

*Original papers***Effects of the deposit-feeding benthic bivalve *Macoma balthica* on meiobenthos**Emil Ólafsson¹, Ragnar Elmgren^{1,2}, Ourania Papakosta¹¹Department of Zoology and Askö Laboratory, Stockholm University, S-106 91 Stockholm, Sweden²Department of Systems Ecology, Stockholm University, S-106 91 Stockholm, Sweden

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Abstract. To evaluate the effects of a deposit-feeding bivalve on meiobenthic assemblage structure in muddy habitats, a laboratory experiment was performed at the Askö Laboratory in the northwestern Baltic proper. Microcosms, surface area 104 cm², containing a c. 7-cm thick layer of sieved (0.5 mm) sublittoral mud were established in June 1990. Two months later the tellinid bivalve *Macoma balthica* was added in quantities varying from 0 to 40 individuals per microcosm. After 5 months the effects of the bivalves on the meiofauna were surprisingly small. The density of harpacticoid copepods was lowest ($P < 0.05$) in microcosms containing a high density of *M. balthica*. It is suggested that competition for food resources was responsible for this pattern. For all other meiofaunal groups, including nematodes which were the most abundant taxon (99%), no significant differences ($P > 0.05$) were observed among treatments. The assemblage structure of the nematodes was similar between treatments. The vertical distribution of both major taxa and nematode species appeared to be unaffected by the presence of the bivalve.

Key words: Microcosm – Meiofauna – *Macoma balthica* – Biological interactions

In soft-bottom habitats the macrofauna is known to alter physical and chemical characteristics of the surroundings by bioturbation and creating various formations like tubes, burrows, casts, and funnels in or on the sediment (e.g. Rhoads and Young 1970; Eckman et al. 1981; Nowell et al. 1981; Aller et al. 1983; Lopez and Levinton 1987). The fauna is often enhanced around such structures as these habitats can provide a refuge from predators (Woodin 1978, 1981), increased microbial food (Aller and Yingst 1978; Reise 1983; Warwick et al. 1986) and/or create favourable physical conditions such as higher oxygen tension (Reise and Ax 1979). Macrofauna may also have

negative effects on the meiobenthos. Numerous studies indicate lower abundances due to predation (e.g. Reise 1979; Smith and Coull 1987; Palmer 1988; Ólafsson and Moore 1990) and some due to physical disturbance of the sediment surface (Thistle 1980; Creed and Coull 1984; Ólafsson et al. 1990). In the feeding area of detritus-feeding macrofauna a reduction in the numbers of meiofaunal animals due to competition for food resources is likely to occur as many nematode and copepod species are also detritus feeders (see for review: Hicks and Coull 1983; Heip et al. 1985). However, negative effects on the meiobenthos due to competition over food resources have not yet been demonstrated in field or laboratory experiments.

The soft bottoms of the Baltic Sea have a species-poor macrofaunal community, where the amphipod *Monoporeia affinis* (Lindström) and the bivalve *Macoma balthica* (L.) are generally the dominant macrobenthic species (Elmgren et al. 1986). These species are often found in very high numbers and therefore seem likely to exert a biological pressure on the meiobenthos. In earlier contributions (Ólafsson and Elmgren 1991; Sundelin and Elmgren 1991) the effects of the dominant amphipod on the meiobenthos were studied in laboratory experiments.

In muddy substrata *Macoma balthica* is a deposit-feeder (Ólafsson 1986) utilizing detritus, microflora and microfauna as food (Newell 1965; Fenchel 1972; Tunnicliffe and Risk 1977). They live buried in the sediment at c. 2–5 cm depth and the inhalant siphon is extended up to the surface where food particles are gathered (Hulscher 1973). It appears that *M. balthica* does not select deposits according to particle size (Self and Jumars 1988), though there may be an upper limit (Brey 1991). Brey (1991) concluded after looking at the potential feeding area of *M. balthica* populations in Kiel Bay and the German Wadden Sea that both inter- and intraspecific competition over food resources was likely to occur. Indeed, intraspecific competition between adults and newly settled larvae has been demonstrated both in field and laboratory experiments (Bonsdorff et al. 1986; Ólafsson 1989). There are also some data indicating that interspecific competition can take place. Thus Ólafsson (1989) found that *M. balthica* at very high densities had negative effects on the deposit-feeding

