevent the fish from escaping and we placed a rock in each one to weigh it down. The containers were placed facing the direction of flow with several holes drilled into each to allow water to flow through. This procedure allowed the fish to recover from the effects of anaesthesia without being able to sample their new surroundings. We removed the mesh from each container the following morning, allowing the fish to enter the main part of the arena simultaneously.

We observed each group of fish over the 5 days following release. Each day was split into eight 3-h periods and the fish observed for three to five of these periods per day. During each selected 3-h period we observed the fish twice, with an hour separating the observation periods. During each observation period we individually identified each fish and noted its position in terms of zone. In addition, we recorded the vertical position of the fish (either resting on the bottom or swimming in the water column) and whether it was sheltering adjacent to a boulder. We then watched the fish for 1 min during which we counted feeding attempts and recorded the aggressive interactions initiated and received, along with the identity of the other fish involved in each bout. The aggression witnessed varied from displays to charges and nips (see Keenleyside & Yamamoto 1962 for more details of aggressive interactions in young salmonids).

Light intensity was measured during each observation period, with a photometer (Skye Instruments SKL 300, range 0.01–2000 lx), and recorded as the mean of two measurements made just above the water surface, in the middle of the straight section on either side of the channel. Water temperature was measured with a digital thermometer placed permanently in the stream.

After collecting the data on each group, we removed the fish and placed a different group of fish in the test arena. In total, the sympatry and salmon in allopatry treatments were replicated eight times and the trout in allopatry treatment six times, with new fish in each trial. The experiments were carried out between 30 August and 15 October 1999.

Ethical Note

All experimental procedures, including anaesthesia and marking, were carried out under U.K. Home Office Licence. Fish were kept at densities similar to those that would be experienced in the wild (see Grant & Kramer 1990), and we monitored them closely to ensure we could remove them if contests escalated to a point where injury could occur. However, this was required on only one occasion when one individual sustained a degree of fin damage. The fish was removed and returned to the holding tank where it subsequently recovered, and was returned to the wild along with all other experimental fish at the end of the trials.

Data Analysis

For data analysis we combined the eight 3-h periods during which observations were made to give the following periods: morning (0600–1200 hours), afternoon (1200–1500 hours), evening (1500–2100 hours) and night (2100–0600 hours). We split the data into the following categories for comparison: salmon in allopatry, trout in allopatry, salmon in sympatry (with trout) and trout in sympatry (with salmon). To evaluate the effect of body size on behaviour while standardizing for size differences between trials, we calculated the relative body length of each fish as its body length as a proportion of that of the largest in its group of six fish. To determine the influence of relative size on behaviour while comparing fish in different treatments, we performed analyses of covariance (ANCOVA) with relative length as the covariate, category of fish as the fixed factor and individual feeding rate and aggression initiated as the dependent variables. We also used analysis of covariance to determine whether feeding rate (dependent factor) could be predicted from the rate of aggression initiated (log $x+1$ transformed).

To test for patterns in feeding rates over a 24-h period and over the course of the experiment, we split the four categories of fish on the basis of social status, with two dominants being defined in each replicate group as the two most aggressive fish over the 5 days of observation. Their feeding rate, during each time period or on each day, was then averaged to give a single mean score for the dominants of that particular replicate group. In sympatric trials where the two dominant fish were a salmon and a trout, an average was not taken, to maintain the integrity of the species data. In these cases, we obtained values for dominant salmon in sympatry and dominant trout in sympatry. We calculated mean scores for the remaining subordinate fish of each species in each replicate in a similar manner. Repeated measures analysis of variance (ANOVA) was then carried out on feeding rate with either time period or day of experiment as the within-subject factor, and treatment (allopatry and sympatry), species (salmon and trout) and social status (dominant and subordinate) as the between-subject factors. Repeated measures ANOVAs were also carried out on the two allopatric treatments alone to determine species differences in behaviour without treatment as a confounding variable.

