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Tittel:
AGGRESSIVE BEHAVIOUR OF FOUR SALMONID SPECIES IN DUOCULTURE

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Sammendrag:

Aggressive behaviour of groups of eight parr in different species combinations was studied to investigate the potential of duoculture in rearing of salmonids. The species used were Atlantic salmon (*Salmo salar* L.), sea trout (*Salmo trutta* L.), Arctic charr (*Salvelinus alpinus* L.) and domesticated rainbow trout (*Oncorhynchus mykiss Walbaum*). Aggression was assessed by recording seven behavioural patterns.

The dominant species in each duocombination can roughly be deduced from decreasing aggressive potential in the following ranking: 1. Rainbow trout (high); 2. Sea trout; 3. Atlantic salmon; 4. Arctic charr (low).
Each combination was investigated within and between species as: relative interspecific and intraspecific aggression, size hierarchy effect, and general characteristics of each combination.

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

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

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Prosjektleder

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I. INTRODUCTION

Polyculture of fish is common in carp farming in Asia, where two or more species using different feeding niches, are given favourable feeding conditions to improve quantitative, qualitative and economic production in comparison with monoculture (Huet, 1975; Pillay, 1993).

Also under intensive rearing conditions, duocultures of fish can decrease intraspecific aggression and stimulate growth (Nortvedt and Holm, 1991). Increased growth occurs even when the possible niches are limited, as in a rearing tank (Mork, 1982; Holm, 1988). The goal of the present study was to compare aggressive behaviour in two size classes of Atlantic salmon, sea trout, Arctic charr and rainbow trout, in duoculture, so as to find the most suitable combination of species for productive fish farming.

II. MATERIALS AND METHODS

The investigation was conducted at the Institute of Aquaculture Research (AKVAFORSK) at Sunndalsøra. Two 1-m^2 rectangular fibreglass tanks were equipped with a plexiglass window for observation. For more detailed information on experimental conditions, see Mork (1995, submitted). The fish used were progeny of wild Atlantic salmon , sea trout, Arctic charr and domesticated rainbow trout. Two sizes of fish were used, 7±1 g and 14±1 g, classified as small and large, respectively. Each duoculture group consisted of two small and two large individuals of each of two species. The fish were taken from rearing tanks, of the same size as used in the experiment. The fish were fed to satiation each day with commercial dry pellets delivered every 7.5 minutes for 20 h per day, using automatic feeders. Observations were made between 10 am and 3 pm, and total observation time was 8-27 hours in the different combinations. Number of replicates were 2-5. The behaviour patterns recorded were:

1. *Intention movements* (Approach and body-bending)
2. *Lateral display* (including wigwag display)
3. *Charge*
4. *Chase*
5. *Bite*
6. *Frontal display* (not in rainbow trout)
7. *Fight* (only in rainbow trout)

For definitions of the behaviour patterns, see Mork (1995, submitted).

Each species showed six behavioural patterns. Total aggressive activity was calculated as the sum of all behaviour patterns. The sum of aggression was recorded in three categories, between fish of the same size, small fish towards large fish and vice versa. Comparisons of aggressive activity between size categories and between species were made by t-tests.

III. RESULTS

The four species showed roughly decreasing aggression in the following order: 1. Rainbow trout (high); 2. Sea trout; 3. Atlantic salmon; 4. Arctic charr (low). Interspecific dominance and its corresponding interspecific part of total aggression within a species conformed with each other in all groups, except in the combination of sea trout-rainbow trout. (Table 1).

TABLE 1. *Dominance. Comparative interspecific aggression and part of aggression shown between species in duoculture. (Frequency means)*