Hydrobia spp. suggesting competition for food resources. In a colonization experiment, Bonsdorff et al. (1986) showed that *M. balthica* had negative effects on settling *Cardium glaucum* whereas ostracods were found in higher densities in the presence of adult *M. balthica*. In a sandy tidal flat aggregates of the clam attracted meiobenthos both at the sediment surface and also deeper down in the sediment indicating a biotic enrichment by the bivalve (Reise 1983). Such enrichment is thought to be due to termination of exhalant siphons below the surface, which produces micro-oxic zones and localized concentrations of nutrients. This will stimulate growth in microorganisms, hence the bivalve is thought to activate the growth of its own food source (Reise 1983).

In this experiment we tested the following hypotheses:

1. A reduction in surface dwelling meiofauna occurs in the presence of *M. balthica* due to competition over food resources.
2. Gardening effects' *sensu* Reise (1983) result in a different trophic structure of the nematode assemblage both at the sediment surface and deeper down.
3. The presence of *M. balthica* alters the vertical distribution of the meiobenthos due to bioturbation, e.g. we expected that deep-dwelling species such as the nematode *Sabatieria pulchra* would have a shallower vertical distribution in sediments where bivalves are not present.

Material and methods

Small aquaria were established at the Askö Laboratory field station in the northwestern Baltic proper (58° 49'N, 17° 38'E) in June 1990. Each microcosm consisted of a 2-l glass jar with a total surface area of about 104 cm², as described by Elmgren et al. (1986). Brackish water was pumped from a depth of 16 m into a cooling tank and distributed to the microcosms through dripping needles. Outflow water from the microcosms was not recycled. Temperature and salinity were kept near levels at 30–40 m depth in the field, i.e. 2–5°C and 6.5–7.2‰, and a dim green light, controlled by an outdoor photocell, approximated *in situ* light conditions.

Sediment was collected using a benthic dredge from a 34 m deep station, approximately 3 km south of the Askö Laboratory. Kajak cores (Blomqvist and Abrahamsson 1985) were also obtained and the top layer of each core used to enrich the meiofauna in the microcosms. The mud was sieved through a 0.5-mm mesh to exclude macrofauna, allowed to settle, homogenized by stirring and added to the glass jars. Each microcosm contained a c. 7 cm thick layer of mud. A total of 40 microcosms were used, to permit four treatment levels of ten replicates each, arranged in a randomized block design.

At the start of the experiment on 28 August 1990, 2 months after sediment collection, adult bivalves (average wet weight: 650 mg, size range: 1.2–2.0 cm) were gathered from the same location as the sediment. Ten microcosms were set up without bivalves, and the remainder used for three bivalve treatment levels: 10, 20 and 40 individuals of standard size per microcosm, corresponding to medium, high and very high field densities.

The experiment was terminated after 5 months. From each microcosm a 4 cm deep core sample (5.3 cm²) was taken. About half of the replicate cores of each treatment were sectioned into three layers: 0–1, 1–2 and 2–4 cm, while the rest were preserved whole. The core samples and the remainder of the sediment from each microcosm were fixed in 4% buffered formalin. The core samples were sieved through 500-µm and 40-µm mesh sieves while the rest of the sediment was sieved through 500-µm and 100-µm mesh. The 40-µm and 100-µm screenings were transferred separately to 2-l conical flasks and suspended in Ludox (colloidal silica polymer) at a specific