We calculated the percentage of time spent in deeper water for each individual by determining the number of times that the fish occurred in zones 6–10 (deeper area), as opposed to zones 1–5 and 11–15 (shallow areas), and calculating this as a percentage of the overall number of observations. The percentage of time spent touching the substrate, as opposed to swimming in the water column, was also calculated for each individual. We then calculated replicate means for these behavioural variables in

Table 1. Summary of results from a series of analyses of covariance to determine the influence of relative size and treatment on level of aggression initiated and feeding rate

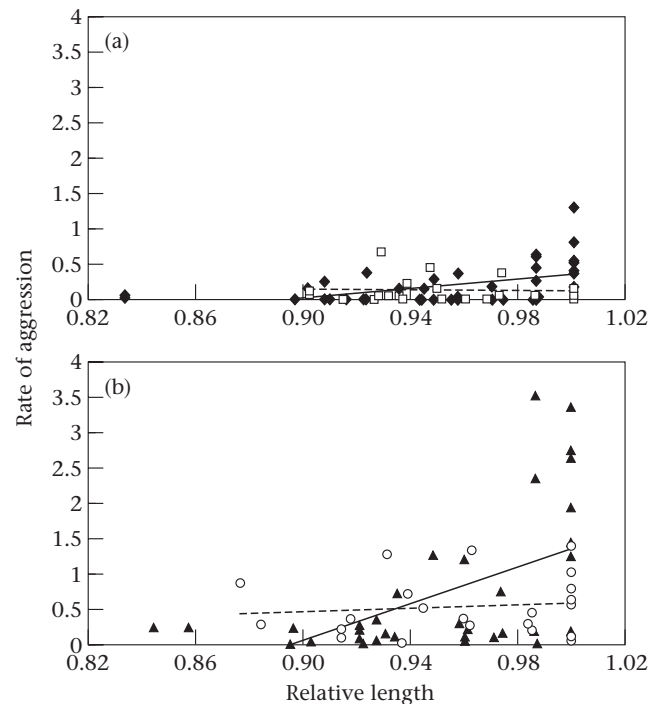| Source of variation	df	F	P
Level of aggression initiated			
Salmon in allopatry versus salmon in sympatry			
Comparison of regression slopes	1,67	4.58	0.036
Trout in allopatry versus trout in sympatry			
Comparison of regression slopes	1,54	6.00	0.018
Feeding rate			
Salmon in allopatry versus salmon in sympatry			
Comparison of regression slopes	1,67	1.27	0.263
Effect of relative length	1,68	3.17	0.079
Effect of category of fish	1,68	0.55	0.463
Trout in allopatry versus trout in sympatry			
Comparison of regression slopes	1,54	1.33	0.255
Effect of relative length	1,55	2.06	0.157
Effect of category of fish	1,55	3.25	0.077

the manner described above. We used analysis of covariance to determine the influence of species, treatment and social status (fixed factors) on the percentage of time in deep water and the percentage of time spent on the substrate (dependent factors).

To test for patterns of aggression over a 24-h period and over the course of the experiment, we conducted separate analyses that took account of the varying levels of opportunity to attack different categories of fish. For example, individual salmon in allopatry and trout in allopatry had the same level of opportunity to attack other individuals of their own species, and these two levels of aggression could therefore be directly compared. In contrast, a salmon in sympatry with trout had the opportunity to attack three trout but only two other salmon. For this reason, we analysed aggression in sympatry by comparing levels of salmon–salmon aggression with trout–trout aggression, and salmon–trout aggression with trout–salmon aggression. The replicate mean for each category of fish was found and then analysed with repeated measures ANOVA to test for patterns of aggression through the day and over the course of the experiment. Social status was not included in the analysis of aggression data as status was itself defined by the level of aggression. We used chi-square analysis to compare the numbers of displays, chases, charges and nips used in each treatment by each species, to test for possible variation in the nature of aggression used under different environmental conditions. All percentage data were normalized by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for two-tailed tests of significance.

