Structuring zoobenthos: the importance of predation, siphon cropping and physical disturbance

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Abstract

In a set of field and laboratory experiments, the relative importance of (1) direct predation (measured as mortality in the prey populations), (2) physical disturbance of the sediment (sand and mud), and the combined effects of disturbance and predation, and (3) sublethal siphon cropping, were tested on an infaunal food web in the low-saline northern Baltic Sea. The predators used (*Saduria entomon* and *Crangon crangon*) are the major epibenthic crustacean predators of the northern Baltic coastal waters, and the prey organism in the experiments (the bivalve *Macoma balthica*) is, by frequency of occurrence and by biomass, the dominant infaunal organism among the zoobenthos. In the field the predatory effect of *Saduria* was tested on the entire infaunal community.

The field experiment on direct predation by *Saduria* on the entire infaunal assemblage significantly reduced the density of the polychaete *Manayunkia aestuarina*. Aquarium experiments show that although direct predation by *Saduria* or physical sediment disturbance alone had little effects on juvenile (< 3 mm) *Macoma*, the combined effects of these factors were significant, and more important than the sum of the two single factors, demonstrating synergistic negative effects. Experiments with *Saduria* and *Crangon* in relation to adult (7–17 mm) *Macoma* showed sublethal effects on length-weight relationships and on a general index of condition in the mussels. The experiments illustrate that intricate combinations of biotic and physical (environmental) mechanisms may play important roles in the organization of zoobenthic communities.

Keywords: Crangon crangon; Disturbance; *Macoma*; Predation; *Saduria*; Siphon cropping; Zoobenthos

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1. Introduction

The community structure and dynamics of the benthic infauna show great variation in space and time, depending primarily on factors such as spatial heterogeneity of the habitat and seasonality of the environment. Apart from food supply, shelter, risk for predation, reproduction and recruitment, more or less unpredictable combinations of factors may affect both the structure and functioning of zoobenthic assemblages (Menge & Sutherland, 1976, 1987; Reise, 1985; Pearson & Rosenberg, 1987). In extreme environments the importance of these factors is pronounced, as many species experience the limits of their physiological tolerance. This is the case in the Baltic Sea, which is non-tidal and characterized by steep vertical and horizontal physical, hydrographical and biological gradients on both local and basin-wide scales (Leppäkoski & Bonsdorff, 1989). In the northern parts of the central Baltic Sea (about 60°N) in the coastal waters of Finland, the seasonality is pronounced, with ice cover for 3–5 months of the year, and a summer period with long days and warm water. In shallow (< 10 m) archipelago waters the annual amplitude in temperature may range from close to 0°C to around 20°C, while salinity varies from about 4 to 7 ppt. Oxygen conditions are generally good, and normally not limiting the zoobenthos, except for cases with high amounts of drifting algae possibly causing temporary oxygen depletion (Bonsdorff, 1992), which may have profound effects on, e.g. predator-prey relationships among the zoobenthos (Sandberg, 1994). The organic content of the sediment ranges from < 0.5% on sandy bottoms to 5–10% in muddy sediments, causing shifts in the gross faunal composition, although many of the major taxa are the same in all habitats, due to the low overall number of benthic species present (Bonsdorff & Blomqvist, 1993).

The role of predation and interspecific competition for the infauna has been studied extensively in different environments (e.g. Commito & Ambrose, 1985a,b; Jensen & Jensen, 1985; Reise, 1985; Hill et al., 1990; Ambrose, 1991; Hall & Raffaelli, 1991; Wilson, 1991a,b). Previous results indicate that the effects of biological interference in the maintenance of community dynamics are of significant importance also in the naturally stressed northern Baltic Sea with low functional diversity (Bonsdorff & Blomqvist, 1993). The aim of the present investigation was to study the importance of biotic couplings in relation to common abiotic mechanisms (sediment quality and the effects of sediment disturbance) on shallow coastal soft bottoms in the northern Baltic Sea. Predation, in spite of the low diversity and low overall size of the predators of the Baltic Sea, may indeed affect the community in both promotive (increased diversity; Rönn et al., 1988) and repressive (losses in abundance; Bonsdorff et al., 1986; Rönn et al., 1988; Ejdung & Bonsdorff, 1992; Sandberg & Bonsdorff, 1992) ways. Thus, we wanted to experimentally test the effects of predation in relation to other factors, which possibly mask the outcome of predation in the field. The factors studied were: (a) sediment disturbance, (b) combinations of sediment disturbance and predation, and (c) sublethal siphon cropping on adult prey organisms. Some mechanisms for and implications of disturbance and siphon cropping have been

illustrated by e.g. De Vlas (1981, 1985), Hodgson (1982), Pekkarinen (1984), Hopkinson et al. (1985), Savidge & Taghon (1988), Lake (1990), and Kamermans & Huitema (1994). Sandberg et al. (1995) illustrated the effects of hypoxia on siphon cropping for the same test species as used in the present experiments. Ecological consequences of combinations of disturbance and biotic interactions have been documented by Möller (1986), Palmer (1988), Pickett et al. (1989) and Brey (1991), and their hierarchical importance was examplified by Barry & Dayton (1991). All the present experiments were conducted with key species for the shallow near-shore waters of the northern Baltic Sea, with the isopod *Saduria entomon* and the decapod *Crangon crangon* as predators, and the bivalve *Macoma balthica* as prey. The combinations of test situations were chosen in order to facilitate correct interpretation on different environmental and biological scales (Kneib, 1991; Duttileul, 1993). The problems with interpretation of results are further demonstrated by a simple field experiment on predation.