	Interspecific fraction a)	Between species aggression b)	Intraspecific fraction c)
Salmon (1)	30	33.5	74
Sea trout (2)	70	77.5	26
Salmon (1)	22.5	60	23
Rainbow trout (2)	77.5	60.5	77
Salmon (1)	71.5	72	24.5
Arctic charr (2)	28.5	24.5	75.5
Sea trout (1)	46	80.5	11
Rainbow trout (2)	54	37.5	89
Sea trout (1)	72.5	65.5	57
Arctic charr (2)	27.5	49	43
Rainbow trout (1)	75.5	61.5	71.5
Arctic charr (2)	24.5	56	28.5

a) *Interspecific fraction*, comparison of the aggressive behaviour between species, calculated as

$$\frac{X_{1.er}}{X_{1.er} + X_{2.er}} * 100$$

b) *Between species aggression*, interspecific aggression as part of total aggression in each species, calculated as

$$\frac{X_{1.2er}}{X_{1.2er} + X_{1.2ra}} * 100$$

c) *Intraspecific fraction*, comparative part of intraspecific behavior between two duospecies, calculated as

$$\frac{X_{1.ra}}{X_{1.ra} + X_{2.ra}} * 100$$

X_{er} = frequency mean of interspecific aggression. X_{ra} = frequency mean of intraspecific aggression

Salmon + sea trout

Sea trout were more aggressive than Atlantic salmon within the different size categories ($P<0.01$, Figure 1). Size hierarchy relations developed between species as well as between conspecifics (Figure 2). Salmon directed most of its aggression towards conspecifics, whereas interspecific aggression was predominant in trout (Table 1).

Salmon + rainbow trout