RESULTS

Aggression

Comparison of the relationship between relative length and the rate of aggression initiated for salmon in allopatry versus salmon in sympatry revealed a significant

Figure 1. The rate of aggression initiated/min by individual fish against their length for (a) salmon in allopatry (◆, ——) and salmon in sympatry (□, – – –) and (b) trout in allopatry (▲, ——) and trout in sympatry (○, – – –). Length is expressed relative to the largest fish in the group (=1.0).

difference between the categories of fish, with the largest salmon in allopatry being the most aggressive fish, while this was not the case for salmon in the presence of trout (Table 1, Fig. 1a). We found the same pattern for trout in allopatry versus trout in sympatry (Table 1, Fig. 1b). There was also a significant difference between the species in the rate of aggression that they initiated when in sympatry, with trout being significantly more likely to be defined as dominants than salmon ($\chi^2_1=6.25$, $P=0.012$). In addition, when testing for time of day effects we found a

Table 2. Summary of results from repeated measures ANOVAs for the effect of time period and day of experiment on the level of aggression initiated

Category of fish	Source of variation	df	F	P
Within-subject effect: time period				
Salmon in allopatry versus trout in allopatry	Time period	2,24	1.23	0.311
	Category of fish	1,12	43.55	<0.001
	Time period*category of fish	2,24	0.39	0.682
Salmon–salmon versus trout–trout	Time period	2,28	2.54	0.097
	Category of fish	1,14	4.73	0.047
	Time period*category of fish	2,28	0.37	0.691
Salmon–trout versus trout–salmon	Time period	2,13	0.46	0.643
	Category of fish	1,14	8.44	0.012
	Time period*category of fish	2,13	0.64	0.544
Within-subject effect: day of experiment				
Salmon in allopatry versus trout in allopatry	Day of experiment	4,7	2.34	0.154
	Category of fish	1,10	30.88	<0.001
	Day*category of fish	4,7	2.97	0.099
Salmon–salmon versus trout–trout	Day of experiment	4,9	5.44	0.017
	Category of fish	1,12	1.74	0.211
	Day*category of fish	4,9	7.70	0.006
Salmon–trout versus trout–salmon	Day of experiment	4,9	0.89	0.507
	Category of fish	1,12	10.57	0.007
	Day*category of fish	4,9	1.99	0.179

significant effect of fish category in each of the three interspecific comparisons: salmon in allopatry versus trout in allopatry, salmon–trout versus trout–salmon, and salmon–salmon versus trout–trout, with trout initiating more aggression than salmon in each case (Table 2). A comparison of the percentage of times salmon attacked salmon and trout attacked trout in sympatry revealed that salmon directed more aggression to members of their own species than trout (independent samples t test: $t_{22.5}=2.20$, $P=0.038$). These results confirm that trout were generally more aggressive and tended to dominate salmon.
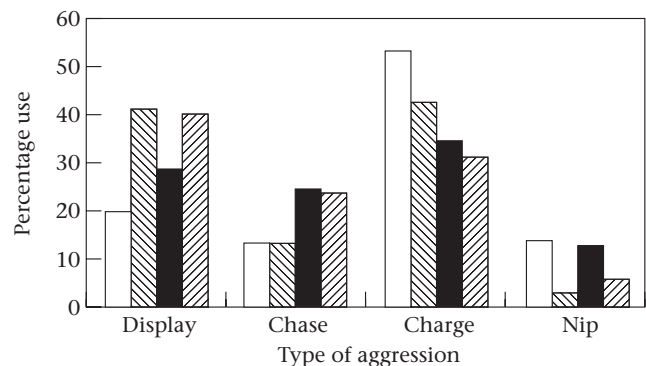
There was no significant time of day effect in the amount of aggression initiated for any category of aggression (Table 2). There was also no consistent decline in aggression over the 5 days of the experiment, with the significant day effect for salmon–salmon and trout–trout aggression representing a decreased level of aggression on day 2 in relation to days 1, 3, 4 and 5 (cubic term of polynomial contrasts: $F_{1,12}=8.27$, $P=0.014$).