gravity of 1.15. After settling for 1 h the supernatant liquid was decanted through a 40-µm mesh. The sediment was then resuspended in Ludox and the process repeated once more. Ólafsson and Elmgren (1991), using a very similar extraction technique on sediments from the same site, found that average extraction efficiency for nematodes, copepods and other groups combined was 98% (range 97–99%), 87% (range 70–100%) and 71% (range 58–84%) respectively. Apart from nematodes all meiofaunal groups were found in very low numbers within the core samples. The major meiofaunal taxa were identified and enumerated from the whole-microcosm sample (100-µm screenings) using a stereo dissecting microscope. Foraminifera were excluded from the study as they were not reliably extracted with the flotation method used. The extracted meiofauna core samples (40 µm) were resuspended in 500 ml of tap water and vigorously agitated. Sub-samples were then taken with a syringe, to allow c. 100 nematodes (numbers permitting) to be impregnated with anhydrous glycerine (Platt and Warwick 1983) and mounted on slides for identification under a high-power microscope. Given the small differences in the abundance of the nematode species in zero, medium and high bivalve treatments, nematodes were not determined to species in the low treatment, to save time.

For each taxon, differences in density between the treatments were investigated by one-way analyses of variance. Paired *a posteriori* comparisons of density estimates were carried out with the Tukey test using 95% confidence limits. Prior to the analysis of variance, all data were first log₁₀(x+1) transformed and Bartlett's test used to check the assumption of homoscedasticity.

Nematode species abundance data were double square-root transformed, and subjected to detrended correspondence analysis using DECORANA adapted for microcomputers (Hill 1979). A computer program by Moore (1983) was used to calculate various species diversity indices.

Results

The survival rate of the bivalves inside the microcosm was 97.5% on average and very similar in all treatments (Table 1). Visual observations during the experiment revealed that the bivalves extended their inhalant siphon up to the sediment surface while buried at 2–5 cm depth. One of the high-density treatment microcosms was accidentally disconnected from the water supply and was hence excluded from the experiment.

The meiofauna inside the microcosms was highly dominated by nematodes (99%) while harpacticoid copepods (0.3%) were usually the second most abundant group. Compared to field densities (Ólafsson and Elmgren 1991) all taxa were in lower numbers inside the microcosms, nematode and harpacticoid numbers being one-half and 1/25 of field values respectively.

Major taxa

Average numbers of the major meiofaunal taxa in each treatment are shown in Table 1. Numbers of harpacticoid copepods [mainly *Microarthridion littorale* (Poppe)] were significantly different among experimental treatments (one-way ANOVA, $P=0.015$). They were on average half as abundant in the high-density treatment as in other treatments. For no other group were significant differences observed among treatments (one-way ANOVA, $P>0.05$). Meiofaunal numbers in core samples with no *M. balthica* were not significantly different (one-way ANOVA, $P>0.05$) from core samples containing one or more *Macoma*.

Table 1. Average (AVG) number per microcosm ($n=10$ for all but High where $n=9$) and standard error of the major meiofaunal taxa in 4 treatments

	Zero AVG	SE	Low AVG	SE	Medium AVG	SE	High AVG	SE	ANOVA Sig. level
<i>M. balthica</i> initial	0		10		20		40		
<i>M. balthica</i> final	0		9.7		19.6		39		
Nematoda	21292	1665	20176	1254	21743	2233	18668	1312	0.5981
Harpacticoida	79	12	88	14	73	15	41	14	0.0150 ^a
Ostracoda	88	8	73	9	78	11	57	10	0.1374
Turbellaria	40	6	54	7	64	10	44	10	0.1698
Kinorhyncha	24	6	15	2	22	5	17	4	0.6685
Oligochaeta	23	12	37	10	34	11	26	11	0.1117
Priapulida	9	1	9	1	9	1	6	1	0.1659
Others	7	1	5	1	7	1	7	1	0.5767

^aA posteriori Tukey test: High < Low, Zero

The *P* values from the 1-way ANOVA are also presented

Table 2. Average (AVG) number per 10 cm² standard deviation (SD) and percentage of nematode species in three treatments

