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Aquaculture 167 (1998) 17–26

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**Aquaculture**

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# Alternative competitive strategies and the cost of food acquisition in juvenile Atlantic salmon (*Salmo salar*)

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Accepted 15 June 1998

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## Abstract

Aggressive interactions were recorded for 3 h per day in 11 groups of 10, 1+, juvenile Atlantic salmon given access to a limited food supply. Observations were made over nine-day periods in which the dominant (most aggressive) fish on each day was identified and removed. In all groups at the start of the study, one (usually relatively large) fish performed most (67% overall) of the aggressive acts. Feeding activity was also polarised, though less strongly so, with the two most actively feeding fish taking on average 41% of the food supplied. Behavioural polarisation was also marked at a later stage in the study, when five fishes remained in each group, but rates of aggression per fish increased markedly over successive days. Food intake was positively related to aggression, but not to relative size once the size/aggression relationship was corrected statistically. The relationship between aggression and food intake on the first day of testing was weak ( $R^2 = 8\%$ ); in particular, 30% gained no food in spite of behaving aggressively, while 11% obtained food even though they showed no aggression. The proportion of attacks received was positively, but weakly ( $R^2 = 5\%$ ) related to feeding rates, but not to level of aggression. As a consequence, fishes that engaged in neither feeding nor fighting were attacked less frequently than others in the group. These results, which suggest that the risk of injury may act as a counter-selec-

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tion against some strategies for food acquisition, are discussed in the context of previous work on resource competition in salmonid fishes. © 1998 Elsevier Science B.V. All rights reserved.

*Keywords:* Aggression; Competition; Atlantic salmon; Salmonids

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## 1. Introduction

There are many well-documented examples of variability in aggressiveness among animals of the same species that can be explained from a cost–benefit perspective, with the potential risks of injury degrading the benefits of preferential access to resources (Archer, 1987; Huntingford and Turner, 1987). Such behavioural variability has been relatively well-studied in salmonid fishes. In nature, aggression may be used in competitive interactions to exclude conspecifics from favourable feeding areas or to suppress their foraging activity. Depending on species (e.g., Nakano and Furukawa-Tanaka, 1994), fish density (e.g., Christiansen et al., 1992), food abundance (e.g., Ryer and Olla, 1995) and food distribution (e.g., Ryer and Olla, 1996), such behavioural mechanisms may allow a small number of aggressive fish to monopolise available food (e.g., Chapman, 1966; Gotceitas and Godin, 1992; Dumbrack et al., 1996).

It is clear that fishes vary greatly in competitive ability, as reflected in their capacity to monopolise a limited food supply. Using direct behavioural observation, Metcalfe et al. (1989) were able to identify dominant Atlantic salmon (*Salmo salar*) on the basis of position with respect to a localised food supply and ability to acquire contested food pellets. Aggressive interactions were not monitored systematically, but frequency of attacks initiated by an individual broadly correlated with status as assigned by foraging station and food acquisition. Further, direct observations made on food intake in farmed Atlantic salmon in sea cages showed that a few individuals were able to monopolise a localised food source (e.g., Kadri et al., 1996). Other workers have also used food acquisition as a measure of hierarchy development and to assign dominance status with groups of fish (e.g., McCarthy et al., 1992, for rainbow trout; Brännäs and Alanärä, 1994 and Jobling and Baardvik, 1994, for Arctic charr).

In these studies, conducted under a wide variety of conditions, access to food tended to be highly polarised, with one or a few fishes gaining the greatest share of available resources. These are important results from a practical point of view and methods for assessing monopolisation of food provide a valuable tool for identifying ways of ameliorating its effects in production systems (e.g., McCarthy et al., 1992; Alanärä and Brännäs, 1996). However, from both a fundamental and an applied perspective, it is important to understand the basis of such differences in resource acquisition. For example, preferential access to food may stem from a high level of aggressiveness or from particularly effective foraging, but there may be costs associated with maintaining a high level of food acquisition at high densities when competition is strong. As part of a study designed to examine the relationship between aggressiveness and subsequent performance in production conditions, we examined the behaviour of juvenile Atlantic salmon housed in small groups at densities typical of culture systems. This allowed examination of variation in aggressiveness, of the relationship between size, aggression

and acquisition of food in this social context and assessment of one possible cost of engaging in aggressive interactions.