Generally, rainbow trout showed more interspecific aggression than salmon ($P<0.01$, Figure 1, Table 1). Both species showed more aggression towards the other species than between conspecifics (Table 1). Salmon showed no size hierarchy between conspecifics, while larger fish were dominant in rainbow trout ($P<0.05$, Figure 2).

Salmon + Arctic charr

Salmon was the most aggressive species (Figure 1) when considering aggression between large fish ($P<0.01$) and between small fish of even size ($P<0.05$, Table 1). This was consistent with salmon, which used most of its aggression against charr (Table 1). There were no size hierarchy effects between conspecifics (Figure 2).

Sea trout + rainbow trout

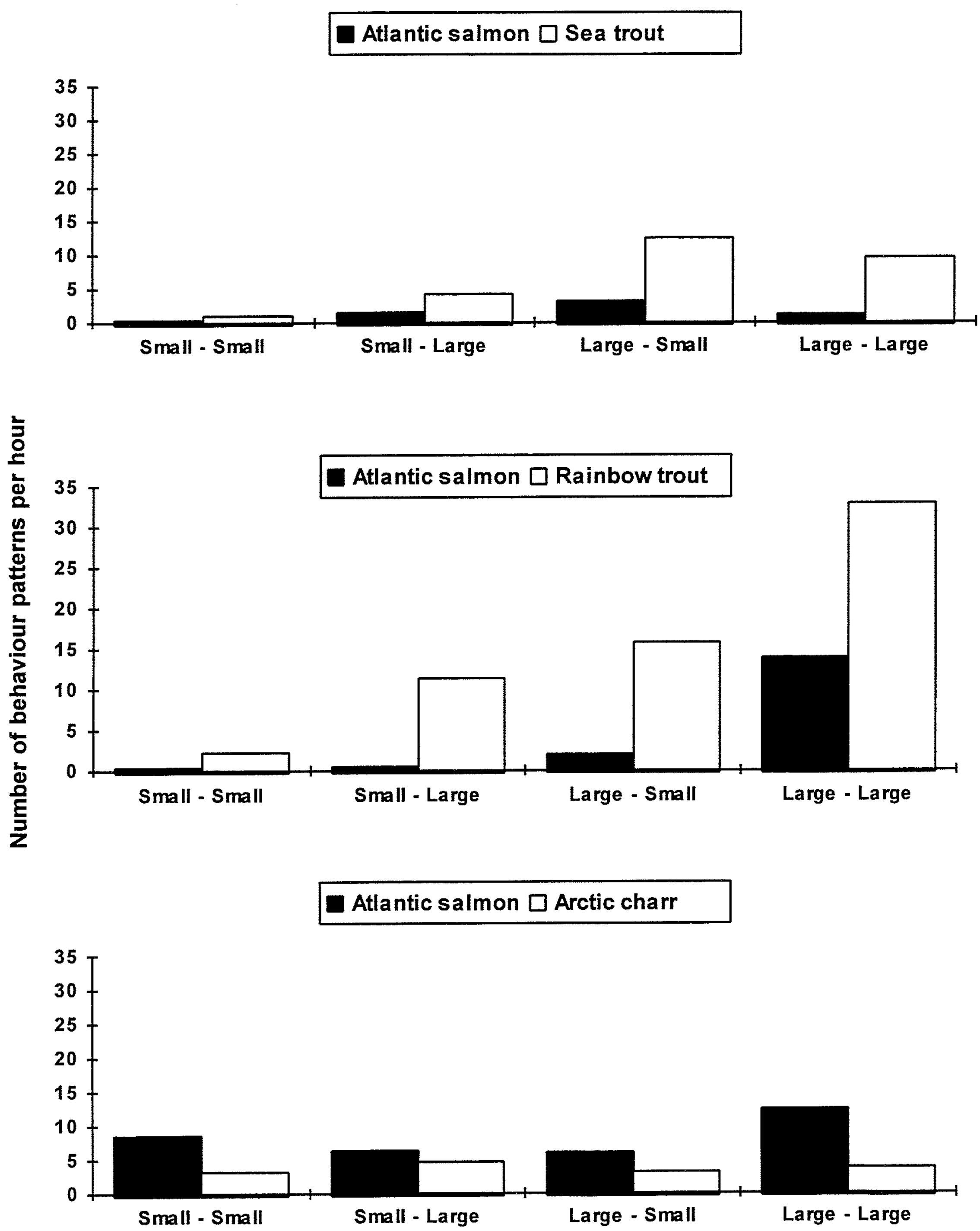
Large rainbow trout showed more frequent interspecific aggression towards small sea trout than large sea trout did towards small rainbow trout ($P<0.01$, Figure 1). On the other hand, small sea trout were more aggressive towards large rainbow trout than small rainbow trout were towards large sea trout. There were no differences in aggression between species of equal size. Generally, sea trout directed most of their aggression towards rainbow trout (Table 1), while rainbow trout were predominantly aggressive towards each other. Intraspecific aggressivity showed a normal one step size hierarchy, as larger fish dominated small fish in both species (Figure 2). Intraspecific aggression in rainbow trout was more frequent than in sea trout (Table 1).

