

Benthic predation on shallow-water macro- and meiofauna in the Baltic Sea: an experimental comparison between *Pomatoschistus minutus* (Pisces) and *Saduria entomon* (Crustacea)

Katri Aarnio, Eva Sandberg & Erik Bonsdorff

Aarnio, K., Sandberg, E. & Bonsdorff, E., Dept. of Biology and Husö Biological Station, Åbo Akademi University, SF-20500 Åbo, Finland

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The effects of the sand goby, *Pomatoschistus minutus* (Pallas) and the isopod, *Saduria entomon* (L.), on the zoobenthic community succession were examined in a field experiment conducted in the northern archipelago of Åland (Baltic Sea). In an enclosure colonization experiment two hypotheses were tested: 1) predation by *Pomatoschistus* and *Saduria* will have little structuring effect on benthic meio- and macrofaunal colonization, and 2) there will be no difference between the effects of *Pomatoschistus* and *Saduria* on the structure of the meio- and macrofaunal communities. After a two-week colonization period, the enclosures with *Pomatoschistus* contained 4.8 meiofauna taxa and had a meiofaunal abundance of 484 ind/10 cm² compared to 4.5 taxa and 428 ind/10 cm² with *Saduria*. With *Pomatoschistus*, the macrofauna species totalled 4.9 and a macrofaunal density of 45776 ind/ m² was reached, compared to 3.7 species and 20782 ind/m² with *Saduria*. A difference was thus evident between the predators in their effect on the macrofauna. At community level in the meiofauna, no differences were found between the predators. The results partly support the first hypothesis, as *Pomatoschistus* and *Saduria* have little effect on meiofaunal colonization, whereas *Saduria* does affect colonization by the macrofauna. No difference was apparent in the structuring role of the predators.

1. Introduction

During the last 20 years, biotic interactions have been studied extensively on marine intertidal soft bottoms (e.g. Schoener 1983, Ambrose 1984,

Reise 1985, 1987), but studies of this kind in non-tidal brackish areas are relatively few (Blomqvist 1986, Blomqvist & Bonsdorff 1986, Olafsson & Persson 1986, Zander & Hagemann 1987, Bonsdorff & Blomqvist 1989). In the

northern Baltic Sea, studies on biotic interactions have focused on inter- and intraspecific interactions in the benthic macrofauna (Bonsdorff & Rönn 1985, Bonsdorff et al. 1986, Elmgren et al. 1986, Rönn et al. 1988) and on fish predation on the benthic macrofauna (Mattila & Bonsdorff 1988, 1989). Most previous studies have tried to explain the structure of biological communities in terms of predation, competition, disturbance and adult-larval interactions.

This study is a comparison between two epibenthic predators, the sand goby *Pomatoschistus minutus* (Pallas) and the isopod *Saduria entomon* (L.) (syn. *Mesidotea entomon*). *Pomatoschistus* is a very common fish on shallow soft bottoms (Aneer & Nellbring 1977, Thorman & Wiederholm 1983, Nellbring 1985, Zander & Hagemann 1986) and *Saduria* is one of the most important benthic invertebrate predators in the northern Baltic Sea (Sellerberg 1961, Bagge & Ilus 1973). Consequently, these two predators

should play an important role in structuring the benthic community, but no competition for food can be expected between them as they differ in feeding behaviour, *Pomatoschistus* being a visual predator, whereas *Saduria* is more omnivorous.

The possible effects of predation by these two species on the establishment and early succession of a benthic community were examined in a short-term (2 weeks) colonization study. The following nullhypotheses were tested: Although the individual predation intensity of these two species may be high (Zander & Hagemann 1986, Gee 1987, Nellbring 1988, Sandberg & Bonsdorff 1990),

- 1) predation by *Pomatoschistus* and *Saduria* will have little direct structuring effect on meio- and macrofaunal colonization, and
- 2) there will be little difference between the predatory pressure of *Pomatoschistus* and *Saduria* on meio- and macrofaunal colonization.

Table 1. The composition (%) of the meio- and macrofauna in the study area and in the experimental trays (3 with *Pomatoschistus*, 1 with *Saduria*, and two controls with net cover).

