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International Council for
the Exploration of the Sea

C.M. 1976/E:37
Fisheries Improvement
Committee
Ref.: Anadromous and Catadromous Committee

AGGRESSION AND GROWTH OF ATLANTIC SALMON IN DIFFERENT STOCKING DENSITIES

by

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INTRODUCTION

Parr of the Atlantic salmon (Salmo salar L.) are territorial and defend some kind of feeding territory by a variety of aggressive actions (KALLEBERG 1958). This aggressiveness might be a negative factor in connection with cultivation of salmon parr. Even if the kind of territoriality seen under natural conditions is not observed under crowded rearing conditions, salmon parr nevertheless display several kinds of aggressive behaviour patterns under high densities as will be reported in the present study.

Aggressive behaviour of salmon parr in relation to density has earlier been studied under laboratory conditions. KEENLEYSIDE and YAMOMOTO (1962) compared the aggressiveness with 2 to 34 parr in aquaria of about 200 litres and found maximal aggression with 8 individuals present. An increase of aggression with increasing density was observed by FENDERSEN and CARPENTER (1971).

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However, in these two studies the investigated densities were considerably lower than the densities used in aquaculture.

Aggression in relation to density has to some extent also been studied in other species of fish. In the guppy (*Poecilia reticulata*) the aggressiveness increases with increasing density (WARREN 1973, FARR and HERRNKIND 1974). Among medaka (*Oryzias latipes*) and green sunfish (*Lepomis cyanellus*) the highest frequency of aggression occurs, however, at intermediate densities (MAGNUSON 1962, GREENBERG 1947).

A negative correlation between growth and population density in salmon parr has been found by LINDROTH (1972). However, using a wider variation in density, BROWN (1946 a) demonstrated that maximum growth in early stages of brown trout (*Salmo trutta*) was achieved under moderate densities. Low densities lead to a suppressed growth of the smallest individuals presumably due to some kind of social hierarchy while there was a general suppression of growth in connection with too high densities. An optimum degree of crowding was also found in 2-year-old trout (BROWN 1946 b).

So far, there has been no systematic study on aggressive behaviour of salmon parr under crowded rearing conditions. Therefore, the present study was undertaken. The investigation compares the aggressive behaviour under different densities, describes the distribution of aggressive actions between individuals of different size and attempts to correlate aggressiveness with growth.

MATERIALS AND METHODS

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

The aquaria used were semioval fiberglass tanks with a window pane (Fig. 1). The water inlet was on the back side with an inflow of about 4 l/min. and the water surface was kept in level with the inlet pipes. The outlet was at the concave bottom, which was covered with a perforated aluminium plate providing a horizontal floor of 4840 cm^2 in level with the bottom of the window. The water depth was 40 cm, thus giving a volume of about 200 l. The temperature was $10 \pm 0,2^{\circ}$ C and the oxygen saturation varied between 82% and 94%. The photoperiod was 12 hours starting at 8.00 a.m. and the source of illumination was 100 W white fluorescent lights placed on top of each aquarium.

The aquaria were stocked with 255 g (120 parr) in density A, 505 g (229 parr) in density B, 1005 g (393 parr) in density C and 2000 g (878 parr) in density D. The initial length of the parr varied from 40 to 94 mm. In order to distinguish large fish from small fish all fish $\geq$ 71 mm were cold branded with liquid nitrogen on both sides under the adipose fin.

The fish were fed to satiation by hand three times a day during week days at approximately 8.30 and 12.00 a.m. and 3.00 p.m. On Saturdays the fish were fed only once at about 12.00 a.m., while no feeding was made on Sundays.

The observation time was 10 min/aquarium/day for the whole aquarium and 5 min/aquarium/day for the special observation area. This area (Fig. 1) was limited by two parallel lines on the window pane and on the bottom at 20 cm distance from each other. The observations from the special areas were made because here the observer could watch all fishes with reasonable accuracy,and the reliability of the observations from the whole aquaria with high numbers of fishes present could in this way be estimated. The observations started at 10.00 a.m. and the aquaria were observed in a rotating order to avoid systematical errors. The fishes were observed by the same person 4 days a week for 8 weeks. During the observations the laboratory was in darkness to prevent the fishes from being disturbed. The observations were recorded on magnetic tape and later transcribed.

The aggressive behaviour was recorded as follows:

Attack - an approach towards another fish followed by a bite

Charge - an approach not followed by a bite

Nip - a bite not preceded by an approach

Chase - a succession of at least two attacks towards the same fleeing fish.