Sea trout + Arctic charr

Large sea trout were significantly more aggressive towards large charr than the reverse ($P<0.05$, Figure 1). There was no significant difference interspecifically in aggression from large fish towards small fish. However, small sea trout were more aggressive towards large charr than small charr were against large sea trout. While sea trout showed a significant difference between large and small conspecifics, this was not the case for charr (Figure 2). Trout also directed most of its aggression towards interspecifics ($P<0.01$, Table 1).

Rainbow trout + Arctic charr

Rainbow trout displayed more interspecific aggression than charr in most size relations (Figure 1), except between small fish. Rainbow trout also showed most of its total aggressive activity towards interspecifics (Table I). Both species had a size hierarchy between conspecifics (Figure 2).


Atlantic salmon
Sea trout
Atlantic salmon
Rainbow trout
Atlantic salmon
Arctic charr
Number of behaviour patterns per hour
0
5
10
15
20
25
30
35
Small - Small
Small - Large
Large - Small
Large - Large

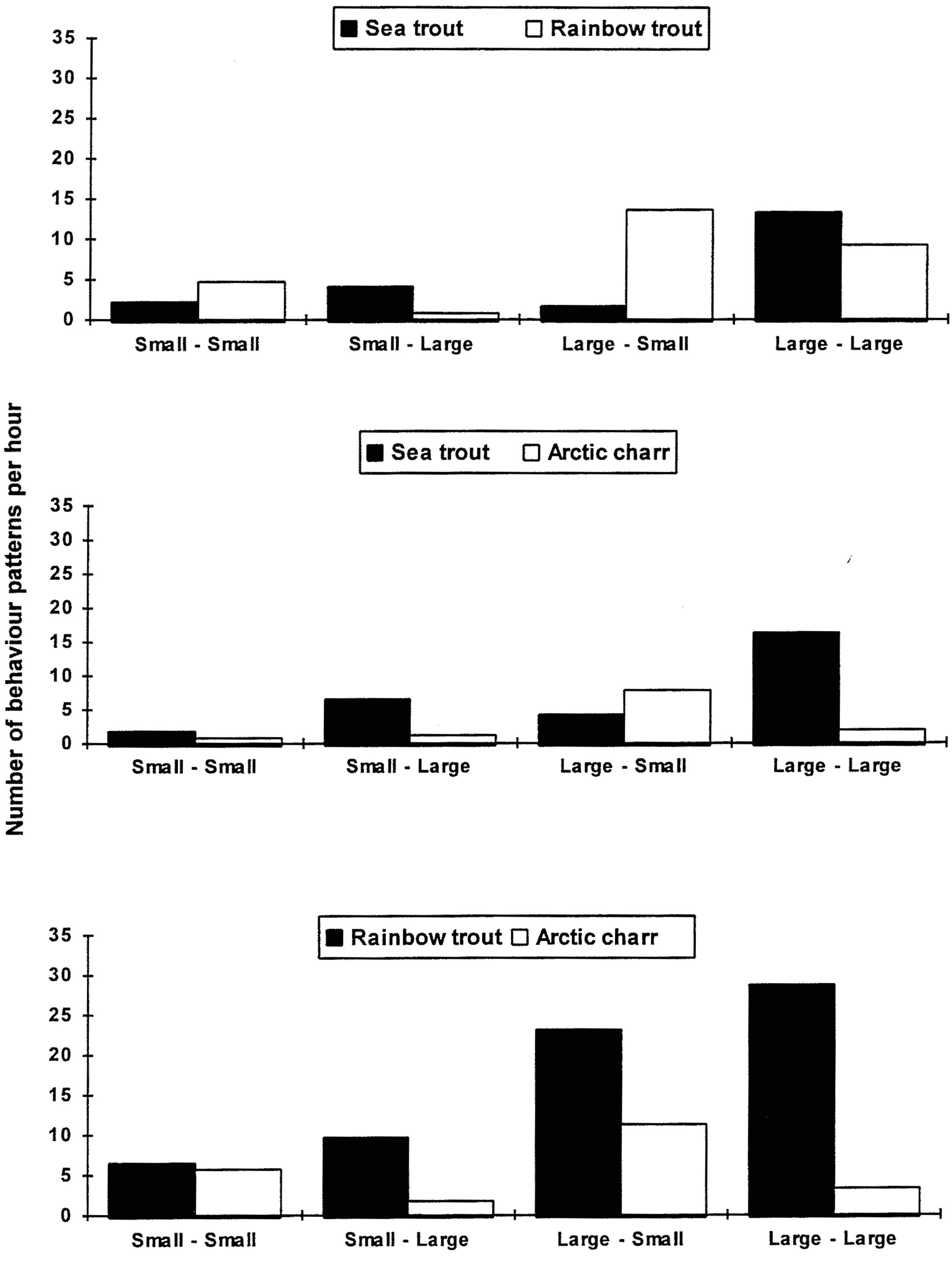
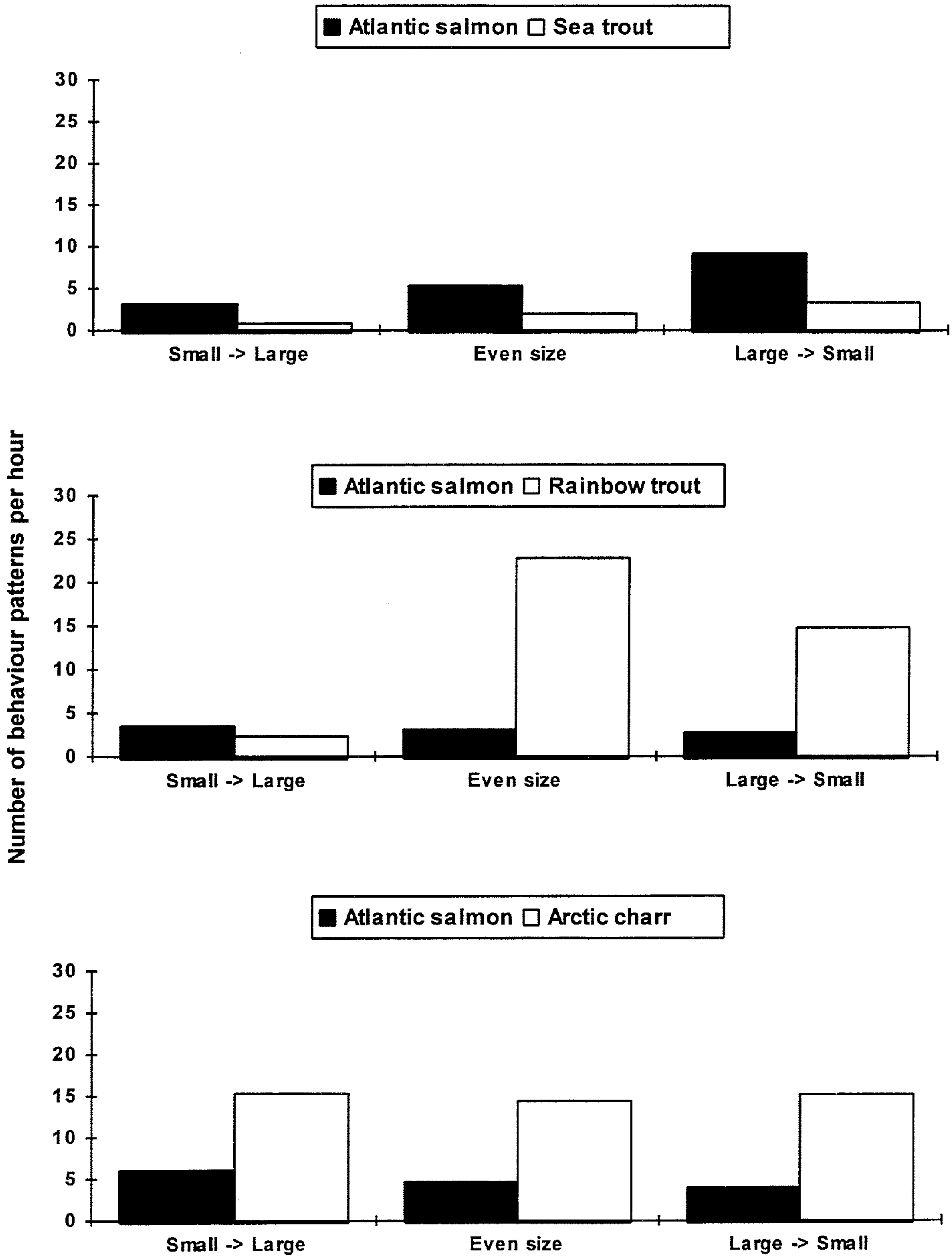