	Surroundings		<i>Pomatoschistus</i>		<i>Saduria</i>		Control (C+N)	
	Meio	Macro	Meio	Macro	Meio	Macro	Meio	Macro
Foraminifera	7.1	—	41.2	—	58.7	—	50.9	—
Turbellaria	6.0	—	5.5	—	4.4	—	6.0	—
<i>Prostoma obscurum</i>	—	+	—	—	—	—	—	—
Nematoda	65.9	5.6	9.3	—	6.2	—	8.4	—
<i>Halicryptus spinulosus</i>	+	+	—	—	—	—	—	—
<i>Nereis diversicolor</i>	—	1.2	—	—	—	—	—	—
Oligochaeta	3.8	9.3	+	8.0	+	18.9	1.3	19.0
Hydrachnidae	1.4	—	4.4	—	5.5	—	3.1	—
Ostracoda	1.2	—	+	11.0	+	34.6	+	16.0
Calanoida	+	—	+	—	+	—	+	—
Cyclopoida	—	—	+	—	—	—	+	—
Harpacticoida	4.5	—	18.1	—	12.3	—	11.8	—
Copepoda nauplii	—	—	1.5	—	1.6	—	1.0	—
Mysidae	1.6	—	+	—	—	—	—	—
Isopoda	—	—	+	—	—	—	—	—
<i>Gammarus</i> sp.	—	1.2	—	+	—	—	—	+
<i>Bathyporeia pilosa</i>	1.3	31.7	—	—	—	—	—	—
<i>Corophium volutator</i>	—	14.9	+	10.0	+	13.7	1.0	7.0
Chironomidae	+	4.3	4.6	23.0	2.5	8.5	4.1	23.0
<i>Cardium</i> sp.	+	—	+	+	+	—	+	+
<i>Macoma balthica</i>	6.4	28.6	12.6	48.0	7.1	23.5	10.6	32.0
<i>Mya arenaria</i>	—	+	—	—	—	—	—	—
<i>Hydrobia</i> sp.	—	1.2	—	+	—	+	—	+

2. Material and methods

2.1. Study area

The field colonization experiment was conducted in the outer archipelago of Åland (N. Baltic Sea; 60°17'N, 19° 49'E) in the vicinity of Husö Biological Station.

The study site is a shallow (1–2 m) soft-bottom bay (sand and clay; loss on ignition 0.31%). The hydrographical conditions during the experiment (21 June to 5 July 1988) were as follows: 12–20 °C, pH 8.2–8.4, S‰ 5.7–5.9 and O₂% 101–114. In the area, a total of 14 meiofauna taxa and a mean abundance (\pm SE) of 354 ± 35 ind/10 cm² were recorded. The dominant taxa were Nematoda, Turbellaria and Harpacticoida. The total number of macrofauna taxa was 12 and the corresponding abundance 6583 ± 1285 ind/m². The dominant species among the macrofauna were *Bathyporeia pilosa*, *Macoma balthica* and *Corophium volutator* (Table 1).

2.2. Test organisms

Pomatoschistus minutus is a small (in the Baltic Sea up to 6 cm), littoral fish found in the zone from less than 0.5 m to the sublittoral. It is very common in shallow coastal waters (2–12 ind/m²) and has a relatively short life span of one to two years. It migrates to shallow littoral waters in early summer to spawn from June through August (Nellbring 1986). Its main food consists of small benthic animals such as larval chironomids and *Macoma balthica*, free-swimming crustaceans (e.g. mysids) and members of the benthic meiofauna, such as Harpacticoida (Nellbring 1988). *Pomatoschistus* hunts its prey actively just above the sediment surface.

Saduria entomon is commonly found in the zone from 0 to 20 m in the northern Baltic Sea (1–30 ind/m²). It is common in both shallow and deeper waters, and is considered one of the most important mobile invertebrate predators in the northern Baltic (Leonardsson 1986). Its main food is the benthic macrofauna, for instance *Pontoporeia affinis* (Hessle 1924). It is an omnivorous predator and has three strategies for catching its prey: 1) active fast hunting (Pynnönen 1985), 2) sit-and-wait

behaviour (Green 1957), and 3) active slow hunting.