	Zero ($n=6$)			Medium ($n=6$)			High ($n=7$)		
	AVG	SD	%	AVG	SD	%	AVG	SD	%
<i>Leptolaimus elegans</i>	482	170	26.2	511	170	23.7	382	77	21.1
<i>Leptolaimus papilliger</i>	375	107	20.4	320	43	14.8	377	140	20.8
<i>Calomicrolaimus honestus</i>	312	171	17.0	345	265	16.0	231	75	12.7
<i>Sabatieria pulchra</i>	287	140	15.6	385	176	17.8	303	189	16.7
<i>Microlaimus globiceps</i>	109	45	5.9	114	30	5.3	146	38	8.1
<i>Desmolaimus</i> sp.	102	30	5.5	222	161	10.3	168	102	9.2
<i>Paracanthocheilus</i> spp.	61	40	3.3	99	131	4.6	65	46	3.6
<i>Eleutherolaimus</i> sp.	24	17	1.3	15	25	0.7	17	28	0.9
Species Y	20	31	1.1	33	55	1.5	24	30	1.3
<i>Campylaimus</i> sp.	19	21	1.0	21	14	1.0	22	19	1.2
<i>Monhystera disjuncta</i>	12	14	0.7	0	1	0.0	0	0	0.0
<i>Daptonema</i> sp.1	12	15	0.6	15	14	0.7	9	23	0.5
<i>Dichromadora</i> sp.	6	11	0.3	9	10	0.4	9	16	0.5
<i>Paramonhystera</i> sp.	4	7	0.2	38	16	1.7	24	29	1.3
<i>Axonolaimus</i> sp.	3	7	0.2	7	11	0.3	2	6	0.1
Species X	3	6	0.2	0	0	0.0	0	0	0.0
<i>Adoncholaimus</i> sp.	3	7	0.2	3	6	0.1	2	6	0.1
<i>Sphaerolaimus</i> sp.	3	6	0.1	10	23	0.5	23	30	1.3
<i>Chromadorita fennica</i>	2	6	0.1	6	9	0.3	0	0	0.0
<i>Anoplostoma</i> sp.	0	0	0.0	0	0	0.0	1	2	0.0
<i>Camacolaimus</i> sp.	0	0	0.0	0	0	0.0	6	11	0.3
<i>Halalaimus</i> sp.3	0	0	0.0	3	8	0.1	4	7	0.2
total	1838	507	100	2155	881		1816	369	
Richness - <i>S</i>	8.58	0.61		9.07	1.22		8.89	1.36	
Simpson - <i>D</i>	0.81	0.01		0.83	0.03		0.83	0.02	
Shannon - Wiener - <i>H</i> ^a	2.75	0.10		2.88	0.24		2.86	0.20	
Pielou - <i>J</i> ^a	0.78	0.05		0.79	0.03		0.83	0.04	

^a using \log_2

Average species diversity (Shannon-Wiener, Simpson), evenness (Pielou) and richness (Sanders rarefaction at the 50 individual level) are also presented

Nematode assemblage structure

Altogether 22 nematode species were found in the microcosms. The congeneric species *Leptolaimus elegans* (Schuurmans Stekhoven & De Coninck) and *L. papilliger* De Man along with *Calomicrolaimus honestus* De Man and *Sabatieria pulchra* G. Schneider were the dominant

species (Table 2). No significant differences were observed among treatments for the 10 most abundant species (one-way ANOVA, $P>0.05$). Detrended correspondence analyses failed to show any groupings of treatments (Fig. 1) and only a small proportion of the variance was attributable to the first two axes, with eigenvalues of 0.11 and 0.07, respectively. Average species diversity (Shannon-

would have expected a reduction in the medium high density treatment as well. (2) During the experiment *M. balthica* may have reduced recruitment of harpacticoids in the high-density treatment by feeding on nauplii. At the end of the experiment nauplii were almost absent in all microcosms so this hypothesis could not be tested by analysing gut contents of *Macoma* individuals from the microcosms. However when there is a high density of nauplii in the field *M. balthica* does not appear to be feeding on nauplii, as they were not observed in the gut contents (pers. obs.). As far as we know nauplii have not been reported in the gut contents of *M. balthica* although in a related species *Macoma nausta* harpacticoids have been detected in the mantle cavity (Hylleberg and Gallucci 1975). Hence we believe that this explanation is inadequate. (3) There is competition between *M. balthica* and copepods over food resources. Data collected by Ankar and Elmgren (1976) from the muddy sediment of the Askö area reveal that when the number of macrofaunal *M. balthica* was over a certain limit (200 per m²), the abundance of bivalves was negatively correlated with the abundance of harpacticoid copepods (Fig. 4, Correlation coefficient = -0.85, r² = 0.72, = 12, P < 0.001). In our experiment we found a decrease only at very high bivalve densities. As the abundance of the harpacticoids in the microcosms was only a fraction (1/25) of the field density one would expect higher numbers of *M. balthica* to be required before competition over food resources occurs. This, however, remains speculative and needs to be tested experimentally.