## 2. Materials and methods

Hatchery-reared, 1 + , juvenile Atlantic salmon (*S. salar*) of a domestic strain were reared on a commercial unit (Loch Sween, Argyll) and transported to the University Field Station, Rowardennan, Loch Lomondside. Fish were weighed, given individual alcian blue dye marks and randomly placed in groups of 10, in round observations tank (diameter = 46 cm; depth = 15 cm). Water flow was 2.5 l/min and the inlet was angled to maintain a current speed equivalent to approximately 0.75 body lengths per second. The fishes were left to settle for three days, during which they were not fed. Subsequently, the fishes were fed for 1 h each day, during which 12 live chironomid larvae (blood worms) were presented one at a time, at a fixed point in the tank at 5-min intervals. The tank was filmed from above during feeding and for 2 h afterwards. The video film was examined and the occurrence of each aggressive act (charge, nip and chase—see Adams et al., 1995), the fish instigating the attack and the target individual were noted. In addition, the fish that gained each food item, was recorded and contestants in any feeding events were noted. Because of either the orientation of fish or the prey item introduced into the tank, some feeding events were not recorded on film and, thus, were not included in subsequent analysis. Analysis was continued until 100 aggressive acts had been recorded or until the full 3 h period had elapsed, whichever occurred sooner. The fish that delivered most attacks (and this was always more than 60%) was removed from the group of 10 in the tank and given a dominance rank of 1. This procedure was repeated daily until all the fishes had been removed, with the most aggressive fish on each day being given a successively higher rank number. Assignment of social rank in terms of order of serial removal in this manner follows Metcalfe et al. (1989). Mean stocking density on day 1 when the fish were in groups of 10 was 8.4 kg/m<sup>2</sup>.

In all, 11 groups were examined in this way, between April and July, 1995. Fishes used in these experiments ranged from 3.0 to 15.9 g in weight reflecting the full range of sizes of fish in the group over this four-month period. Temperature and light conditions were ambient for latitude 56°N, temperature ranging from 7 to 20°C over the experimental period. The fishes were killed in November 1995 (as part of a separate study relating gonadal status to behavioural traits) and their genders were determined. Two fishes, both males, were found to be sexually mature in November; all other fishes were immature.

As fishes in the holding unit grew over the course of these trials, to enable a comparison of size between groups, the weight of each fish during the period of behavioural observation was expressed as a percentage of the total biomass of fish in the relevant group. To look for changes in behaviour with the progression of the trial, the number of attacks given and received by each fish on day 1 and day 6 of the study were expressed as a percentage of the total number of attacks observed on that day. Similarly, the number of prey items eaten by each fish was expressed as a percentage of the total number eaten on that day. The relationships between food intake, aggression and weight

on day 1 and day 6 of the study and between the proportions of attacks received, food intake, aggression and relative weight on day 1 only, were examined by stepwise multiple regression on arcsine transformed data. Properties of fishes identified by their status with respect to food acquisition and the performance of attacks were compared by two-way analysis of variance, again using arcsine transformed data.