2.3. Field methods

To study early colonization by the meio- and macrofauna, trays with initially defaunated sediment were used, as described by Bonsdorff & Österman (1985) and Bonsdorff (1989). The trays (30 × 40 × 11 cm) were filled with a 3 cm thick layer of azoic sediment consisting of sieved (\varnothing 0.5 mm) sand and clay. The sediment was made azoic by deep-freezing (–20 °C) for at least 48 h before the start of the experiment. The numbers of trays were: three with *Pomatoschistus*, one with *Saduria*, two control trays with a net (C+N) and two control trays without a net (C–N). The predators (2 *Pomatoschistus* = 17 ind/m², mean length 4.1 cm, or 5 *Saduria* = 42 ind/m², mean length 5.0 cm) were enclosed in the trays with a 2 mm mesh net. The densities of the predators were chosen to equal the maximal field densities recorded in the experimental area. The controls were used to examine possible effects of caging (Virnstein 1977, 1978, Hulberg & Oliver 1980, Schmidt & Warner 1984). In the results we will compare the different predator treatments with each other and with the control tray with a net. The predator trays will not be compared with the control tray with no net, because it allows free entrance for predators from the surrounding area. The duration of the experiment was two weeks and the trays were put at a depth of 1.5 meters by using a snorkel. At the end of the experiment, 15 core samples (\varnothing 1.0 cm) for the meiofauna were taken from each tray (3 *Pomatoschistus*, 1 *Saduria*, 2 C+N and 2 C–N), preserved in buffered 4% formaldehyde solution, stained with Rose Bengal (Dybern et al. 1976) and later sieved on two different screens: 0.125 and 0.063 mm. Similarly, 15 core samples (\varnothing 2.5 cm) for the macrofauna were taken from one tray of each treatment (1 *Pomatoschistus*, 1 *Saduria*, 1 C+N and 1 C–N), preserved in 4 % buffered formaldehyde and sieved through a 0.25 mm screen. To obtain a general view of the rate of community establishment and succession, both meio- and macrofauna samples were taken from the surrounding area.

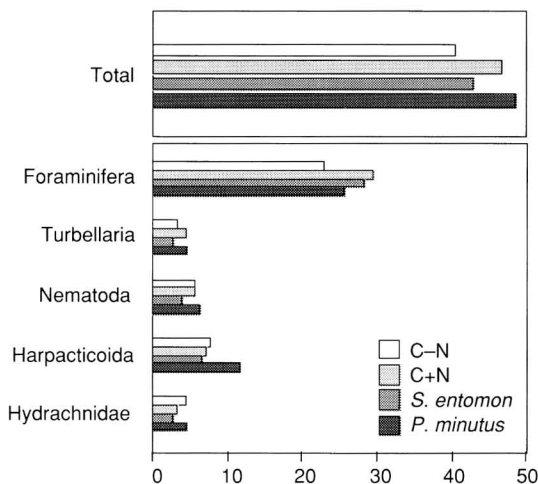


Fig. 1. Total abundance and abundance of dominant meiofauna groups per 10 cm² after two weeks of colonization in the different treatments. C-N = control tray with no net, C+N = control tray with net, *S. entomon* = tray enclosing five *Saduria entomon*, and *P. minutus* = tray enclosing two *Pomatoschistus minutus*

The total organic matter (loss on ignition; 500°C for three hours after drying according to Dybern et al. 1976) was measured in each tray and in the surrounding area.

2.4. Numerical analyses

The meio- and macrofauna were compared descriptively between the treatments: *Pomatoschistus* / *Saduria* and *Saduria* / control. Standard statistical methods (Sokal & Rohlf 1981) were applied in the analyses of the meiofauna from the control and the treatment with *Pomatoschistus*. Shannon-Wiener's index of diversity H' ($H' \geq 0$) and its evenness component (Pielou's J ; $0 \leq J \leq 1$) were used to detect structural differences between treatments.

3. Results

3.1. Predators

All predators, both *Pomatoschistus* and *Saduria*, were alive at the end of the experiment. The mean length and weight of *Saduria* had in-

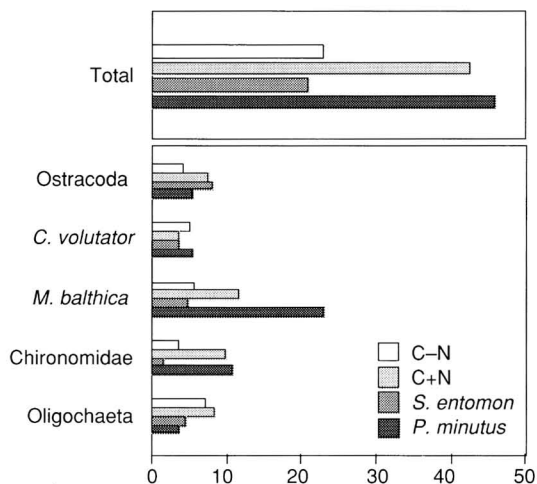


Fig. 2. Total abundance and abundance of dominant macrofauna species per m² after two weeks of colonization in the different treatments (for explanations, see Fig. 1).

creased during the experimental period, while *Pomatoschistus* was measured only at the end of the experiment. The good condition of *Pomatoschistus* was shown by the stomach analysis, which contained both meio- and macrofauna. No stomach analysis was made on *Saduria*.

