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AGGRESSION AND GROWTH OF ATLANTIC SALMON PARR.* I. DIFFERENT STOCKING DENSITIES AND SIZE GROUPS

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ABSTRACT

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The aggressive behaviour and growth of salmon parr under crowded rearing conditions was studied at four different densities. One or several fish per aquarium was dominant, displaying a kind of territorial defence and committing a significant part of the observed aggressive acts. Large subordinate fish were more aggressive than small fish at all densities. The ratio between the number of performed and received aggressive actions was about the same for large and small subordinate fish at the lowest density, but with increasing density this ratio became higher for large parr. Small fish grew slower than large fish at the highest density and suffered generally from a higher mortality. Factors other than aggression also seemed to influence growth, as both the growth rate and number of aggressive acts per fish decreased with increasing density.

INTRODUCTION

Parr of the Atlantic salmon (*Salmo salar* L.) are territorial under natural conditions (KEENLEYSIDE and YAMAMOTO 1962). The aggressive behaviour might be a negative factor in the cultivation of salmon parr.

A negative correlation between growth rate and density under crowded rearing conditions has been found in salmon (LINDROTH 1972, REFSTIE and KITTELSEN 1976), rainbow trout (BRAUHN, SIMON and BRIDGES 1976, KILAMBI,

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ADAMS, BROWN and WICKIZER 1977, REFSTIE 1977), and coho salmon (FAGERLUND, MCBRIDE and STONE 1981). It has often been assumed (e.g. REFSTIE and KITTELSEN 1976) that suppression of growth by aggressive behaviour was involved. BROWN (1946a) demonstrated that maximum growth in early stages of brown trout took place under moderate densities. Low densities led to suppressed growth of the smallest individuals, presumably due to some kind of social hierarchy, whereas there was a general suppression of growth at high densities. An optimum degree of crowding was also found in 2-year-old trout (BROWN 1946b).

The aggressive behaviour of salmon parr has earlier been studied in the laboratory (e.g. KEENLEYSIDE and YAMOMOTO 1962, FENDERSON and CARPENTER 1971), but until now, there has been no systematic study on the aggressive behaviour of salmon parr under the crowded conditions typical in aquaculture. The present study was therefore undertaken. The aggressive behaviour at different densities was investigated, and the aggressive activity of large and small parr was compared. The relationship between the aggressive behaviour and the growth rate was also studied.

MATERIALS AND METHODS

Second-generation hatchery-reared fish were used in the experiment. The eggs came from a commercial fish farmer at Hitra in middle Norway, and the parent fish originated from a river in the same area. The eggs were hatched in January 1975 at the field experiment station in Matre, near Bergen. The fish were about one year old at the start of the experiment in January 1976.

The aquaria were semi-oval fiber glass tanks with a glass front. The water inlet was on the backside, with an inflow of about 4 l/min, and the outlet was on the concave bottom. The bottom was covered with a perforated aluminium plate providing a horizontal floor of 4820 cm^2 level with the bottom of the window. The water depth was 40 cm, giving a volume of about 200 l. The temperature was around 10° C, and the oxygen saturation varied between 82 and 94%. The source of illumination was 100 W white fluorescent lights placed on top of each aquarium, and the photoperiod was 12 hrs starting at 0800 hours. The fish were fed to satiation by hand three times a day during week days, at 0830, 1200, and 1500 hours. On Saturdays the fish were fed only once, at 1200. No feeding was done on Sundays.

The aquaria were stocked at initial densities of 255 g (120 parr) at density A, 505 g (229 parr) at density B, 1005 g (393 parr) at density C, and 2000 g (878 parr) at density D. The initial length of the parr varied between 40 and 94 mm.

In order to distinguish large fish from small fish, all fish of the least 71 mm length were freeze-branded with liquid nitrogen on both sides of the body under the adipose fin. The estimation of growth rate of large and small parr was based directly on the freeze-branding. When comparing the aggressive activity, the fact that some of the unmarked fish had outgrown some of the marked fish, during the course of the experiment, had to be considered. The number of large fish in each aquarium was therefore defined as the mean between number of marked fish at the beginning of the experiment and number of marked fish plus number of unmarked fish larger than the smallest marked fish at the end of the experiment. Unmarked fish clearly larger than the smallest marked fish were recorded as «large» during the observations.