The almost total lack of response of the meiofauna in this experiment may reflect the limitations of the approach. The microcosms used do not allow faunal immigration or emigration. Additionally we found a very shallow vertical distribution of the nematodes with all the species almost confined to the top 1 cm. In the field the vertical distribution appears to be deeper (Ólafsson and Elmgren 1991) probably because of different sediment characteristics (fine sieved mud in microcosms). Furthermore the densities of the major non-nematode taxa in the microcosms were far below normal field levels. There may be several reasons for this e.g. time of sediment collection,

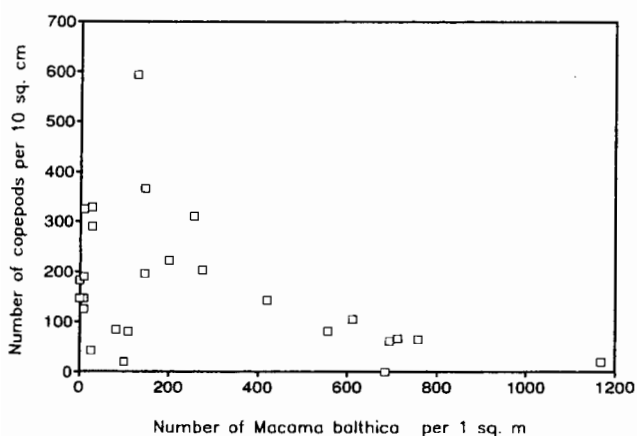


Fig. 4. Number of copepods and *Macoma balthica* in subtidal muddy sediment stations from the Askö area. Data from Ankar and Elmgren (1976)

lack of sufficient food resources or high initial mortality due to sieving.

Deposit-feeding animals generally move throughout the substrate when searching for food. *M. balthica* not only moves vertically but also horizontally, up to 5 cm per 4 min (Brafield and Newell 1961). However crawling behaviour of *M. balthica* is thought to be associated with trematode infections (Swennen 1969) and "healthy" individuals tend to be more stationary (Swennen 1969; Hulscher 1973). In the Askö area a high percentage of *M. balthica* seem to be infested with trematodes (Ankar and Elmgren 1976). After the introduction of the bivalves to the microcosms they all burrowed into the sediment within 24 h. If they then stayed at the same place for the rest of the experiment this could explain the lack of significant effects on the vertical distribution of the meiofauna. The tendency of *Sabatieria pulchra* to have relatively deeper vertical distributions within microcosms containing the bivalves compared with microcosms without is in accordance with Ólafsson (1992). He found, when implanting shells of *M. balthica*, that sediment became black indicating anoxic conditions and that *S. pulchra* became more abundant there than in control areas.

Biotic enrichment by the bivalve was not detected in this experiment and is in direct contrast with the findings of Reise (1983) from a sandy tidal flat area. This may reflect the different habitats where these experiments were performed. It is likely that water percolation in the sediment is much more limited in muddy substrata than in sand, hence dispersion of nutrients (and oxygen) may be negligible within muddy sediments. Another possibility is that biotic enrichment is based on outside input not present in the microcosms.

Despite the limited effects of the *Macoma* on the meiofauna in this experiment, our data indicate the presence of interspecific competition over food resources between the bivalves and harpacticoid copepods. Such competition could be ecologically significant in the field where harpacticoid copepods are a major link between microbes and higher trophic levels, and present in higher abundance than in our microcosms.

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