2. Materials and methods

2.1. Test organisms

The valviferan isopod *Saduria (*syn. *Mesidotea) entomon* (L.) is a large (4–10 cm) widely dispersed omnivorous predator (Green, 1957), occurring in fully marine, brackish and limnic waters (Haahtela, 1990 and references therein). In the Baltic Sea *Saduria* is a glacial relict species found throughout the depth gradient (in the Åland area it is found from 1–290 m). *Saduria* is considered an important community regulator in a large variety of benthic assemblages (Leonardsson, 1986; Ejdung & Bonsdorff, 1992; Hill & Elmgren, 1992), ranging from the species-poor deep bottoms with periodic hypoxia to the species-rich and productive littoral communities (Sandberg & Bonsdorff, 1990, 1992; Sandberg, 1994). Thus *Saduria* is the only benthic invertebrate predator occurring on all bottom types, at all depths and in virtually every habitat, probably utilizing any available food item as prey or food. Due to this potential role as "universal regulator" for the infauna, *Saduria* was used as the predator in all three experiments in this paper. They were captured with baited traps at 5–10 m depth and stored in collecting tanks. They were fed with crushed mussels and dead fish, and starved two to three days prior to each experiment. No *Saduria* carrying a brood were used in the experiments as these individuals can be expected to behave differently from the others.

The brown shrimp *Crangon crangon* (L.) together with *Palaemon adspersus* (Rathke) are the only decapods which have adapted to the brackish water environment in the northern Baltic Sea. *Crangon* is an important epibenthic predator on shallow sandy bottoms in the southern Baltic Sea (Mattila et al., 1990), but information on the ecology of *Crangon* in the northern Baltic Sea is still sparce, although it is known to be an effective predator on both crustaceans and bivalves (Lindell, 1993; Sandberg et al., 1995). *Crangon* is an omnivorous

predator (Pihl & Rosenberg, 1984; Raffaelli et al., 1989) and known to prey upon bivalve siphon tips (De Vlas, 1985; Kamermans & Huitema, 1994; Sandberg et al., 1995).

The tellinid bivalve *Macoma balthica* (L.) is a brackish-water bivalve widely distributed over the northern hemisphere (e.g. Beukema & Meeham, 1985) occurring on soft or mixed shallow bottoms (Muus, 1967). In brackish areas such as Chesapeake Bay and the Baltic Sea it is commonly found subtidally, and down to more than 100 m, in a broad range of sediment types (Segerstråle, 1957; Bonsdorff, 1988; Eggleston et al., 1992), although settling is concentrated to shallow waters (Bonsdorff et al., 1995). The low species diversity in the brackish Baltic Sea reduces the occurrence of normal marine subtidal competitors of *Macoma* (Segerstråle, 1962; Remane & Schlieper, 1971), giving this bivalve species a wide range of ecological roles (Bonsdorff & Blomqvist, 1993; Bonsdorff et al., 1995). Both juvenile and adult *Macoma* were used as prey in the aquarium experiments.

2.2. Field experiment

A field enclosure experiment (Experiment 1) was conducted in the outer Åland archipelago (N. Baltic Sea; 60°17'N, 19°49'E). The locality is semi-exposed (depth ranging from 5–10 m), and the sediment consists of sand and clay (loss on ignition ~ 0.4%). Dominating macrofauna are *Macoma balthica*, gastropods (*Hydrobia* spp.), the amhipod *Corophium volutator* (Pallas), polychaetes (*Pygospio elegans* Claparéde and *Manayunkia aestuarina* (Bourne)) and oligochaetes. Common invertebrate epibenthic predators in the area are *Saduria entomon* and *Crangon crangon*. The main benthic feeders in the area are flounder [*Platichtys flesus* (L.)], and other benthivorous fish (Mattila, 1992; Aarnio & Bonsdorff, 1993; Bonsdorff & Blomqvist, 1993).

The hydrographical conditions during the experiment (21th of June to 2nd of August 1991) were: S‰ ≈ 5.6, temp. 8.5–15 °C, pH ≈ 8 and O_2 % 92–102 (bottom water), and the organic content of the sediment was 0.19–0.23% during the experiment (all treatments). In the field enclosure experiment a natural benthic community was exposed to enhanced predator densities by enclosing *Saduria*. This was done using PVC-cylinders as enclosures (height = 15 cm, Ø = 16 cm) covered with a 5 mm mesh-net to avoid migration (in/out) and to make possible cage artefacts similar for both (control and predation) treatments (Hulberg & Oliver 1980, Peterson & Black 1994). The experiment consisted of two treatments: predation (3 *Saduria* per enclosure) and control (no predator). The predator density in the enclosure was equivalent to 150 ind · m^{-2}, a density somewhat higher than normal background values (Haahtela, 1990). Densities higher than normal in experimental set-ups are, however, considered appropriate for detecting predation effects (Hall et al., 1990a,b; Kennedy, 1993). Personal observations during SCUBA-diving have shown that *Saduria* can occur in high densities; the scavenging behavior of *Saduria* allows them to forage collectively on

a carcass without disturbing each other, although adult-juvenile predation (cannibalism) may occur (Leonardsson, 1991).