The general behaviour and positions in the tanks especially of dominant fishes were also recorded. Frontal display was frequently observed while lateral display was observed more seldom. It was not possible to record these behaviour patterns systematically under the high densities of the experiment.

Standard methods (e.g. SOKAL and ROHLF 1969) were used for calculating X^2.

RESULTS

Aggressive behaviour

The number of aggressive actions per fish was greater in the special area than in the whole aquarium (Table 1). This is considered to be due to that there actually occurred most aggression in the middle of an aquarium. The tendencies in the material were similar to the observations of the special area and the whole aquarium which proves the validity of the observation technique. In this context no further data from the observations of the special area will be presented. It was possible to observe the behaviour of that many fishes simultaneously because the fish were mostly standing rather motionless making the movements of single fishes easily detectable.

The total number of aggressive encounters increased somewhat with increasing density (Table 1). When the number of fish per aquarium is taken into account, it appears that the frequency of aggression per individual was highest in the lowest density and decreased markedly with increasing density.

Table 1. Comparison of the number of aggressive actions between different densities in the whole aquarium and the special area.

	Whole aquarium				Special area			
Density	A	B	C	D	A	B	C	D
Total No. of aggressive actions	779	820	972	1279	220	236	224	314
Aggressive actions per fish and minute of obser- vation	0,0229	0.0124	0.0082	0.0049	0.0669	0.0401	0.0208	0.0169

Although aggressive behaviour patterns were often observed during the observation periods, there seemed to be few aggressive en- counters during feeding. This speaks against direct competition for food, when food is abundant.

It was possible to distinguish one or several dominant indivi- duals during most of the observation periods. These fishes defended a kind of territory and the density of other fish was lower in the vicinity of a dominant fish than elsewhere in the aquarium. A volume of some dm^3 could be completely devoid of other fish. Especially with increasing density, however, some fishes were usually present in the vicinity of a dominant without being attacked. Dominant fishes were often swimming around in the territory in contrast to the relative immobility of the other fishes which were generally standing tail-beating against the current at the same spot. Dominants were also characterized by a great number of attacks performed and a low number of attacks received.

The dominant fishes were often standing 5 - 10 cm above the bottom but could also defend a territory elsewhere in the water volume. If more than one individual defended a territory in the same aquarium, these dominants were seldom aggressive towards each other. They could have territories in different areas near the bottom but also in different levels. A certain fish, often the largest individual, was often dominant for several weeks defending the same place but new individuals could also become dominant. Due to the difficulty to distinguish individuals among the great number of fishes present, these observations could not be carried out systematically.

In the lowest density (A), there was during most of the observation periods one dominant fish ($\bar{x}$ = 1,13) and dominants performed no less than 47% of the total number of aggressive actions (Table 2). In the next density (B), there was also most of the time one dominant fish ($\bar{x}$ = 1,10) making 17.4% of the aggressive actions. In density C, a mean of 1,74 dominant fishes made 6,5% of the aggressive actions, while in the highest density (D) a mean of 1,90 dominant fishes made 25,6% of the aggression.

Table 2. Number of observed aggressive behaviour patterns between different categories in different densities.

	Attacks				Charges				Nips				Chases				Total number of aggressive actions			
	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
																	779	820	972	1279

It is also of great interest to compare the aggressive activity of large and small nondominant fish. The number of large fish in each density was defined as the mean of the number of cold branded fish in the beginning of the experiment, and the number of branded fish together with the number of unmarked fish of the same size at the end of the experiment. Unmarked individuals as large as the smallest branded fishes were recorded as large during the observations. The percentages of large nondominants of the total number of not dominant fish in densities A, B, C and D were 13,3, 24,4, 40,6 and 30,6 respectively. The corresponding percentages of aggressive actions made by large nondominants of the total number of aggressive actions made by not dominant fish were 17,4 for density A ($p > 0,10$), 45,9 for density B ($p < 0,001$), 56,5 for density C ($p < 0,001$) and 38,4 for density D ($p < 0,001$). Consequently, it seems as if large fish were generally somewhat more aggressive than small fish.