There were significant differences in the nature of aggression used both between species and between treatments. For fish in allopatry, salmon were more likely to charge than trout, using correspondingly fewer displays and chases ($\chi^2_3=31.21$, $P<0.001$). For both species we found significantly more displays, and fewer charges and nips, in allopatry than in sympatry ($\chi^2_3=32.47$, $P<0.001$; Fig. 2). There was also a significant difference in the aggression used by salmon and trout against their own species in sympatry. As in allopatry, salmon attacking salmon were less likely to display or chase and more likely to charge than trout attacking trout ($\chi^2_3=14.76$, $P=0.002$). However, there was no significant difference between the type of aggression used by salmon to attack trout and trout to attack salmon ($\chi^2_3=3.86$, $P=0.277$).
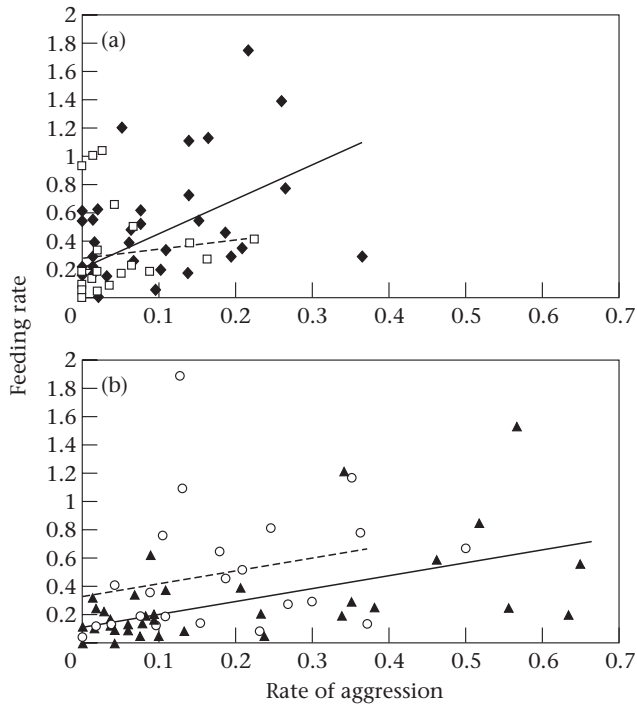
Feeding

There was a nonsignificant trend for larger fish to feed at a higher rate than smaller fish for salmon in allopatry ($r^2=0.081$, $F_{1,45}=3.96$, $P=0.053$) and a significant trend for trout in allopatry ($r^2=0.128$, $F_{1,34}=5.00$, $P=0.032$). However, when salmon in allopatry were compared with salmon in sympatry, and trout in allopatry with trout in sympatry, there was no significant effect of length on feeding rate, and no significant difference in the slopes of the regression lines (Table 1).

There was a positive relationship between the rate of aggression initiated and feeding rate for both salmon in allopatry and salmon in sympatry (ANCOVA: comparison of regression slopes: $F_{1,67}=1.69$, $P=0.198$; comparison of regression elevations: $F_{1,68}=0.03$, $P=0.860$), with more aggressive fish gaining significantly more food than less aggressive fish (effect of rate of aggression: $F_{1,68}=17.36$,

Figure 2. Percentage use of displays, chases, charges and nips by salmon in allopatry (□), salmon in sympatry (▨), trout in allopatry (■) and trout in sympatry (▧).

Figure 3. Feeding rates (items attacked/min) of individual fish plotted against their rate of initiated aggression/min (log $x+1$ transformed) for (a) salmon in allopatry (◆, ——) and sympatry (□, – – –) and (b) trout in allopatry (▲, ——) and sympatry (○, – – –).

$P<0.001$; Fig. 3a). There was a similar relationship for trout in allopatry and trout in sympatry (ANCOVA: comparison of regression slopes: $F_{1,54}<0.01$, $P=0.999$; effect of rate of aggression: $F_{1,55}=11.34$, $P=0.001$). Trout in sympatry also gained significantly more food than trout in allopatry for an equivalent amount of aggression (comparison of regression elevations: $F_{1,55}=4.99$, $P=0.030$; Fig. 3b).