A statistical power analysis was performed a priori (Sokal & Rohlf, 1981) based on previous field experiments with *Saduria*. Accordingly, 15 replicates per treatment were used, getting sufficient power for detecting a 35% change in abundance of the natural infauna enclosed by the cylinders with a power of 80%. The cylinders were semi-randomly placed at a depth of 7 m in a clustered pattern 0.5 m apart to avoid topographic heterogeneity and disturbance by the divers. The enclosures were pushed 5 cm into the sediment. At the beginning and at the end of the experiment, five replicate reference samples (core-sampler $\emptyset = 4.7$ cm) were taken in the ambient area. During the course of the experiment the enclosures were checked weekly, with possible drifting algae removed from the nets covering the cylinders. At the end of the experiment the nets were removed, and one 4.7 cm diameter core-sample was taken from the center of each enclosure to avoid possible edge effects (Hall et al., 1990b). After the sampling any remaining predators were caught for length and weight measurements. All manipulations and samplings were done by SCUBA-diving. The samples were preserved in 4% buffered formalin. The macrofauna samples were washed on a 0.5 mm mesh sieve, and the remaining animals were identified to species and counted under a preparation microscope ($15 \times$ magnification). The treatments were compared using one-way ANOVA, and the Bray-Curtis similarity (Bray & Curtis, 1957). For each treatment maximum diversity and evenness were calculated from pooled samples according to Shannon & Weaver (1963).

2.3. Predation vs disturbance vs sediment-type

The aim of this experiment (Experiment 2) was to compare predation with physical disturbance, and to evaluate whether the combined effect of predation and disturbance would deviate from the added effects of the single factors. This was conducted using two different sediment-types (pure sand with loss on ignition of 0.16%, and a mixture of mud and sand with loss on ignition of 0.70%) simulating an exposed (sand bottoms) and sheltered (muddy bottoms) locality with different sediment properties behaving differently under the exposure of waves (Table 1). The pure sand sediment consisted of sieved (0.5 mm) sand and the mud-sand mixture of 50% sieved sand mixed with 50% mud (sieved, 0.5 mm and deep frozen in $-20°C$ for 48 h).

Saduria was used as predator (mean length 37.2 mm $\pm$ 0.5 SE, and mean wwt 1.10 g ± 0.04 SE), and 1-yr-old individuals of *Macoma balthica* (length range 1.0–3.0 mm) as prey. Glass-aquaria (290 mm $\times$ 210 mm $\times$ 220 mm, volume 13.4 l), placed in a common cooling system, were used. The individual aquaria were randomized. The depth of the sediment layer in the aquaria was 3 cm, and the water was aerated with aquarium air-pumps. The hydrographical conditions were measured every second day during the experiment (Table 1). A light:dark period of 12:12 h was used throughout the experiment. When starting the experiment, 100 *Macoma* where placed in each aquarium, allowing the clams to acclimatize for 12

Table 1
Hydrographical conditions during three separate runs (I, II, III) of Experiment 2 (predation, disturbance and sediment type). The suspended matter (mg/l) in the water immediately after disturbance (0) and after 1, 3 and 6 h

	Hydrographical conditions			Suspended material (mg/l)		
	I	II	III	(h)	Sand	Mud
Temp. °C	14.4–15.7	13.6–15.6	14.3–16.4	0	2.4	5182
pH	7.67–8.06	8.02–8.17	7.98–8.13	1	1.3	524
Salinity ‰	5.2–5.5	5.3–5.4	5.3–5.4	3	1.6	295
Oxygen %	63–99	95–98	95–107	6	0.7	164

h before adding the predators. The predators were randomly chosen for each aquarium and treatment. Four treatments (in two sediment types) were compared with two replicates for each run (3 repeated runs). For both sediment types (sand and mud/sand) the following treatments were done (Table 2): (1) direct predation (4 *Saduria* per aquarium), (2) physical disturbance of the sediment (no predator), (3) predation (4 *Saduria* per aquarium) + physical disturbance of the sediment, and (4) a control treatment (no predation, no physical disturbance). Physical disturbance was simulated in terms of sediment resuspension, achieved by rapid hand motion just above the sediment, causing instant and complete resuspension of the sediment, thus mimicking effects of waves and currents, and also of digging benthivorous fish. The resuspension was done for 30 seconds every 6th hour over a period of 3 days (72 h). While picking the bivalves for the experiment, random reference samples of 100 *Macoma* were collected for every run for size frequency analysis. After each run the remaining live *Macoma* were counted and the length measured (to the nearest 0.1 mm with an ocular-micrometer). The suspended matter in the water (mg·l^{-1}) was measured for both sediment types immediately after disturbance and after 1, 3 and 6 h (Anon., 1973).

2.4. Siphon cropping experiment

A long-term (27 days) aquarium experiment was run to study whether *Saduria* and the brown shrimp *Crangon crangon* prey upon *Macoma* siphons and thus reduce the fitness of adult clams, i.e. sublethal effects of predation (De Vlas, 1981,

Table 2
The experimental set-up for Experiment 2

	Control		Predation		Disturbance		Pred. + Dist.	
	sand	mud	sand	mud	sand	mud	sand	mud
Predator (*Saduria*)	–	–	4	4	–	–	4	4
Prey (*Macoma*)	100	100	100	100	100	100	100	100
Disturbance	–	–	–	–	+	+	+	+
Replicates	2	2	6	6	6	6	6	6

Table 3

Hydrographical conditions in the different treatments during Experiment 3. Nutrients (tot. P and tot. N), chlorophyll-*a*, and loss on ignition were measured at the beginning and at the end of the experiment