Dominant fish were seldom objects of aggressive actions (Table 2). Of the total number of aggressive actions against not dominant fish, large nondominant fish were attacked in 16,5% (A), 36,7% (B), 44,6% (C) and 25,4% (D). This means that large fish were attacked more than small fish in density B ($p < 0,001$) and less in density D ($p < 0,01$), while there was no difference in densities A and C ($p > 0,10$). If all densities are considered together, the risk to be the object of an aggressive action is consequently about the same for a small and for a large fish.

In order to get a more accurate idea of the dominance relationship it is essential to know between which categories of fish aggression occurs most frequently. Dominants almost never attacked each other (Table 2). 23,7% of the aggressive actions by dominants towards nondominant fish were directed at large fish in density A ($p < 0,05$) add the corresponding figures for density B and C were 48,3% ($p < 0,001$) and 64,5% ($p < 0,001$). In these densities, dominants made more aggressive actions against large fish than they would do if aggression was directed at fish irrespective of size. In density D, 26,3% of the attacks were directed at large fish constituting 31% of the total number of fish ($p > 0,10$).

Large not dominant fish were generally significantly more aggressive towards large than towards small fish and directed 20,3% ($p > 0,20$), 45,6 ($p < 0,001$), 53,0% ($p < 0,001$) and 37,2% ($p < 0,05$) of the aggression towards large fish in densities A - D. Small fish were generally more aggressive towards small than towards large fish and directed only 8,0% ($p < 0,05$), 24,6% ($p > 0,90$), 30,6% ($p < 0,001$) and 17,5% ($p < 0,001$) of the aggression towards large fish in densities A - D.

Of the different aggressive actions, attacks and charges were observed most frequently (Table 2). Dominants had an obvious tendency to perform charges. If all densities are considered together, dominants performed 1,25 times as many attacks as charges while large fish made 4,37 and small fish 5,87 times as many attacks as charges.

Growth rate and mortality.

The maximum total weight gain during the experiment was found in density D and became less with decreasing density (Table 3). However, when the growth is considered in relation to the original weight, the population in density A grew most rapidly. The efficiency of food utilization (gross efficiency) was highest in density C.

Table 3. Growth and utilization of food in different densities during 10 weeks.

Density	A	B	C	D
Total weight increment in g	188	285	545	683
Relative weight gain (% of original weight)	73,7	56,4	54,2	34,2
Gross efficiency	0,49	0,41	0.59	0,48

Large fish had a greater absolute weight gain than small fish. If the specific growth rates of marked and unmarked fish are compared (Table 4), it appears that small fish grew as fast as large fish.

Table 4. Specific growth rate (G) based on changes of mean individual weights of large and small fish in different densities.

$$G = \frac{\log Y_T - \log Y_t}{T - t} \times 100$$

$\log Y_T'$ = weight at start
$\log Y_t$ = weight at end of experiment
$T - t$ = time of experiment (8 weeks)

Density	A	B	C	D
Large fish	8,38	6,73	6,49	5,09
Small fish	8,47	6,96	6,24	4,56

Small fish suffered from a higher mortality than large fish (Table 5). The difference is significant if the densities are considered together ($p < 0,001$). The eyes of small fish were often damaged indicating aggression as a cause of death. Fishes still alive but with damaged eyes were repeatedly observed.

Table 5. Mortalities of large and small fish in different densities.

	Small fish ≤ 70 mm		Large fish ≥ 71 mm	
Density/ aquarium	Number at start	Number of dead	Number at start	Number of dead
255 g (A)	106	9	14	1
505 g (B)	189	21	40	2
1005 g (C)	287	18	106	1
2000 g (D)	697	67	181	4
Total	1279	115	341	8

DISCUSSION

The finding that some individuals of salmon parr defend a kind of territory even under high population densities is not in accordance with the suggestion of KALLEBERG (1958) that territoriality of salmon parr as a rule is not observed under crowded rearing conditions. Under the conditions of the present study, we observed an incomplete territorial defence as the territory holder often accepted other fish in the territory. The reason for the relatively weak defence of the territory is possibly a habituation of the aggressive response of a dominant fish. THORPE (1963) defined habituation as "the relative permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement". In our case a dominant fish could not effectively chase away other fish from the territory and a reinforcement in connection with an aggressive action may therefore be lacking. Dominants also had a tendency to perform the behaviour pattern 'charge' which can be looked upon as a partially habituated incomplete response to repeated stimulation. In other words, the presence of multiple stimuli may have an inhibiting or confusing effect on the directed attacks of the dominants, as proposed by MAGNUSON (1962) for similar findings in the medaka.