The observations of fish behaviour started three days after stocking. Observations were made four days a week for eight weeks. The experiment was then terminated, and the length and weight of the fish were recorded.

During the observations, the laboratory was in darkness. The observations began at 1000 hours. The aquaria were observed in rotation to avoid systematic errors. The observation time was 15 min/aquarium/observation day. This was divided into two periods: 10 min for observation of the whole aquarium and 5 min for observation of the special observation volume. This volume was delineated by two parallel lines 20 cm apart on the window pane and bottom at the center of each aquarium, All fish could be observed with reasonable accuracy in this restricted volume, and the reliability of the observations from the whole aquarium could in this way be estimated. The number of fish in the special observation volume was recorded before an observation. The observations were recorded on magnetic tape and later transcribed. The following aggressive behaviour patterns were recorded:

Attack – an approach towards another fish followed by a bite
Charge – an approach not followed by bite
Nip – a bite not preceded by an approch
Chase – at least two successive attacks towards a fleeing fish

Frontal and lateral displays (Keenleyside and Yamomoto 1962) were also observed, but it was not possible to record these behaviour patterns systematically under the high densities in the experiment.

RESULTS

AGGRESSIVE BEHAVIOUR

Aggressive behaviour patterns were observed relatively frequently with no systematic change in aggressive activity during the eight weeks of observation. The total number of aggressive acts per aquarium increased somewhat with increasing density (Table 1). The aggressive activity per fish was, however, highest at the lowest density and decreased markedly with increasing density.

Table 1. The aggressive activity at densities A–D (initial densities 255–2000 g per 200 l).

	Whole aquarium				Special observation volume			
Density	A	B	C	D	A	B	C	D
Total no. of aggressive acts	779	820	972	1279	220	236	224	314
Aggressive acts per fish per minute observation	0,023	0,012	0,008	0,005	0,067	0,040	0,021	0,017

Table 1 also shows the results from the observations in the special observation volume. The number of aggressive acts per fish in this volume was at all densities higher than in the observations from the whole aquarium. This was probably because passive fish had a tendency to cluster along the tank walls, but unrecorded aggression during observations of the whole aquarium may also contribute to this difference. The observation technique was, however, regarded as valid since similar tendencies were found for both types of observation.

A large number of fish could be observed simultaneously with reasonable accuracy because most fish kept their position, quietly tail-beating against the current. This made movements of single fish easily detectable. Only the observations of the total water volume are considered hereafter.

One or several dominant fish per aquarium could be distinguished during most observations. One fish could be dominant for several weeks, but could also be displaced by a challenger. Dominant fish were generally large and had a pale overall colouration with black vertical bands through the eyes.They defended a kind of territory in which the density of other fish was lower than elsewhere in the aquarium. A dominant often patrolled its territory from a position 5–10 cm above the bottom, but could also defend a territory higher up. In the lowest density, the dominant fish often defended the whole bottom area as its territory, but at higher densities some fish were usually present in the vicinity of a dominant without being attacked. Dominants seemed to selectively attack fish that moved.

At the lowest densities, there was usually one dominant fish (mean per observation = 1.1 in both A and B) committing 47% (A) and 17% (B) of the aggressive acts. At densities C ($\overline{x}$= 1.7) and D ($\overline{x}$= 1.9) there were often several dominants (up to four) committing respectively 7% and 25% of the aggressive acts.

Table 2 shows all observed aggressive acts by both dominant and subordinate fish. Of the different aggressive behaviour patterns, attacks were observed most frequently, followed by charges, nips and chases. With increasing density, attacks became relatively more frequent ($p<0.001$, chi-square test) and charges less frequent ($p<0.001$). The proportion of chases was highest at the lowest density ($p<0.001$). The mean intensity of the aggressive

Table 2. The number of different aggressive behaviour patterns between different categories of fish at densities A-D (initial densities 250-2000g per 200 l)