There was no significant variation in feeding rate through the day for any category of fish (Table 3). There was a significant status effect, with dominant fish feeding at a higher rate than subordinates. However, a significant interaction between treatment and status indicates that the effect of status was not the same in all treatments, with there being a negligible effect of status in the sympatric treatment but a large difference in feeding rates of fish of different status in allopatry (Fig. 4a, b).

When the analysis was repeated with the data from just the two allopatric trials there was no significant effect of time of day on feeding rates for either salmon or trout (Table 3). However, there was a highly significant status effect with dominant fish feeding at a higher rate than subordinates. There was also a significant time by species by status effect, indicating that the effect of status on the diel pattern of feeding was different for the two species. Subordinate trout ate more when dominant trout reduced their feeding rate, while the relationship between the feeding patterns of dominant and subordinate salmon was less clear (Fig. 4a). There was no significant temporal pattern in the level of feeding across the 5 days of each experiment.

Habitat Use

There were significant species and status effects on both the percentage of time spent in deeper water and the percentage of time spent on the substrate. Trout spent significantly more time in deeper water than salmon, but less time touching the substrate. Similarly, dominant fish of both species spent more of their time in deeper water than subordinates, but significantly less time holding position on the substrate (Table 4, Fig. 5a, b).

DISCUSSION

Although there was a trend for larger salmon and trout to feed at a higher rate than smaller individuals in allopatry, this was not evident when we compared the behaviour of fish between treatments. These results, therefore, provide no support for our first hypothesis that food acquisition correlates positively with size in single- and mixed-species groups of Atlantic salmon and brown trout. Furthermore, our results enlarge the growing sample of contrasting results obtained for the relationship between size and dominance in terms of feeding success: if we had been interested only in single-species groups we would have assumed a significant correlation between size and dominance. Such a positive correlation has been witnessed under a range of conditions (Jenkins 1969; Abbott et al. 1985; Nakano 1995a, b), while other studies have found no relationship between food acquisition and body size (Metcalfe & Thorpe 1992; Adams & Huntingford 1996). The conclusion that size is a consequence rather than a cause of dominance, with dominant fish becoming large rather than vice versa (Huntingford et al. 1990) may go some way to explaining our results. This is because large fish in sympatry did not acquire more food than smaller fish, but might have been dominant in past social experiences and thus attained large size. This argument relies on the assumption that fish can adopt different behavioural strategies that promote success in different competitive environments (Adams & Huntingford 1996; Pettersson et al. 1996).

The positive correlation between rate of aggression and food intake has been documented before (Grant 1990; Adams et al. 1998; Cutts et al. 2001), and was present in both species in allopatry and when the two species coexisted. These results therefore provide support for our second hypothesis that aggressiveness and food intake are positively correlated in single- and mixed-species groups of Atlantic salmon and brown trout. However, although there was a clear positive relationship between size and aggressiveness for both salmon and trout in allopatry (see also Elliott 1990; Nakano 1995b), this was not the case in sympatry and raises the question: why were the largest fish in sympatry not the most aggressive, especially when the most aggressive fish obtained the most food? This may relate to the different competitive abilities of Atlantic salmon and brown trout. Trout are more aggressive than salmon of a similar size (Kalleberg 1958; this study), and this dominance affects both the spatial (Kennedy & Strange 1986a) and temporal (Harwood et al.

Table 3. Summary of results from repeated measures ANOVAs for the effect of time of day on feeding rate with treatment included as a between-subject factor and treatment excluded, thus comparing only the two allopatric trials