	Hydrographical conditions		
	Control	*Saduria*	*Crangon*
Temp. °C	12.0–18.2	12.0–18.7	11.8–18.7
pH	8.4–8.7	8.2–8.7	8.5–8.8
Salinity ‰	5.2–5.4	5.3–5.4	5.3–5.4
Oxygen %	86–110	73–97	79–92
Tot. P μg/l	31.2–25.8	31.2–39.8	31.2–33.8
Tot. N μg/l	564.4–560.9	564.4–738.2	564.4–633.2
Chlorophyll-*a* μg/l	1.10–1.75	0.93–2.26	1.26–1.96
Loss of ignition %	0.7–0.6	0.9–0.9	0.5–0.5

1985; Kamermans & Huitema, 1994). The aquaria used were PVC containors ($435 \times 335 \times 300$ mm, volume 44 l), filled with a 10 cm layer of sieved azoic sand- and clay mixture, covered by 15 cm of running sea water. The hydrographical conditions were measured every second day (Table 3). To follow the activity in the aquaria the content of basic nutrients (tot-P, tot-N) and chlorophyll-a were analysed from each aquarium. Sediment samples for loss on ignition were taken at the beginning and at the end of the experiment.

The experiment consisted of three treatments; (1) the *Saduria* treatment with five *Saduria* (mean length 35.4 mm ± 0.9 SE , mean wwt 0.88 g ± 0.06 SE), (2) the *Crangon* treatment with five *Crangon* (mean total length 35 mm ± 2.53, mean wwt 0.50 g ± 0.11), and (3) a control treatment without predators. Each tank, one for each treatment, was supplied with 100 adult *Macoma*, with shell length ranging from 7.0 to 17.0 mm (mean size: 11.6 mm ± 0.11). The clams were allowed to acclimatize for 24 h before adding the predators. During the experiment the behavior of the prey was observed by counting bivalves forced to the sediment surface by the activity of predators.

At the end of the experiment the predators were removed for length and weight measurements. The sediment was sieved and all bivalves collected and counted. The shell-free dwt/shell dwt (mg) and a condition index (CI-1) were determined according to Wenne & Styczynska-Jurewicz (1985), Bonsdorff & Wenne (1989), and Sandberg et al. (1995), and differences between treatments were analysed according to Fowler & Cohen (1992) for the length/weight-relationships.

3. Results

3.1. Field enclosure experiment (Experiment 1)

At the end of the experiment, 34 of the initial 45 predators were found, all of them in good condition. Remaining predators were probably buried deep in the

sediment and not retrieved (length at start was 41.9 ± 0.85 mm and weight 1.54 ± 0.09 g; length at the end was 41.6 ± 0.97 mm and weight 1.42 ± 0.09 g). The total abundance in the control treatment was similar to that in the predation treatment (Table 4, Fig. 1). Both treatments had higher abundance values than in the ambient area (Table 4). None of these differences were significant, however. When comparing the predation effects on the dominating macrofauna (Fig. 1) a significant negative effect ($p < 0.01$) by *Saduria* on the polychaete *Manayunkia aestuarina* was found. *Saduria* also had a negative effect on oligochaetes. The total number of species (Table 4) was highest in the predation treatment compared to the control (n.s.) and the ambient area ($p < 0.01$). For the Shannon-Wiener diversity (H') and evenness (J) the highest values were found in the control, and the lowest in the predation treatment (n.s.; one-sample sign test). The similarity between treatments and ambient area was high, ranging from 70 to 90% (Table 4).

3.2. Predation vs disturbance vs sediment-type (Experiment 2)

The hydrographical conditions were stable throughout the three consecutive runs in Experiment 2, and the sediment types were highly different, as illustrated by sedimentation rates (Table 1) and organic content. There were no significant differences between runs within treatments ($p = 0.22$). The survival in the control for both sediment types (sand and mud) was $99.9 \pm 0.5\%$ with no significant difference between control-sand and control-mud. For the treatments predation-sand and predation-mud the survival was $95.3 \pm 2.8\%$ and $81.8 \pm 7.5\%$, respectively, and for disturbance-sand and disturbance-mud $97.8 \pm 0.9\%$ and $98.3 \pm 1.1\%$ with no significant differences between either treatments (Fig. 2). Significant differences ($p < 0.0001$) in the *Macoma* survival-rate were found between the combined predation and disturbance treatments (both with sand and mud, survival being $51.7 \pm 8.2\%$ and $44.3 \pm 6.8\%$, respectively) and all other treatments (Table 5). There were no significant differences between the predation + disturbance-sand and -mud ($p = 0.33$) or between the two different predation treatments (sand and mud, $p = 0.08$), however. No significant effects of only predation or disturbance were found compared to the control treatment. In the treatments with predation + disturbance, significant effects were also found on the size-distribution of *Macoma* (Fig. 3). In both sediment-types used, a shift in length distribution was recorded, with small sizes (1.35–1.75 mm) being negatively ($p < 0.05$) affected by predation, with a significant shift towards larger in the median size classes for the different treatments (Fowler & Cohen, 1992).

The combined effects of predation + disturbance thus induced synergistic negative effects on the survival of the juvenile *Macoma*. The resuspension of the sediment seemingly exposed the juvenile bivalves making them more susceptible to predation. In these treatments the predators were also visibly more active than in the ordinary predation treatments.