	Attack				Charge				Nip				Chase				Total			
Aggressor-Target	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Dom.-Dom.	12														1		12		1	
Dom.-Large	55	29	25	65	23	36	15	20	2				4	4		1	84	69	40	86
Dom.-Small	116	24	17	116	126	44	5	99	1	3		1	27	3		25	270	74	22	241
Large-Dom.	7	2	5	6	1		1										8	2	6	6
Small-Dom.	14	4	1	9			1		1		1						15	4	3	9
Large-Large	10	88	199	116	2	30	38	11	1	19	27	5		4	5	2	13	141	269	134
Large-Small	34	108	159	188	11	41	53	23	6	16	23	10		3	4	5	51	168	239	226
Small-Large	14	66	86	83	7	15	13	5	4	7	19	12	1	1	2	1	26	89	120	101
Small-Small	193	190	191	381	54	46	28	41	37	34	53	46	16	3		8	300	273	272	476
Sum	455	511	683	964	224	212	154	199	52	79	123	74	48	18	12	42	779	820	972	1279
% of total	58,4	62,3	70,3	75,4	28,8	25,9	15,8	15,6	6,7	9,6	12,7	5,8	6,2	2,2	1,2	3,3				

behaviour (regarding chase as the most intensive and charge as the least intensive behaviour patterns) was therefore not systematically changed with an increase in density.

Dominant fish had a tendency to make relatively more charges and chases (41% and 7% of all aggressive acts) than subordinate fish (14% and 2%, $p<0.001$, chi-square test), whereas the reverse was true for attacks and nips (dominant fish 51% and 1%, subordinate fish 73% and 11%, $p<0.001$).

There was also a significant difference between large and small subordinate parr in the relative occurrence of different behaviour patterns ($p<0.001$), with large parr performing more charges and small parr more nips. There was also a difference in the target of the aggressive actions of the different categories ($p<0.05$), with large parr receiving more attacks and small parr more chases and charges. All aggressive behaviour patterns will, in the following, generally be treated together.

Large fish constituted 13% (A), 24% (B), 41% (C) and 31% (D) of the total number of subordinate fish in the different densities. Large fish were generally more aggressive than small fish, and made 17% of the total number of aggressive acts of subordinate fish at density A ($p>0.10$, chi-square test), 46% at density B ($p<0.001$), 57% at density C ($p<0.001$), and 38% at density D ($p<0.001$).

Of the total number of aggressive acts aimed at subordinate fish at the different densities, large fish were the targets in 17% (A), 37% (B), 45% (C) and 25% (D). This means that large fish were attacked more than small fish at density B ($p<0.001$) and less at density D ($p<0.01$), whereas no significant difference was found at densities A and C. When all densities are regarded together, large and small fish were observed equally often to be the object of aggression, but there also seemed to be a tendency for small fish to be attacked relatively more with increasing density.

Table 3 shows the ratios between the number of performed and received aggressive acts of large and small fish. At the highest densities, small parr seemed to have a less favourable situation than large parr.

To get a better idea of the dominance relationship in the aquaria, it is important to know between which categories of fish aggression occurred most frequently (see Table 2). Dominant fish were seldom aggressive towards each other. Dominants directed more aggression towards large than small subordi-

Table 3. The ratio between the number of performed and received aggressive acts of large and small fish at densities A–D (initial densities 255–2000 g per 200 l).

	Density			
	A	B	C	D
Large fish	0.59	1.04	1.20	1.14
Small fish	0.55	0.71	0.74	0.62

Table 4. Growth and food utilization at densities A–D (initial densities 255–2000 g per 200 l).
$$\text{Food conversion factor} = \frac{\text{weight of feed (g)}}{\text{growth (g)}}$$

	Density			
	A	B	C	D
Total weight gain (g)	188	285	545	683
Relative weight gain (% of original weight)	73.7	56.4	54.2	34.2
Food conversion factor	2.0	2.4	1.7	2.1

nate fish at the three lowest densities (A: 24%, $p<0.05$, B: 48%, $p<0.001$ and C: 65%, $p<0.001$). No difference was found at the highest density (26%, $p>0.10$). Dominants also had a tendency to make more attacks towards large fish and more charges towards small fish ($p<0.01$).

Large subordinate fish were significantly more aggressive towards large fish at three of four densities, and directed 20% ($p>0.20$), 46% ($p<0.001$), 53% ($p<0.001$) and 37% ($p<0.05$) of the aggressive acts towards them at densities A–D. Small fish were generally more aggressive towards small fish, while directing only 8% ($p<0.05$), 25% ($p>0.90$), 31% ($p<0.001$) and 18% ($p<0.001$) of their aggression towards large fish at densities A–D, respectively.