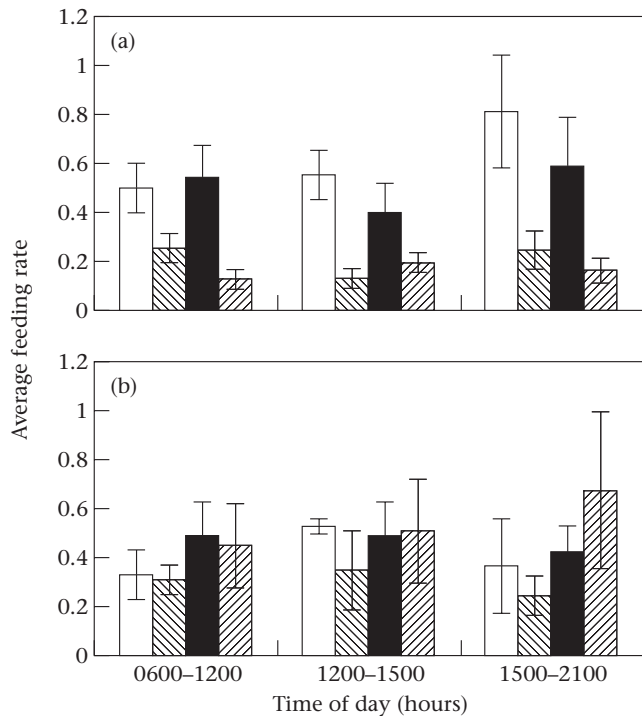| Category of fish	Source of variation	df	F	P
Treatment included as between-subject factor				
Within-subject effects	Time	2,46	0.93	0.404
	Time*treatment	2,46	0.87	0.424
	Time*species	2,46	0.11	0.896
	Time*status	2,46	0.08	0.922
	Time*treatment*species	2,46	0.63	0.539
	Time*treatment*status	2,46	0.96	0.390
	Time*species*status	2,46	2.67	0.080
	Time*treatment*species*status	2,46	0.13	0.883
Between-subject effects	Treatment	1,47	0.30	0.588
	Species	1,47	0.14	0.715
	Status	1,47	4.81	0.033
	Treatment*species	1,47	1.63	0.209
	Treatment*status	1,47	4.11	0.048
	Species*status	1,47	0.46	0.500
	Treatment*species*status	1,47	0.12	0.732
Treatment excluded as between-subject factor				
Within-subject effects	Time	2,23	1.98	0.160
	Time*species	2,23	0.31	0.733
	Time*status	2,23	0.78	0.470
	Time*species*status	2,23	7.41	0.003
Between-subject effects	Species	1,24	0.72	0.404
	Status	1,24	15.63	0.001
	Species*status	1,24	0.10	0.756

2001) resource use of salmon in sympatry with trout. Given the presence of the competitively inferior salmon, large trout in sympatry may not need to engage in high levels of aggression. This is supported by the fact that trout in sympatry did not need to be as aggressive as trout in allopatry to acquire a given amount of food. Salmonids adjust their methods of resource acquisition based on their relative costs and benefits. For example, brook charr, *Salvelinus fontinalis* (McNicol & Noakes 1981) and Arctic charr (Adams et al. 1995) reduce their rate of aggression when current velocity increases, because the cost of defending their territory outweighs the benefit gained in terms of food acquisition.

The largest salmon in allopatry may have similarly reduced their level of aggression because in the presence of competitively superior trout they were unable to monopolize the resource in the same manner as when only smaller salmon were present. They were therefore forced to adopt alternative strategies to acquire sufficient resources. In this instance, salmon were perhaps able to obtain more food by initiating little aggression and holding position on the substrate within deeper water, than they were by being aggressive. The nonaggressive individuals might have been able to remain vigilant and capture any food that aggressive trout higher in the water column missed while fighting. In contrast, salmon that were aggressive in sympatry were the only category of fish that spent less time in deep water in sympatry than in allopatry, presumably because they were displaced by competitively superior trout.