Table 4
The number of species/groups and their abundance per m^2 ($\pm$SE) from Experiment 1

Species/groups	Ambient area		Control	Predation
	I	II		
Mollusca				
Macoma balthica	806.9 ± 230.5	691.7 ± 336.1	1460.2 ± 231.0	1631.9 ± 196.5
Cerastoderma glaucum	–	115.3 ± 115.3	–	+
Mytilus edulis	+	–	999.1 ± 330.2	576.4 ± 168.7
Hydrobia spp.	10375.0 ± 1719.5	11297.2 ± 3252.4	14601.8 ± 1470.8	20634.6 ± 1520.3
Limapontia capitata	–	–	–	+
Crustacea				
Monoporeia affinis	–	–	76.8 ± 52.4	76.8 ± 52.4
Gammarus spp.	–	–	–	+
Corophium volutator	–	461.1 ± 282.4	422.7 ± 153.7	691.7 ± 212.0
Jaera albifrons coll.	–	–	76.8 ± 52.4	115.3 ± 61.6
Polychaeta				
Nereis diversicolor	345.8 ± 230.5	+	76.8 ± 52.4	230.5 ± 123.2
Pygospio elegans	3573.6 ± 423.5	3573.6 ± 495.8	1921.3 ± 340.7	1921.3 ± 358.7
Manayunkia aestuarina	1613.9 ± 336.1	1152.8 ± 257.8	2382.4 ± 263.0	999.1 ± 206.4
Oligochaeta	6340.3 ± 1351.7	7954.1 ± 2837.8	9606.4 ± 770.6	7493.0 ± 1151.4
Priapulida				
Halicryptus spinulosus	–	–	–	+
Nemertina				
Prostoma obscurum	+	–	+	+
Turbellaria	+	806.9 ± 431.3	422.7 ± 153.7	538.0 ± 198.6
Insecta				
Chironomus sp.	–	–	691.7 ± 100.6	1652.3 ± 368.3
Hydrachnida	–	–	153.7 ± 118.9	+
Total abundance	23055.5 ± 1015.0	25937.5 ± 4298.1	33276.5 ± 2162.0	36351.0 ± 2650.2
Total number of species	9	8	13	16
Diversity (H')	2.05	2.10	1.51	1.99
Eveness (J)	0.68	0.66	0.70	0.52

Similarity	90%
	75%
	70%
	80%
	75%
	83%

The total number of species, Shannon-Wiener diversity index (H') and its evenness component (J') are given for the ambient area and the treatments. Ambient area I and II describe the natural population (untreated) at the beginning and at the end of the experiment. Control = control treatment without predator, and Predation = predation treatment with *Saduria entomon*.
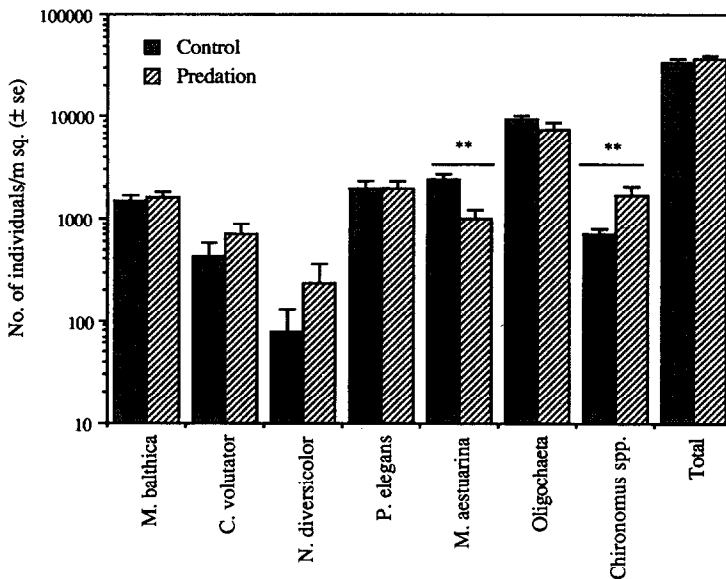
Fig. 1. The number of dominating species/groups and total abundance (ind · m^{-2}; log-scale) in the field enclosure experiment (Experiment 1). Control = no predator; Predation = 3 *Saduria* enclosed. Significant differences between treatments ($p < 0.01$) were found for the polychaete *Manayunkia aestuarina* and chironomid larvae.
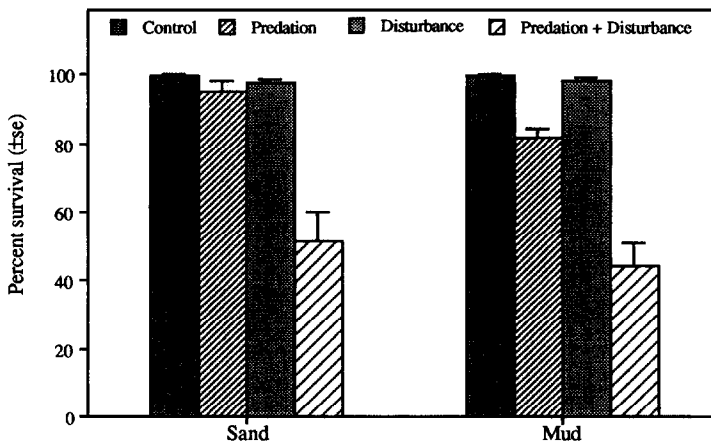

Fig. 2. The survival rate (% ± SE) of 1- yr-old *Macoma balthica* in the aquarium experiment with predation and sediment disturbance (Experiment 2). Control = no predator/no physical disturbance; Predation = 4 *Saduria*/ no disturbance; Disturbance = *Macoma*/disturbance (sediment resuspension); Predation + Disturbance = 4 *Saduria*/disturbance.