FIGURE 1. *Frequency per hour of interspecific aggression in duoculture.*)*

**) Fish categories: Small-Small and Large-Large = aggressive acts between fish of even size.*

Small-Large and Large-Small = aggressive acts of small fish towards large fish and vice versa.

The fish category to the left is the initiator.



Atlantic salmon
Sea trout
Number of behaviour patterns per hour
30
25
20
15
10
5
0
Small -> Large
Even size
Large -> Small
Atlantic salmon
Rainbow trout
Atlantic salmon
Arctic charr

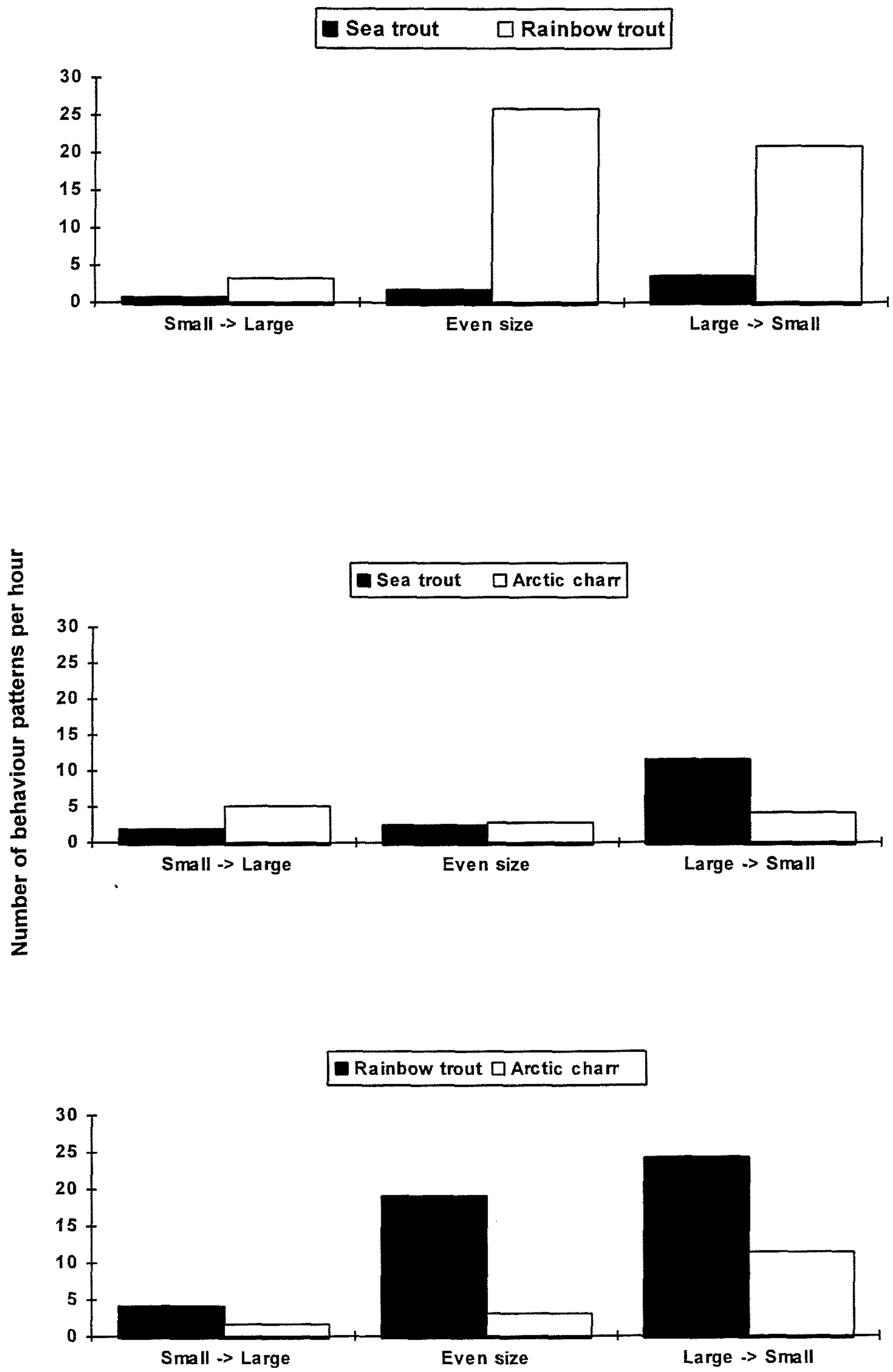


FIGURE 2. *Frequency per hour of intraspecific aggression in duoculture **)*

***) Frequency of total aggressive acts among two size categories. Large -> Small, Small -> Large = aggressive acts of larger fish towards smaller fish and vice versa. Even size = aggressive acts of fish of equal size towards each other.*

IV. DISCUSSION

Increased knowledge about the social life of salmonids may contribute to their eventual application in duoculture. It may also teach some fundamental knowledge to scientists researching salmonids that live together in nature.

When looking for candidate species for duoculture, those species that have minimized interspecific competition through a long history of coevolution will be of particular interest (Connell, 1980; Holm, 1988). In Norway, Atlantic salmon, sea trout and Arctic charr live sympatrically in many coastal streams, at least two species in each location in streams or lakes. More seldom all three species live sympatrically. Sympatric salmonids do not overlap completely, but are segregated into different niches which decrease competition (Nilsson, 1967). Nilsson (1967) also suggests that segregation is typical of "young faunas" not yet stabilized, where ecosystems are still in a relatively rapid process of evolution.

The mixed groups of salmonids in this study were considered to be more or less suitable combinations for duoculture, based on aggression displayed between and within the species. Conformity between interspecific fraction, between species aggression, as well as intraspecific fraction was found (Table 1).

A suitable duoculture combination might be characterized by a minor or moderate frequency of interspecific fraction and between species aggression, and a complementary intraspecific fraction to counteract the interspecific part of aggression (Table 1).