Small fish were generally not objects of aggressive actions more often than large fish, even if large fish were somewhat more aggressive than small fish. The specific growth rate of small fish was not different from that of large fish, and this is in contrast to the findings of BROWN (1946 a, b) in the brown trout. However, the small fish in the present experiment suffered from a considerably higher mortality than the large fish. This effect can evidently not be correlated with the number of attacks directed against small fish, and the possibility therefore exists that open aggressiveness does not have a very strong influence under the densities in question. An attack from a larger fish could, however, influence an individual more than an attack from a smaller fish or a fish of equal size because of a greater risk of damage. Even if the small ones are not attacked more often than the large ones, attacks from large fish might inhibit small fish more than large ones because of some kind of psychological stress effect. BROWN (1946a) proposed psychological stress as an explanation of poor growth of small brown trout fry. We did not find any significant differences in growth between small and large fish, but some negative effect of aggression is obviously present leading to a higher mortality among the small fish.

The size hierarchy concept by BROWN (1946) implies that some kind of hierarchy should exist under rearing conditions. A prerequisite to a true hierarchy is that the fish should know each other individually and this is not likely under the crowded conditions in our experiment. No hierarchy based on open aggressiveness seemed to exist as small fish were not attacked more often than large fish and as the fish generally were aggressive within their own size category, which also was reported by SYMONS (1968).

SUMMARY

(1) In densities of 120-878 salmon parr inn 200 l aquaria the maximum number of aggressive actions per fish was found in the lowest density.

(2) One or several large fishes in each aquarium showed a kind of incomplete territorial defence. Such dominants made a significant part of the aggressive actions especially in the lowest density, and were particularly aggressive towards large not dominant fish.

(3) Large not dominant fish were somewhat more aggressive than small fish. Large and small fish were, however, equally often the objects of aggressive actions by other fish and tended to be aggressive within their own size cathegory.

(4) The gain in weight in percent of initial weight was greatest in the lowest density, while the gross efficiency was highest in the second highest density. The specific growth rate of large fish was about the same as for small fish. Small fish suffered, however, from a considerably higher mortality.

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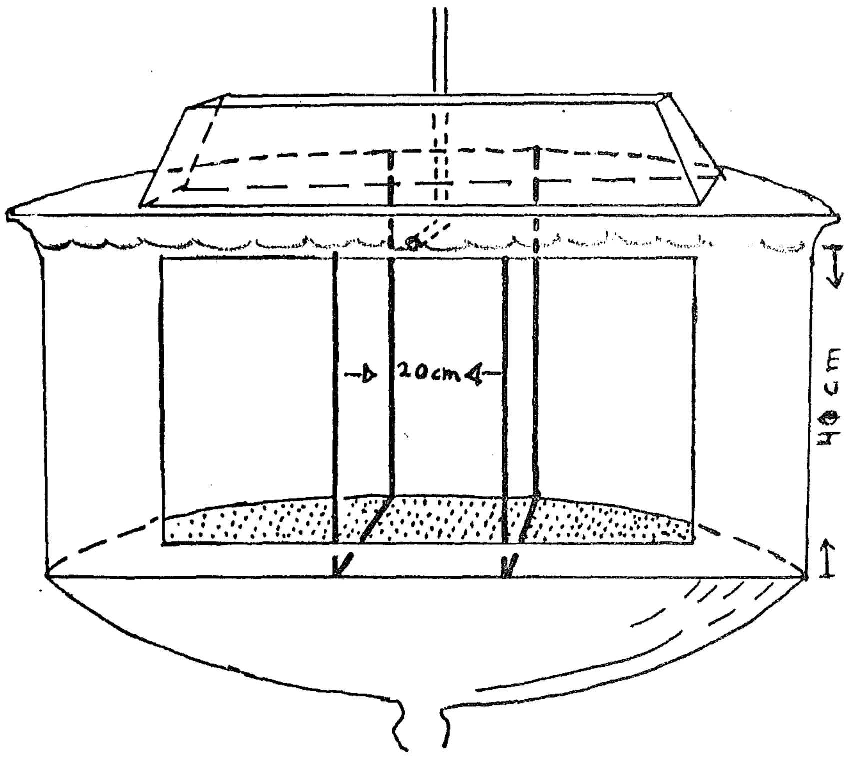

Fig. 1. Experimental tank. Parallell lines (the thick lines in the figure) painted on the front glass, the bottom and on the back wall limited the special observation area.