Table 5
Statistical differences (one-way ANOVA) in the survival of juvenile *Macoma balthica* in Experiment 2

Treatments	Control		Predation		Disturbance		Pred. + Dist.	
	S	M	S	M	S	M	S	M
Control								
S		N.S.	N.S.	N.S.	N.S.	N.S.	***	***
M	(1)		N.S.	N.S.	N.S.	N.S.	***	***
Predation								
S	0.6967	0.6967		N.S.	N.S.	N.S.	***	***
M	0.1051	0.1051	0.0809		N.S.	N.S.	***	***
Disturbance								
S	0.8760	0.8760	0.7407	0.0404		N.S.	***	***
M	0.9130	0.9130	0.6914	0.0349	0.9472		***	***
Pred. + Dist.								
S	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		N.S.
M	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.3349	

(1) The exact p-value was not obtained dur low replication number ($n = 2$).
Control (no treatment), Predation, Disturbance, and Predation + Disturbance in the two sediment types used (S = sand; M = mud); $***p < 0.01$; NS, not significant. Levels of significance and corresponding p-values given for all combinations of factors tested in the experiment.
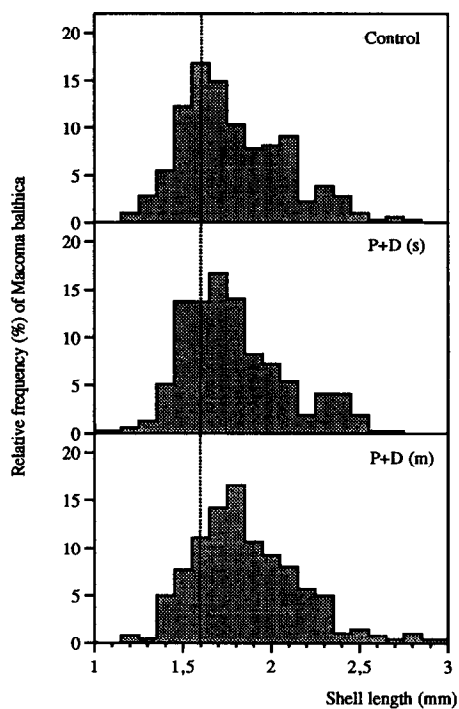
Fig. 3. The length distribution (%; 0.1 mm classes) of juvenile *Macoma balthica* from Experiment 2. Control = reference samples; P + D (s) = predation (4 *Saduria*)/disturbance in sand; P + D (m) = predation/disturbance in mud. The vertical dotted line indicates the median size of the Control.

3.3. Siphon cropping experiment (Experiment 3)

The hydrographical conditions and nutrient dynamics were stable throughout the siphon cropping experiment. No significant differences between treatments were noted and the chlorophyll-a content in the water was comparable to the natural archipelago waters, indicating a sufficient food supply for the bivalves (Table 3).

The slope of the length/weight-relationship of *Macoma* changed with treatment (control > *Saduria* and *Crangon*, $p < 0.01$ with no significant difference between *Saduria* and *Crangon*; Fig. 4), although mean length (11.33 mm; all treatments) and mean weight (26.7 g wwt; all treatments) of the clams did not differ after the experiment. In the control the mean condition index (CI-1) in *Macoma* was 236.4 ± 4.4, which was significantly ($p < 0.05$) higher than in both predator-treatments. In the treatment with *Saduria* as predator the mean condition index was 223.0 ± 4.9 and in the treatment with *Crangon* 218.9 ± 4.0, illustrating that *Crangon* had a
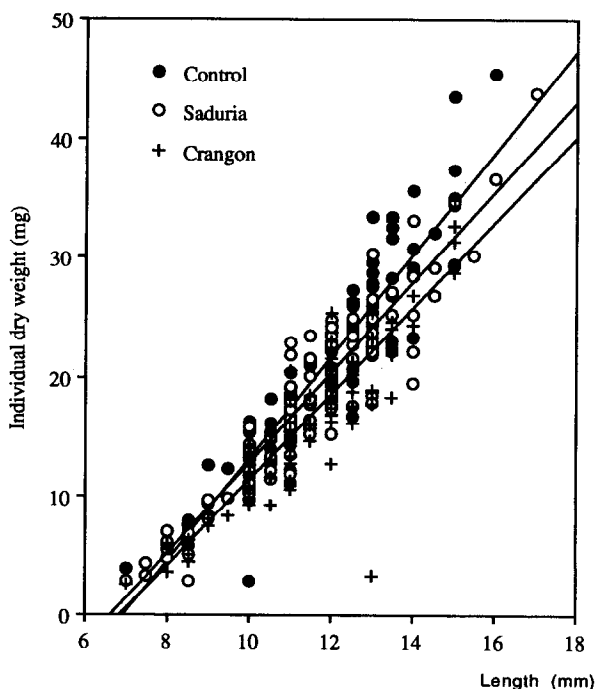

Fig. 4. The length (mm)/body dry weight (mg) -relationships in adult (7–17 mm) *Macoma balthica* after the siphon cropping experiment (Experiment 3). Control = no cropping ($y = 4.271x - 29.704$; $r^2 = 0.86$); *Saduria* = continuous potential cropping by *Saduria entomon* ($y = 3.802x - 25.374$; $r^2 = 0.87$); *Crangon* = continuous potential cropping by *Crangon crangon* ($y = 3.523x - 24.686$; $r^2 = 0.76$).

higher impact on the condition of *Macoma* than *Saduria*, although the difference was not significant (Fig. 5).