### 3. Results

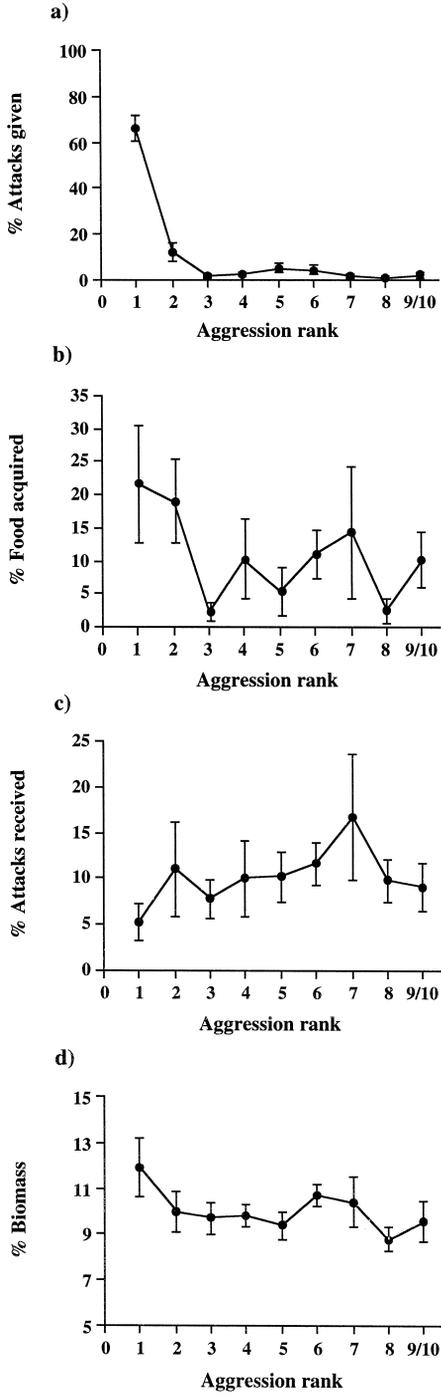
#### 3.1. Individual variability in aggression and food intake

Fig. 1 shows the relationship between assigned aggression rank (determined by the sequence of removal from the group) and the proportion of aggressive interactions initiated (Fig. 1a); the proportion of food items eaten (Fig. 1b); the proportion of attacks received (Fig. 1c); and the average size of fish of a given rank (Fig. 1d), on the first day of testing (when all fishes were present), for all groups combined. Within the group of 10, a single 'despot' consistently emerged that showed high levels of aggression and usually obtained most of the available food (Fig. 1a,b). However, in some groups, one or a few other fishes also engaged in a small amount of attacking. Over all groups, the despot accounted for 67% of all attacks on day 1, with an additional 11% performed by the fish of aggression rank 2. The proportion of attacks received was unrelated to assigned aggression status. The most aggressive fish on day 1 of testing was usually among the largest fish of the group (rank 1 compared to all other ranks,  $F_{1,101} = 4.49$ ,  $P < 0.05$ ). There was a weak association between assigned aggression rank and feeding ( $R_s = 0.82$ ,  $N = 9$ ,  $P < 0.05$ ), with 41% of the food items being eaten by the two highest aggression-ranked fishes. There was a tendency (falling just short of significance at the 5% level) for female fishes to eat more than the male fishes (means  $\pm$  SEM for females and males were  $0.34 \pm 0.09$ ,  $N = 23$  and  $0.15 \pm 0.04$ ,  $N = 31$ , respectively,  $T = 1.84$ ,  $P = 0.07$ ). No other gender differences were found.

To examine changes in aggressive behaviour as the trial progressed, mean levels of aggression per fish were calculated on successive days of the study (Fig. 2). There was a marked increase in rates of aggression per fish with time (Spearman rank order correlation between mean rate of attacks per fish against day  $R_s = 0.98$ ,  $N = 8$ ,  $P < 0.01$ ). Fig. 3 shows mean ( $\pm$  SEM) levels of aggression and food intake on day 6 of the study (when five fishes remained in each group), in relation to assigned aggression rank. Aggression and feeding at this time, were still highly polarised, 86% of attacks being given and 66% of food being eaten by the two fishes with highest assigned aggression rank (6 and 7). However, by this stage in the trial, the correlation between aggression rank and food acquisition observed on day 1 had disappeared ( $R_s = 0.07$ ,  $N = 5$ , NS).

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Fig. 1. The relationship between assigned aggression rank of a fish (day of removal from the group) and (a) the percentage of attacks given, (b) the percentage of food items acquired, (c) the percentage of attacks received and (d) the weight of a fish as a percentage of the total biomass in the tank on day 1 of testing. Data shown are means ( $\pm$  SEM).  $N = 11$ .