A similar nonaggressive strategy was seen in groups of Atlantic salmon (Adams et al. 1998) and rainbow trout

(Pettersson et al. 1996), thus supporting the proposal that minimizing energy expenditure, through low levels of aggression and attempts at feeding, at the expense of maximizing food intake may be the optimum strategy for subordinates (Metcalfe 1986). In support of this argument, Elliott (1990) found high levels of aggression to be extremely costly in terms of feeding. Similarly, Cutts et al. (2001) found no relationship between competitive ability and subsequent growth because dominants achieved a greater energy intake only by expending more energy on increased aggression and feeding attempts. A similar switch to an alternative feeding strategy under different environmental conditions was seen in Dolly Varden, *Salvelinus malma*, competing with white-spotted charr, *Salvelinus leucomaenis*, in Japanese streams. In this instance, a drop in the abundance of drifting prey caused the competitively inferior Dolly Varden to shift to nonterritorial benthic foraging whereas white-spotted charr continued to feed on the drift, thus allowing both species to coexist even when their preferred prey was limited (Nakano et al. 1999).

Another explanation for the change in behaviour of large fish in sympatry is that they were more familiar with conspecifics, having been kept in species-specific holding tanks, and therefore spent longer assessing the fighting ability of unfamiliar heterospecifics before engaging in aggression. However, this is unlikely to be the case as holding tanks initially held 70 fish of each species and trials began less than a week after fish were caught. Furthermore, evidence from previous studies suggests that aggression would be higher among unfamiliar fish (Johnsson 1997; O'Connor et al. 2000).

Figure 4. Average feeding rate (items attacked/min ± SEM) through the day for dominant salmon (□), subordinate salmon (▨), dominant trout (■) and subordinate trout (▨) in (a) allopatry and (b) sympatry.

We found no significant difference in the feeding periodicity of Atlantic salmon and brown trout, although there was no peak in feeding at dawn and dusk, thus providing only partial support for our third hypothesis. A lack of significant diel variation in feeding rates has been seen in wild populations of brook charr (Forrester et al. 1994). However, the overwhelming impression from studies of feeding behaviour of wild salmonids is that the timing of feeding varies greatly between populations and species. For example, Angradi & Griffith (1990) found rainbow trout fed throughout the day, whereas Elliott (1973) found a distinct peak at dusk for the same species in a different river. This variation is likely to stem from behavioural plasticity similar to that discussed above, allowing an opportunistic switch in feeding times or feeding method, dependent on environmental conditions.

There was also only partial support for our fourth hypothesis, because while there was a significant difference in the feeding rates of dominant and subordinates of both species in allopatry, there was no similar discrepancy under sympatric conditions. This result may be related to the differences in behaviour between the two species, both in terms of the nature of aggression used in inter- rather than intraspecific competition, and in terms of their microhabitat choices. There were significantly more displays, and correspondingly fewer charges and nips, in allopatry than in sympatry. The less overt aggression used under sympatric conditions may have allowed subordinates to feed at a higher rate than under allopatric conditions, as the risk of injury may select against some

strategies of food acquisition (Adams et al. 1998). Sabo & Pauley (1997) recorded similar variability in the use of aggression by different populations of fish. They found that in paired size-matched competition between cutthroat trout, *Oncorhynchus clarki*, and coho salmon, *Oncorhynchus kisutch*, cutthroat that had been isolated from coho used chases, whereas cutthroat that naturally coexisted with coho used displays. The use of less overt aggression in sympatry, and the subsequent response in behaviour, may in part be explained by changes in the density of conspecifics. However, this is an inevitable consequence of comparing sympatry and allopatry while maintaining overall biomass (see Fausch 1998) and would not be predicted to alter the rules determining who becomes dominant within species.

The effect that aggression can have on the pattern of feeding was also seen in the comparison of dominant and subordinate trout and salmon in allopatry. Although subordinate trout ate more when dominants reduced their feeding rate, the relationship between the feeding patterns of dominant and subordinate salmon was not as clear. This suggests that the feeding of subordinate trout was repressed to a greater extent than that of subordinate salmon because dominant trout were more aggressive. This finding supports that of Alanärä et al. (2001), who suggested that the degree of temporal segregation in feeding will vary with the intensity of competition, with increased segregation when competition is high.