The effect of *Crangon* was also reflected in the number of bivalves forced to the sediment surface by the end of the experiment. In the treatment with *Crangon* there was an average of 27 ± 1.4 *Macoma* on the sediment-surface, which was
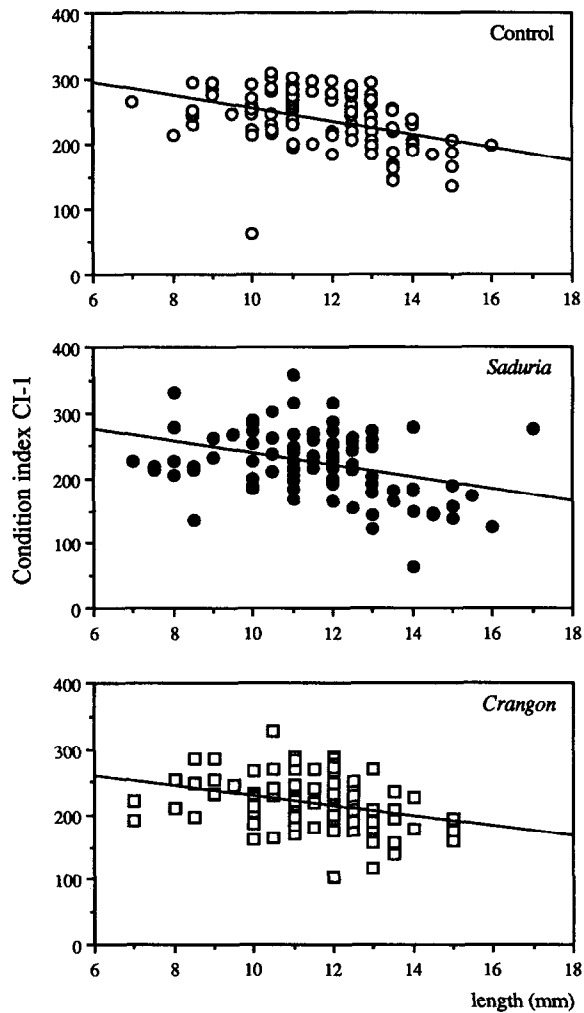

Fig. 5. The relationship between shell length and condition index CI-1 in adult (7–17 mm) *Macoma balthica* after the siphon cropping experiment (Experiment 3). Control = no cropping ($y = 353.39 - 9.99x$; $r^2 = 0.18$); *Saduria* = continuous potential cropping by *Saduria entomon* ($y = 330.30 - 9.25x$; $r^2 = 0.13$); *Crangon* = continuous potential cropping by *Crangon crangon* ($y = 303.34 - 7.38x$; $r^2 = 0.10$).

significantly (p < 0.01) higher than in the treatment with *Saduria* (1.9 ± 0.1) and the control (1.3 ± 0.3). No mortality among the adult *Macoma* was registered in any of the treatments during the experiment.

4. Discussion

4.1. Effects of predation

The field experiment revealed that direct predation has an impact on the benthic ecosystem, although the overall effects may not be significant. At species level the effects were more pronounced, indicating that predators may be prey-selective, and also that some species are more vulnerable to even low levels of stress than others. This is in accordance with our previous experiences from the Baltic Sea, where predation by *Saduria* has been shown to affect small polychaetes (Sandberg & Bonsdorff, 1992) and juvenile bivalves (Ejdung & Bonsdorff, 1992). On the other hand, no negative effect was found on community composition or diversity (Table 4), whereas such an effect was described by Rönn et al. (1988) for a shallow water community with *Nereis diversicolor* as selective predator. The design of the experiment could potentially affect the results (Hall et al., 1990a; Kennedy, 1993; Olafsson et al., 1994; Peterson & Black, 1994), but in our case a pilot test revealed no effects on the biota by the enclosures in comparison to the natural community, or on the predator used, and previous work (Ejdung & Bonsdorff, 1992; Sandberg & Bonsdorff, 1992; Sandberg, 1994) has shown that *Saduria* behaves normally in these experimental conditions. Kennedy (1993) used similar enclosures to study the effects of macrobenthos on meiobenthos, and found negative effects on Annelid-taxa, which supports our results where *Manayunkia aestuarina* and oligochaetes were the only groups significantly reduced by the predator. Gee et al. (1985) also found *Manayunkia aestuarina* vulnerable to predation, as it is confined to the top millimeters of the sediment, and does not withdraw into its tube in response to vibration (caused eg. by movement by the predator). The role of meiofaunal prey cannot be excluded either (Gee, 1987; Kennedy, 1993), although *Saduria* seems to prefer slightly larger prey organisms (Ejdung & Bonsdorff, 1992), which may also explain why no significant predation was recorded in our Experiment 2.

The fact that few direct (negative) effects of predation within the infauna can be detected, does not mean that predation is insignificant as such (Hall et al., 1990b; Bronstein, 1994). Aquarium experiments clearly demonstrate the potential importance of eg. *Saduria* as a population and community regulator in the Baltic Sea (Sandberg & Bonsdorff, 1990, 1992; Leonardsson, 1991; Ejdung & Bonsdorff, 1992). It is quite likely, however, that the detectable effects of predation in the field are masked by other factors, such as community complexity, i.e. multiple interactions within the system (Posey & Hines, 1991) and spatial heterogeneity in the environment (Duttileul, 1993). Hence, several components (both abiotic and biotic) can be expected to interact in community regulation directly and indirectly

(Menge & Sutherland, 1987; Kneib, 1991; Wilson, 1991b; Bonsdorff & Blomqvist, 1993; Kolar & Rahel, 1993; Olafsson et al., 1994).