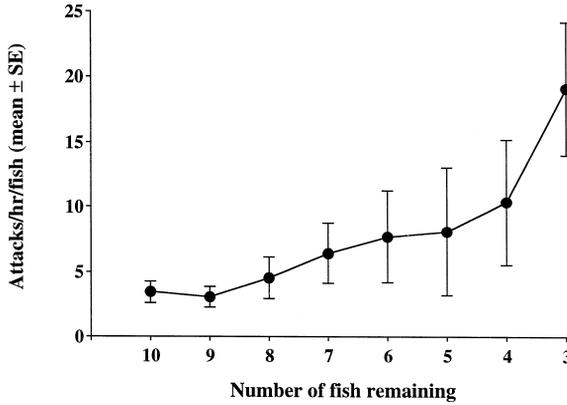


Fig. 2. The frequency of attacks on days 1 to 8 of the observation period. Data shown are mean number of attacks per fish per hour ( $\pm$ SEM).

### 3.2. Aggression and body size as predictors of food intake

Stepwise multiple regression with percentage food acquired as the dependent variable and percentage biomass and percentage attacks as independent variables identified a

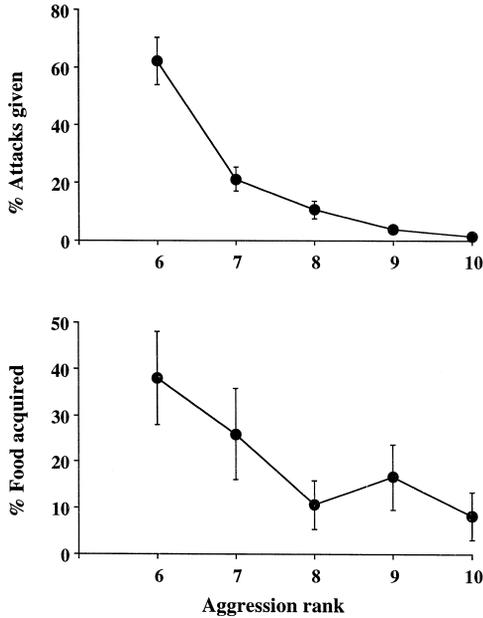


Fig. 3. The relationship between assigned aggression rank of a fish (day of removal from the group) and (a) the percentage of attacks given and (b) the percentage of food items acquired on day 5 of testing with five fishes remaining in observation arena. Data shown are means ( $\pm$ SEM).

Table 1

The relative weight and attacks received by salmon parr classified according to the performance/non-performance of feeding and aggression

	Aggressive and fed	Aggressive, but not fed	Non-aggressive and fed	Neither aggressive nor fed
Number of fish	30	35	11	34
Fish weight as percentage of total biomass	10.5 ± 0.5	10.3 ± 0.6	10.6 ± 0.6	9.4 ± 0.5
Percentage attacks received	11.7 ± 1.6	11.1 ± 2.3	15.4 ± 4.4	5.6 ± 1.0

Weight data are presented as a mean of weight as percentage of total tank biomass ( $\pm$ SEM); attacks received as percentage attacks received.

significant positive relationship between aggression and food intake (regression coefficient = 0.29,  $F_{1,108} = 9.34$ ,  $P < 0.01$ ), but body size had no significant effect, once the relationship between body size and aggression was corrected statistically. However, this regression was weak, accounting for only 8% of the variation in food intake. A similar picture emerged for data for day 6 (regression coefficient = 0.48,  $F_{1,53} = 15.1$ ,  $P < 0.001$ ), with the relationship between aggression and food intake being stronger than on day 1, but only 22% of the variance in food intake was accounted for by this regression.

To examine the factors underlying the scatter in the relationship between aggression and food intake, fishes were classified according to whether they showed any aggression on day 1 and according to whether they obtained any food, also on day 1 (Table 1). Several fishes fell within each of the four possible categories; of particular note, 35 got no food even though they behaved aggressively, whereas 11 were able to obtain food even though they showed no aggression.

### 3.3. Predictors of proportion of attacks received

Table 1 shows the mean ( $\pm$ SEM) body weight (as a proportion of total tank biomass) and the mean ( $\pm$ SEM) number of attacks received by the fish (as a proportion of all attacks) in each food/aggression category. There were no significant differences in relative weight between the four categories of fish ( $F_{3,106} = 3.29$ ,  $P = 0.13$ ). However, there were significant effects of category on the proportion of attacks received ( $F_{3,106} = 4.6$ ,  $P = 0.05$ ). There was a significant interaction effect between food and aggression category, ( $F_{3,106} = 2.78$ ,  $P < 0.05$ ), with fishes that either obtained food or showed some aggression receiving significantly more attacks than those that neither fed nor fought.