3.2. Effects on the meiofauna

The total abundance of the meiofauna was similar in all treatments and there were no marked differences between the treatments or between the different replicates (Table 1). The highest number of individuals, however, was found in the trays with *Pomatoschistus*, which had 484 ± 29 ind/10 cm² (average number of taxa 4.8) compared to 428 ± 51 ind/10 cm² (4.5 taxa) for *Saduria* and 465 ± 33 ind/10 cm² (4.8 taxa) for the control treatment (C+N) (Fig. 1).

At taxon level, differences were found in Harpacticoida and Nematoda when the predator treatments were compared, and the highest abundances of these two taxa were found in the tray with *Pomatoschistus*. The other dominant taxa (Foraminifera, Hydrachnidae and Turbellaria) did not show such clear differences between the predators.

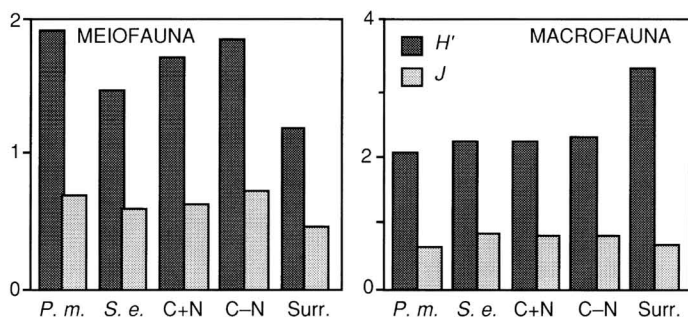


Fig. 3. Shannon-Wiener's diversity index (H') and its evenness component (J) in the different treatments (*P.m.* = *P. minutus*, *S.e.* = *S. entomon*) and in the surrounding area (Surr.).

When these results were compared with those for the control treatment (C+N), no difference was found regarding the total meiofaunal numbers. At taxon level, only the number of Harpacticoida differed significantly ($P < 0.01$) between the control treatment and the tray with *Pomatoschistus*.

3.3. Effects on the macrofauna

For the macrofauna, only descriptive comparisons were made. A clear difference was found between the effects of the predators on the total macrofaunal colonization (Table 1). The highest abundance was recorded with *Pomatoschistus* (45800 ± 4800 ind/m², average number of species 4.9) and the lowest with *Saduria* (20800 ± 2300 ind/m², 3.7 species). In the control treatment (C+N) an abundance of 42200 ± 4700 ind/m² (4.8 species) was recorded (Fig. 2).

At taxon level (Fig. 2), distinctions between the predator treatment could be made in larval chironomids, newly settled *Macoma balthica* and Ostracoda. The highest numbers of larval chironomids and *M. balthica* were found with *Pomatoschistus* while the highest number of Ostracoda was found with *Saduria*. The differences were not so clear as regards the other dominant taxa, such as Oligochaeta and *Corophium volutator*.

The total number of macrofaunal organisms varied between the control treatment (C+N) and the treatment with *Saduria*, but no distinction was found between the control and the treatment with *Pomatoschistus*. At taxon level, the control treatment differed from the treatments with

Pomatoschistus and *Saduria* as regards Oligochaeta species and *M. balthica*. When larval chironomids were considered, a distinction could be made between the control and the tray with *Saduria* (Fig. 2).

3.4. Diversity and evenness

The possible structuring effects on the meio- and macrofauna communities were tested by calculating Shannon-Wiener diversity H' and its evenness component J (Fig. 3). The meiofauna showed no difference between the treatments and the surrounding area, which indicates that two weeks is enough for the establishment of a community structurally close to natural conditions, and also that constant potential predation by *Pomatoschistus* and *Saduria* does not affect this balance. The macrofauna, however, differed clearly between the experimental treatments and the surrounding area. Thus two weeks is not enough for succession resulting in a mature macrofauna community, but on the other hand no structuring by either predator could be detected in the macrofaunal colonization.

4. Discussion

4.1. Methodical aspects

When results from colonization or cage experiments are analysed, attention must be paid to the possibility that the effects of caging may conceal the actual effect of the predators. To examine these effects, control treatments with a net and

with no net were used in our field study. The presence of an unnatural physical structure can alter the physical nature and hydrodynamics of the enclosed area, in our experiment the treatment trays. The decrease in current velocity in the trays allows increasing sedimentation, which may lead to increasing faunal immigration to the trays (Virnstein 1977, 1978, Hulberg & Oliver 1980, Schmidt & Warner 1984). In the two-week period of our study, a slight increase in the loss on ignition ($\sim 0.5\%$) was detected in the trays with a net, but not in the control tray without a net. The abundance of the meio- and macrofauna was higher in the control tray with a net than in the tray without a net. The lower abundance in the latter tray may also have been due to the free entrance of predators (e.g. gobies, flounders, shrimps) into the tray. This experiment, however, was aimed at differentiating the roles of individual predators, and their effect on the zoobenthic community can be expected to be lower than that of free predation.