Another factor that may explain why there was little difference in feeding rates of dominants and subordinates in sympatry was the different microhabitat use of salmon and trout, with salmon spending significantly more time on the substrate than trout. This partitioning of the habitat has been found both in simulated natural streams (Harwood et al. 2001) and in the wild (Bremset & Berg 1999). Harwood et al. (2001) found that dominant salmon occupied preferred deep-water habitats in winter alongside brown trout but were forced to feed at less preferred times during the day, rather than at night, to obtain enough food. The vigilant nonaggressive strategy witnessed in the present study would not have been effective at night. Salmonids defend smaller territories at night (Valdimarsson & Metcalfe 2001), so trout are less likely to be distracted by fighting, and thus more likely to deplete the food supply than during the day.
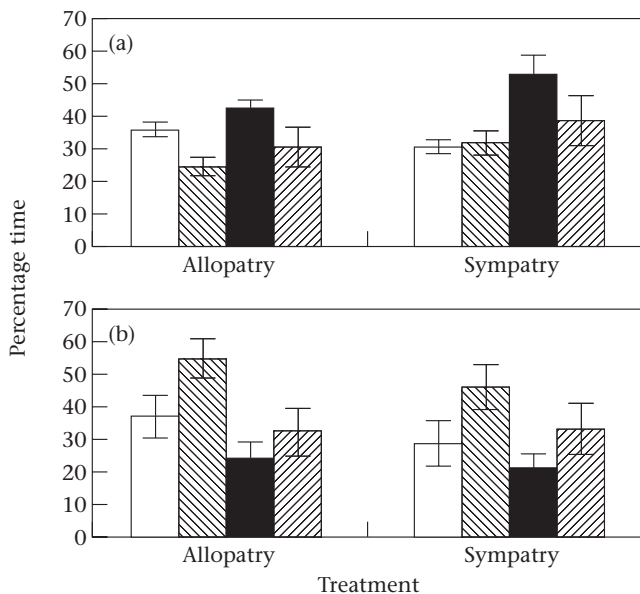
Implications

This study highlights a behavioural plasticity in feeding behaviour that allowed subordinates to obtain enough food in spite of the presence of more dominant individuals, whether of the same or a different species. Strategies to avoid aggressive interactions include feeding at a different time to avoid dominant individuals (Alanärä & Brännäs 1997; Alanärä et al. 2001) or in a different way such as adopting benthic foraging (Fausch et al. 1997; Nakano et al. 1999) or a vigilant nonaggressive foraging strategy (Pettersson et al. 1996; Adams et al. 1998; this study). Alternative feeding strategies such as these are likely to be widespread in animal communities (e.g.

Table 4. Summary of analyses of covariance to determine the influence of species, treatment and social status (fixed factors) on the percentage of time spent in deep water and on the substrate (dependent factors)

Source of variation	df	F	P
Percentage of time spent in deep water			
Species	1,47	7.53	0.009
Treatment	1,47	1.96	0.168
Status	1,47	5.93	0.019
Species*treatment	1,47	1.15	0.290
Species*status	1,47	1.02	0.318
Treatment*status	1,47	0.43	0.515
Species*treatment*status	1,47	0.98	0.328
Percentage of time spent on the substrate			
Species	1,47	8.25	0.006
Treatment	1,47	0.94	0.336
Status	1,47	8.02	0.007
Species*treatment	1,47	0.57	0.453
Species*status	1,47	0.57	0.453
Treatment*status	1,47	0.04	0.851
Species*treatment*status	1,47	0.06	0.816

Figure 5. Habitat use by dominant salmon (□), subordinate salmon (▨), dominant trout (■) and subordinate trout (▨) in terms of (a) percentage time spent in deep water and (b) percentage time on the substrate.

Partridge & Green 1987), especially where social hierarchies prevail. This study provides evidence that, like predation risk (Reinhardt 1999), the presence of a species sharing similar, but not identical, ecological preferences can create the opportunity for these alternative behavioural strategies to be expressed. This study therefore provides the first evidence that the structure of dominance hierarchies can be dependent on the species assemblage, as well as temperature and habitat (Dunson & Travis 1991; Fausch 1998).

Acknowledgments

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