GROWTH RATE AND MORTALITY

The total weight gain was highest at the highest density, and decreased with decreasing density (Table 4). When the growth is considered relative to the original weight (relative weight gain), the most rapid growth was found in the lowest density.

The specific growth rate of large and small fish is presented in Table 5. The growth rate was dependent on density ($p<0.001$, chi-square test), with small fish growing relatively slower with increasing density.

Table 5. The specific growth rate (G) of salmon parr at densities A–D (initial densities 255–2000 g per 200 l).
$$G = \frac{l_n Y_T - l_n Y_t}{T - t}$$
where Y_t = weight (g) at start of experiment, Y_T = weight (g) at end of experiment and T–t = time of experiment in days.

	Density			
	A	B	C	D
Large fish	0.93	0.78	0.76	0.56
Small fish	1.00	0.82	0.74	0.50

Table 6. The percent mortality of large and small parr at densities A–D (initial densities 250–2000 g per 200 l).

Density	Mortality, % Small fish	Large fish	Total
A	9.4	7.1	9.2
B	11.1	5.0	10.0
C	6.3	0.9	4.8
D	9.6	2.2	8.1

The total mortality was not significantly influenced by density (chi-square test, Table 6). Small fish suffered generally from a higher mortality than large fish, and a significant difference was found at densities C ($p<0.05$) and D ($p<0.001$). It was also the smallest fish within the group that died (mean length of dead unmarked fish was 50.1 mm versus 59.6 mm for the mean length of the whole group during the period). The eyes of small fish were often damaged, indicating aggression as the cause of death.

DISCUSSION

A relatively high rate of aggressive activity of salmon parr under crowded rearing conditions was found in this study. One or several fish per aquarium showed a kind of territorial defence although, with increasing density, other fish were accepted in the vicinity of the dominant. This finding is not in accordance with the observation by KALLEBERG (1958), who states that territoriality of salmon parr as a rule is not observed under crowded rearing conditions. The territorial defence observed in the present study may be enhanced by the small size of the aquaria. In larger tanks, the scarcity of points of reference could hinder establishment of territories.

Non-territorial fish also showed aggressive behaviour. Small parr displayed generally less aggressive activity than large parr. If the ratio between the number of performed and received aggressive acts is taken as a measure of the position of the fish in the social hierarchy, the results clearly show that the situation for small parr became less favourable with increasing density. A relationship between the aggressive behaviour and growth is indicated by the finding that, compared to large parr, the growth of small parr became slower with increasing density. Small parr also had a higher mortality than large parr. These observations are in agreement with a study on coho salmon (FAGERLUND *et al.* 1981), where crowding stress particularly affected the growth and stress level (measured as interrenal cell diameter) of small fish. This contrasts with the findings for brown trout (BROWN 1946a), where suppressed growth of small individuals appeared especially at low densities.

Although the total number of observed aggressive acts might seem to be high in the study, an individual fish was seldom the object of aggression due to the high number of fish (a mean of once every 44 to 204 min at the different densities). It could be questioned whether such a low frequency can influence growth, in view of the few aggressive encounters during feeding, an observation which invalidates direct competition for food when food is abundant. However, even such a low level of aggression could induce a level of stress leading to a decreased growth rate – mere visual contact with another fish could in fact influence growth, as demonstrated in *Blennius pholis* (WIRTZ 1975). Another possibility is that physical injuries from aggression depressed growth and increased mortality.

In this study both growth rate and the frequency of aggression per fish were highest at the lowest density. The decrease in growth rate with increasing density found in other studies (e.g. LINDROTH 1972, FAGERLUND *et al.* 1981) was therefore probably not caused by an increase in the level of aggression with increasing density. Factors other than the aggressive behaviour could suppress growth at high densities. One explanation for the present observations is that the water quality was negatively influenced by increases in density, as the inflow of water was the same in all aquaria. The oxygen saturation was, however, never below 82%, and should therefore not be a limiting factor for growth (SMART 1981). The concentration of ammonia nitrogen in the water was not measured. Another explanation is that high densities could have made it difficult for the fish to move and reach the food, as proposed by REFSTIE and KITTELSEN (1976). In the present study, the food utilization was not negatively influenced by an increase in density. Although the fish were fed «to satiation», feeding could apparently have continued for a longer time if food had been given in smaller quantities. This may apply especially to the highest stocking densities. The feeding procedure could therefore have influenced the difference in growth between the densities.

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