4.2. Sediment disturbance promotes predation

In Experiment 2 we demonstrated how potentially important, but principally independent factors, namely predation and sediment quality and disturbance, when acting together lead to enhanced effects that are higher than the sum of the effects of the single factors (Fig. 2). This partly explains why predation alone is not detected as a prime factor in community organization, whereas its effects are pronounced through an abiotic event occurring simultaneously (Möller, 1986; Brey, 1991). The differences between sediment types (Fig. 2) can partly be explained by the differences in sedimentation rates (Table 1), reflecting particle size (in sandy sediments the juvenile bivalves are almost equal in size to the sand grains), but also organic content (Snelgrove & Butman, 1994). Peterson & Black (1988) illustrated a similar phenomenon with dense populations of bivalves, and linked it to sedimentation, which supports our results on increased and differential predation in the muddy sediment (Fig. 3). Similar enhanced effects on predation have also been described in connection with drifting algal mats and/or moderate hypoxia (Kolar & Rahel, 1993; Bonsdorff et al., 1995; Breitburg et al., 1994; Norkko & Bonsdorff, 1995), and as the juvenile *Macoma balthica* are situated at the sediment surface, they will be immediately affected by the sediment disturbance. McClanahan (1992) showed that omnivorous gastropods under stress shift to predation. That was explained as a sign of stressed environments serving as refugia for species that are old on an evolutionary time scale. As *Saduria* is classified as a glacial relict in the Baltic Sea, and it is also known to be omnivorous under conditions with low stress (Green, 1957; Segerstråle, 1966; Haahtela, 1990), the significant increase in predation rates in both sediment types under stress (sediment disturbance) may be such an opportunistic response (Posey & Hines, 1991). Further, the ability of the predator to shift predatory behaviour from passive to active (*Saduria* is able to swim actively), may increase the predation effect (Palmer, 1988). Barry & Dayton (1991) also emphasized the role of the habitat in terms of physical heterogeneity in structuring communities and in species interactions (including predation), and Pickett et al. (1989) regarded disturbance as a natural factor in community control, as also illustrated for hydrodynamic disturbance by Olafsson et al. (1994) and for animal-sediment relationships by Snelgrove et al. (1994). Biotic interaction may not always involve mortality, but rather sublethal effects, and Wilson (1991b) emphasized the role of browsing predation, i.e. siphon cropping (including effects on condition and fitness), which was also covered in our experiments.

4.3. Siphon cropping is important

Sublethal browsing by both *Crangon* and *Saduria* affected the condition of adult *Macoma balthica* (both the length/weight-relationship in Fig. 4, and the

calculated condition index, CI-1). Siphon cropping was not size-dependent (no significant differences in the length/CI-1-relationships between treatments; Fig. 5), although condition factors for *Macoma balthica* have been shown to vary with size and season (Bonsdorff & Wenne 1989). Similar results on various condition factors in *Macoma balthica* were obtained for *Crangon* by Sandberg et al. (1995) in combination with moderate hypoxia. Althogh not significantly, *Crangon* was the more effective browser, which can be explained by its active feeding mode (Pihl & Rosenberg, 1984; DeVlas, 1985; Kamermans & Huitema, 1994). *Macoma balthica*, and other bivalves (but also polychaetes; Woodin, 1982), are known to be cropped upon regularily (De Vlas, 1981, 1985; Peterson & Quammen, 1982; Kamermans & Huitema, 1994; Zwarts et al., 1994), which has been found to directly affect body weight and condition. However, siphons are known to regenerate relatively rapidly at a low energy cost (Hodgson, 1982; Pekkarinen, 1984; De Vlas, 1985). On the other hand, burying depth and feeding radius is directly linked to siphon length (Zwarts & Wanink, 1989; Kamermans & Huitmea, 1994; Zwarts et al., 1994), and burying depth is also linked to chances of escaping epibenthic predation (Wilson, 1991b; Lin & Hines, 1994; Zwarts et al., 1994). Hence, the forcing of bivalves to the sediment surface through siphon cropping or other stress factors (hypoxia, sediment disturbance) may have secondary effects through facilitated epibenthic predation (De Vlas, 1985; Zwarts & Wanink, 1989; Lin & Hines, 1994; Norkko & Bonsdorff, 1995). As siphon cropping is occurring more or less constantly by various epibenthic predators, the predation processes affecting the infaunal community are partly driven by the fact that organisms are made available for predation, which in connection with abiotic factors (sediment disturbance, hypoxia etc.) has an active role in community organization (Hall & Raffaelli, 1991; Wilson, 1991b; Bonsdorff & Blomqvist, 1993).

4.4. The role of synergistic and selective mechanisms in population control

The synergistic effects exemplified by enhanced predation in connection with sediment disturbance, and the effects of siphon cropping and subsequent decrease of burying depth of *Macoma* illustrate the importance of experiments where different factors structuring, regulating and maintaining benthic communities are combined and considered simultaneously. In the case of *Macoma*, the response to stress is age/size-related, in that juvenile individuals up to 1 yr old (about 3 mm; Ejdung & Bonsdorff, 1992) lack siphons and are restricted to the sediment surface. These individuals are easily susceptible to sediment disturbance, whereas adult clams are burrowed into the sediment. On the other hand, siphon cropping will affect only the adult population, and thus different mechanisms affect the biota selectively. Only by creating new experimental situations, both in the lab and in the field, we can begin to understand the intricate mechanisms governing the dynamics of the zoobenthos. It is vital that no single factor alone (apart from catastrophic events) can structure the community, and that various, seemingly independent factors may act together or even counteract or mask the effects of each other.

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