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Tittel:
AGGRESSIVE BEHAVIOUR OF TWO SIZE CLASSES OF FOUR SALMONID SPECIES

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Sammendrag:
Groups of eight parr of hatchery reared Atlantic salmon (*Salmo salar*), sea trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*) were investigated in monoculture with two size groups of fish. Aggression was assessed by recording seven behavioural patterns: Approach and body-bending, lateral display, charge, chase, bite, frontal display, and fight.

Aggression between fish of different size showed one step in a hierarchy where larger fish were most aggressive in all species. Most aggression occurred between fish of similar size. Atlantic salmon most frequently showed charge, bites and intention movements. Sea trout showed most of intention movements and frontal display. Rainbow trout performed charge and bite most frequently, and intention movements and chasing secondly. Body-bending was typically performed by rainbow trout, and this pattern was often intentionnally showed in advance of charge. Arctic charr performed charge, bite and chase at a similar frequency.

Emneord - norsk:
1. Laksefisker
2. Enkeltkultur
3. Aggressiv atferd

Emneord - engelsk:
1. Salmonids
2. Monoculture
3. Aggressive behaviour

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I. INTRODUCTION

The aim of this study was to observe different aggressive behaviour patterns, estimate the frequencies of these patterns and to compare the frequencies of different behaviour patterns among the four species and two sizes of fish. This can predict probable competitive effects of the four phylogenetically related species, and provide scientist and fish farmers with more knowledge about these salmonid species at the juvenile stage.

This experiment was conducted and further developed in accordance with reports on aggression of comparable juvenile salmonid species. Keenleyside and Yamamoto (1962) observed the territorial behaviour of Atlantic salmon. Kalleberg (1958) observed territoriality and competition in Atlantic salmon and trout. Fabricius (1953) and Fabricius and Gustafson (1954) experimented with Arctic charr at the spawning stage. The behaviour of juvenile Kamloops rainbow trout was reported by Stringer and Hoar (1955), and further work on rainbow trout was done by Newman (1956), Hartman (1965) and Jenkins (1969).

This fundamental work of quantifying behaviour was done by recording different behaviour patterns.

It is known that behavioural patterns of small fish can be suppressed by larger conspecifics (Brown, 1946 ab; Stringer and Hoar, 1955; Newman, 1956; Chapman, 1962; Yamagashi, 1962; Fenderson et al., 1968; Symons, 1968; Jenkins, 1969), and this can have effects on growth.

II. MATERIALS AND METHODS

The investigation was conducted at the Institute of Aquacultural Research at Sunndalsøra. Two 1-m^2 rectangular fibreglass tanks were equipped with a plexiglass window for observation. Direct observation of records were made between 10 am and 3 pm.

Lighting and feeders were put on between 4 am and 12 pm. The feeding interval was 7.5 minutes, and the fish were fed in excess with dry pellets. The water passed through a vertically perforated pipe, giving a uniform and circular flow. The water velocity was 7.5 cm per second at the periphery, and the water level was maintained at 34 cm. The water temperature was 12-14^{o}C, and the light intensity was 200 lux at the water surface.

The fish used were progeny of wild Atlantic salmon, sea trout, Arctic charr and domesticated rainbow trout. Each experimental group contained eight conspecific fish, four of each size. Two sizes of fish were used, 7±1 g and 14±1 g, classified as small and large, respectively. Observations were done on duplicate groups of the progeny of the wild fish and on triplicate groups of rainbow trout.

Behavioural patterns recorded are listed in table 1. Except for body-bending, classifications are in accordance with Keenleyside and Yamamoto (1962) and Stringer and Hoar (1955). The aggressive behaviour of each species was classified in six behaviour patterns.

The fish were studied after one to three days of acclimatization. Total aggressive activity (sum of aggression) was calculated as the sum of all behaviour patterns recorded per hour. The observation time was 17,12,16 and 20 hours for Atlantic salmon, sea trout, rainbow trout, and Arctic charr respectively.

The sum of aggression was recorded in three categories, between fish of even size, small fish towards larger fish and large fish towards smaller fish. Comparisons between aggressive activity recorded in size categories were evaluated by a t-test. Statistical significance was classified: $P \leq 0.05$.