Stepwise multiple regression of the proportion of attacks received in relation to the proportion of attacks given, proportion of food eaten and relative body size for day 1 identified proportional food intake as the only significant predictor of attacks received (regression coefficient = 0.13,  $F_{1,108} = 5.23$ ,  $P < 0.05$ ). Although significant, this effect was weak, the regression accounting for only 4.6% of the variance in attacks received.

The ratio of food acquired to attacks received was calculated to give an index of the costs of food acquisition in relation to benefits gained. There was a significant negative

correlation between this index and assigned aggression rank ( $R_s = -0.24$ ,  $N = 89$ ,  $P < 0.05$ ), indicating that more dominant individuals in a small group had a higher rate of food acquisition per attacks received than did lower-ranking fishes.

#### 4. Discussion

This direct behavioural study has confirmed that food acquisition is highly polarised in Atlantic salmon (e.g., Metcalfe et al., 1989; Kadri et al., 1996; Smith et al., 1996), as it is in other species of salmonid fishes (Jobling et al., 1990; McCarthy et al., 1992; Alanärä and Brännäs, 1996). It has also shown that behaviour is even more polarised with respect to the performance of aggressive acts, with one or two fishes aggressively dominating their companions within small groups. This conforms to the view of Symons (1970) that salmonid social hierarchies consist of aggressive, dominant individuals, subdominants and less aggressive, subordinate fishes. For both food acquisition and aggression, the degree of behavioural polarisation was comparable for fishes in groups of 10 (at a stocking density of ca. 8.4 kg/m<sup>2</sup>) and in groups of five (at a stocking density of ca. 3 kg/m<sup>2</sup>). At the start of our serial removal experiments, the most aggressive fish tended to be slightly larger than average; this was not the case later on. Social dominance, as measured in this study, is apparently, therefore, not always a simple consequence of large size (see also Huntingford et al., 1990). Although carried out under very different conditions, the findings of our study agree with those of Alanärä and Brännäs (1996) who found that, in groups of Arctic charr held at higher stocking densities, food is still monopolised, but by several rather than one individual.

Somewhat surprisingly, levels of aggression per fish increased markedly during the process of serial removal. This is contrary to the findings of Metcalfe et al. (1990) that levels of aggression were reduced following the removal of 'despots' from groups of 10 salmon. The increase in attack levels found in the present study could be a group size effect, since aggressive competition among farmed salmonids appears to be lower at high densities (Alanärä and Brännäs, 1996), or a hunger effect (Brännäs and Alanärä, 1994), since by the end of the trial, the fishes had been on restricted rations for up to 13 days. A further possibility is that rates of aggression rose as the study progressed because the strongly dominant fish present in the first half of the trial suppressed aggression in their companions. Such effects have been described for other animal groups, including primates where both the phenomenon and the underlying endocrinological mechanisms are well-documented (e.g., Mendoza et al., 1979).

As in other studies, in which both food intake and aggression have been monitored, there was a significant relationship between aggressiveness and food acquisition, (cf. Grant, 1990), but not between food acquisition and body size (cf. Metcalfe and Thorpe, 1992), once the relationship between aggression and body size had been corrected statistically. The identified relationship between aggression and food intake, though significant, was weak. Two categories of fish complicated the picture: a significant proportion of individuals behaved aggressively, yet failed to acquire food, probably because they were distracted from foraging by fighting, while others were able to feed successfully without fighting at all. The latter were able to obtain food by remaining

vigilant, in visual contact with the feeding site, and darting in and out quickly to intercept food items as soon they became available. There was a cost to feeding in the social context used in this study, in that high food intake was associated with high levels of received attacks, especially in fishes other than the top-ranking individual. This cost is presumably traded-off against the advantages of a high rate of food acquisition in determining the competitive mode adopted.

## Acknowledgements

This study was funded by BBSRC Project Grant number A01405. We would like to thank Vivien Cameron for fish husbandry, Liz Denton for preparation of the figures and two anonymous referees for very helpful comments on an earlier version of this article.

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