Interspecific fraction was roughly ranked in the order rainbow trout, sea trout, salmon and charr, respectively. If interspecific fraction is heavily out of balance and between species aggression significant in both species, the two species should probably not be combined. Salmon and sea trout have a complementary fraction of interspecific and intraspecific aggression. While sea trout displayed most aggression interspecifically, salmon showed most aggression within the species.

This combination is a possible candidate for duoculture. In earlier experimental studies, brown trout have been found to be more aggressive and dominating than Atlantic salmon (Kalleberg, 1958, Pitcher,1986). Salmon and brown trout, living sympatric in nature, primarily compete, but are known to segregate into different niches as a result of magnified interaction (Nilsson, 1967).

Rainbow trout combined with salmon have a majority of interspecific fraction as well as a considerable intraspecific fraction. Although inferior to the rainbow trout, salmon showed more than half of their aggression interspecifically. In contrast to salmon, which were relatively stationary at the bottom, rainbow trout swam extensively. This made them superior to salmon in taking pellets from the automatic feeder. A combination of these two species is not recommended.

Salmon and charr have complementary aggressional fractions, since salmon dominate interspecifically and charr have more intraspecific aggression. Salmon direct most of its aggressive activity towards charr. Salmon and charr might be a good mixing, with one species performing most interspecific aggression and the other species most intraspecific aggression. Nortvedt and Holm (1991) estimated intraspecific aggression of salmon in monoculture to be higher than the sum of salmon aggression in duoculture with charr, whereas charr showed less intraspecific aggression in monoculture than total aggression in duoculture. In a duoculture experiment with salmon and charr, both species showed increased growth rates compared to monoculture (Holm, 1989). Mork (1982) made the same conclusion concerning better growth in duoculture of Atlantic salmon, sea trout and rainbow trout, indicating that this is more than a coincident for the particular combination of salmon and charr.

Rainbow trout combined with sea trout have only a slight majority of interspecific fraction and conform with a distinct intraspecific fraction to rainbow trout. Sea trout directed most of its aggression towards rainbow trout. Since rainbow trout were also in general most active, it did not submit to the territorial sea trout. Deduced from small, experimental groups, this is probably not a good combination. Lewis (1969) observed in nature the importance of current velocity to rainbow trout and cover to brown trout, and this may indicate habitat preference, or may reflect species segregation caused by interspecific competition.

Sea trout had a distinct interspecific fraction over charr, while the intraspecific fraction was fairly equal. The between species aggression of sea trout was most pronounced. Under experimental conditions, Nilsson (1963) found trout to be more aggressive than charr. Interspecific attacks were always more frequent than intraspecific, which may be due to the fact that the pelagic life of the charr makes them more exposed to the attacks by the dominants than the territorial trout. In nature, these two species segregate into separate food niches when living sympatrically (Nilsson, 1967, Langeland et al., 1991).

Rainbow trout had a distinct interspecific fraction towards charr, and also showed more intraspecific aggression. The continuous swimming of charr seemed to act as a releasing stimulus for triggering rainbow trout aggression, and both species use most aggression towards interspecifics. Hence, duoculture using these species is not recommended, deduced from small groups.

The most comparable duoculture experiments are those of Newman (1956), who found brook trout (Salvelinus fontinalis) and rainbow trout to behave as one species. Brook trout nipped more interspecifically than towards conspecifics. Rainbow trout also have been reported to initiate severe competition for food when a new species, redside shiner (Richardsonius balteatus Richardson), were forced to live sympatrically with rainbow trout (Nilsson, 1967).

There has to be a balance between species combined in duo- or polyculture, and it is important to limit the effect of potentially dominating species. Moav and Wohlfarth (1968) pointed out that comparison of growth in polyculture with monoculture is meaningless if species are not corrected for initial difference in weight. According to Dill (1983), foraging strategies of fishes are optimal when the cost of defense is less than the benefits that are gained. Species in this study have been observed to differentiate into separate, local habitats, when living together in small groups (Mork, 1993). That is only the beginning in the development of polyculture with distant species and separate niches (Yashouv,1968; Huet,1975; Lin,1982; Bardach,1986; Pillay, 1993).

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