III. RESULTS.

Each of the six behaviour patterns in each species contributed with different frequency to the total aggressive activity

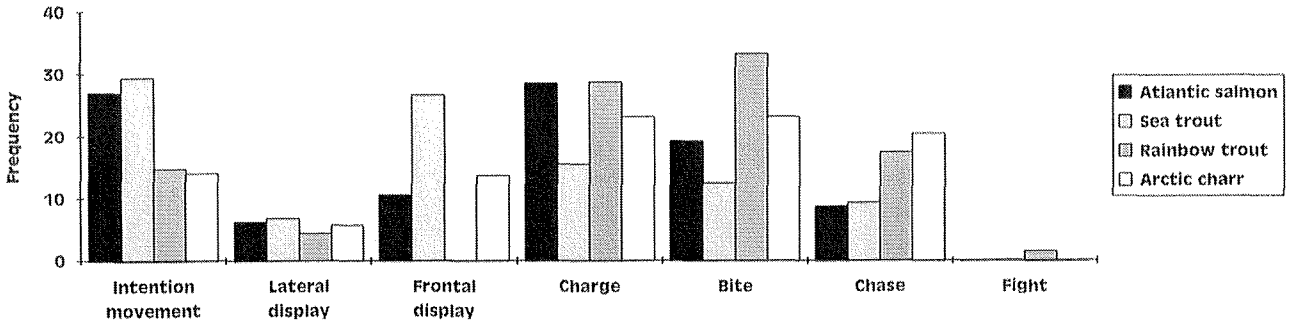

FIGURE 1. *Frequencies of different behaviour patterns in the four species as part of the total aggressive activity.*

Salmon showed most frequently intention movement, charge and bite. The three most frequent behaviour patterns in sea trout were intention movement, frontal display and charge. The aggressive behaviour of Arctic charr was contributed by five patterns, only lateral display had a low mean frequency. The three highest frequencies were charge, bite and chase.

Two main frequency groups of behaviour were evident in the rainbow trout groups: charge and bite, and intention movement and chase. The rainbow trout was peculiar in that it put together "body-bending" behaviour into a circle dance. Frontal display was never observed and was replaced by charge. "Body-bending" behaviour was generally followed by a charge or frontal display and was interpreted as an intention movement. For all species, aggression between fish of similar size was significantly more common than aggression by large fish towards smaller fish ($P \leq 0.05$, Fig. 2). Aggression between even sized fish was of greater frequency than that of small fish towards larger fish in sea trout and rainbow trout ($P \leq 0.05$). Large fish of all species, except salmon, were

significantly more aggressive towards smaller fish than vice versa ($P \leq 0.05$). Total aggressive activity per hour showed species ranking as follows ($P \leq 0.05$): (Arctic charr = rainbow trout) > (Atlantic salmon = sea trout).

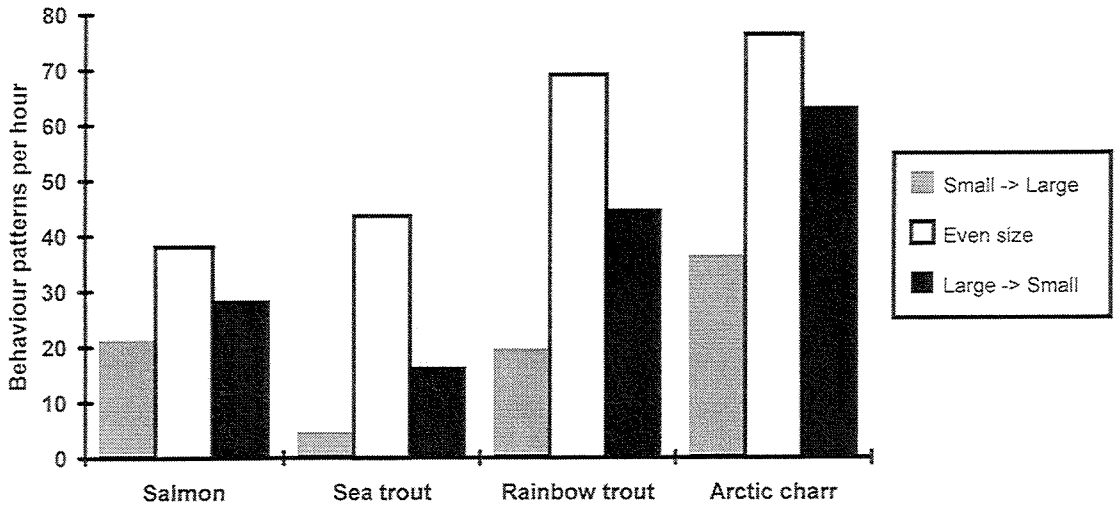

FIGURE 2. *Percentage of total aggression between fish of different size classes. Large -> small and Small -> large = aggressive acts of larger fish towards smaller fish and vice versa. Even size = aggressive acts between fish of equal size.*

IV. DISCUSSION

The aggression of salmon was often dependent on having obtained an area and thereby defending a territory. The most common behaviour patterns were charge, bites and intention movements. Keenleyside and Yamamoto (1962) differentiated between dominant and non-dominant fish. Dominant salmon were generally most aggressive showing charge, bite, chase and frontal display. Non-dominant salmon showed mostly lateral display. The decreasing frequencies from charge, bite to chasing is in accordance with the fact that these patterns demand an increasing aggressional motivation to be expressed (Baerends et al.,1955, Keenleyside and Yamamoto, 1962).