4.2. Colonization by meiofauna

Dense meiofaunal populations can develop in a short time (Widbom 1983, Watzin 1983) and the meiofauna has a high recovery potential (Sherman & Coull 1980, Reidenauer & Thistle 1981, Bonsdorff & Österman 1985). In meiobenthic communities recovering from disturbances harpacticoids usually reach the highest densities (Alongi et al. 1983, Widbom 1983). As harpacticoids are one of the main food sources of *Pomatoschistus* (Nellbring 1988), this fish could be expected to reduce their numbers. In our results, however, the highest number of harpacticoids was reached in the treatment with *Pomatoschistus*. This could be explained by their ability to develop relatively dense populations under favourable predatory and competitive conditions (Widbom 1983, Bonsdorff & Österman 1985, Reise 1985). *Saduria* exerts a deleterious effect on harpacticoids, probably mainly by the strong physical disturbance caused by its burrowing. In this study, however, we were not able to separate the effect of physical disturbance from that of direct predation, as was done for *Nereis diversicolor* from the same area by Rönn et al. (1988). Other meio-

fauna groups, such as nematodes and foraminiferans, are much slower colonizers (Sherman & Coull 1980). In our treatment trays a very large number of foraminiferans was recorded and this may partly be explained by the fact that dead foraminiferans are difficult to distinguish from living ones, or that passive transport of animals is an important means of immigration (Widbom 1983).

4.3. Colonization by macrofauna

In the early phases of colonization, the newly established macrofauna community is very sensitive to both physical disturbance and predation (Connell & Slatyer 1977, Wildish 1977, Bonsdorff 1989). *Saduria* affects the macrofaunal colonization strongly, through both disturbance of the sediment and predation on the colonizing species. *Pomatoschistus* has not as strong an effect as *Saduria*, perhaps because it does not display the same burrowing behaviour. Differences in the feeding behaviour of predators can be detected by examining their choice of food, as they can have a promotive or a repressive effect on their prey organisms. *Pomatoschistus* catches its prey just above the sediment surface, as is evident from its negative effect on ostracods, which are active at the sediment surface (Keyser 1988). The deleterious effect of *Saduria* on some infaunal prey species, such as *Macoma balthica* and larval chironomids, is not apparent in the treatment with *Pomatoschistus*. This is exemplified by the great number of *M. balthica* in the tray with *Pomatoschistus* (22000 ind/m² with *Pomatoschistus* and 4900 ind/m² with *Saduria*). The negative effects on the infaunal prey species exerted by *Saduria* are partly caused by the different prey-catching strategies, but also by its mechanical disturbance (Bonsdorff et al. 1986).

4.4. Community structure

Although the predators do affect some of the colonizing species, as has also been observed in aquarium tests (e.g. Sandberg & Bonsdorff 1990), the diversity and evenness analysis revealed no effect on the structure of the developing com-

munity. There was no measurable difference between the predator treatments in the effect on the meio- and macrofauna colonization, which supports the general conclusions drawn from previous caging experiments using fish (Berge & Hesthagen 1981, Mattila & Bonsdorff 1988, 1989) and invertebrate predators (Sandberg & Bonsdorff 1990). This indicates that food is not the limiting factor for these predators (even at high densities), and that compensatory mechanisms within the infauna are capable of constantly counteracting small-scale disturbance. This could partly explain the relative temporal stability of the fauna in shallow archipelago areas demonstrated by Bonsdorff & Blomqvist (1989). Furthermore, both predators used in these experiments are known to be able to utilize prey organisms of a wide size range and of different taxonomic composition (Green 1957, Thorman & Wiederholm 1983, Zander & Hagemann 1986, 1987, Nellbring 1988, Haahtela 1990, Sandberg & Bonsdorff 1990). To obtain a more complete picture of how the benthic community functions, it is important to study the response of different predators to both the meio- and macrofauna. To be able to understand how the predators may affect the benthic community, it is important to recognize differences in the behaviour of the predators used. Such observations will facilitate the interpretation of experimental data.

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