Sea trout also showed decreasing frequencies from charge, bite to chasing, but the differences were not so marked.

Intention movements and frontal display were frequently observed, while bite was less frequent. Hartman (1963) observed more bites than displays with more rapid streamflow.

Rainbow trout performed charge and bite most frequently, and intention movements and chasing secondly. Stringer and Hoar (1955) found bite and chase as major patterns in Kamloops rainbow trout. Bite was the most frequent aggressive pattern in rainbow trout in this experiment, and this corresponds well with Stringer and Hoar (1955). Hartman (1965) found that steelhead trout (rainbow trout) showed primarily lateral displays, nips and chases.

The term "threat" has been used by Stringer and Hoar (1955) for a similar behaviour pattern as "body-bending" in rainbow trout. Body-bending as an intention movement was frequently followed by charge in rainbow trout. Salmon, sea trout and charr instead showed frontal display following body-bending.

Arctic charr performed charge, bite and chase fairly at a similar frequency, which may indicate that the releasing threshold of these patterns are rather similar. In Arctic charr, in contrast to salmon and sea trout, it was difficult to distinguish between charge and frontal display,

Although Arctic charr showed a high frequency of total aggressive activity, it is probably not correct to compare this species with rainbow trout, since rainbow trout exposed aggressive behaviour very easily in a hard manner.

The intention of using large and small fish in this study was to investigate one step within the size hierarchy that usually develops in concentrated groups of salmonids. Size hierarchy has been studied in several salmonid species (Brown, 1946ab; Stringer and Hoar, 1955; Keenleyside and Yamamoto, 1962; Yamagashi, 1962; Symons, 1968; Chiszar et al.,1975; Fernø and Holm, 1986). In general, hierarchical rank seems to be correlated with size. The tyrannical nature of fish in small groups has the effect of producing some extremely aggressive individuals (Newman, 1956; Yamagashi, 1962; Chiszar et al., 1975). The observations revealed that rainbow trout, and to a lesser degree salmon and trout, showed tyrannical dominance.

Clearly, the highest levels of aggression occurred between fish of the same size in all species. This is in agreement with Newman (1956) and Symons (1968). Symons (1968) reported a stronger hierarchy when juvenile salmon were deprived of food. The results of the present study show that hierarchy developed even when fish were fed in excess.

Intraspecific dominance could favour the dominant fish allowing it to grow more rapidly than subordinates, but could at the same time cause an overall growth depression (Brown, 1946 a; Newman, 1956; Kalleberg, 1958; Magnuson, 1962; Yamagashi, 1962; Symons, 1968; Li and Brocksen, 1977; Jobling and Wandsvik 1983; Abbot et al., 1985; Koebele, 1985).

When using two size classes of fish one could expect frequencies of aggression in accordance with these sizes, but aggressional frequencies were often intermediate. This was concurrent with the fact that small fish could show considerable aggression towards large fish. Thus, dominance could be associated with both costs and benefits to an individual fish (Pitcher, 1986), with the resulting dominance depending on the situation and with the property of the fish.

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1 TABLE. *Behaviour patterns recorded.*

Type of display	Movement and position
1. Intention movement	
1a. Approach	Initiator swims slowly towards another fish and stops.
1b. Body-bending	The fish position is partly parallel with opponent, while anterior and posterior parts of the fish are curved close to the opponent. The back is tilting away from the opponent.
2a. Lateral display	One or two fish are positioned with the flank towards another individual. The back is often tilting towards the opponent.
2b. Wigwag display	The fish swims away from another fish with back-profile concave and the body moving in a wriggling fashion.
3. Frontal display	Initiator swims towards opponent with an arched back profile (in salmon, sea trout and charr).
4. Charge	Initiator swims rapidly towards another fish.
5. Bite	A snap against an opponent with or without contact.
6. Chase	A fish darts towards another fish and pursues it.
7. Fight	A circle dance (in rainbow trout).