Predation on newly settled bivalves by deposit-feeding amphipods: a Baltic Sea case study

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ABSTRACT: In the Baltic Sea, predation on postlarvae of the infaunal clam Macoma balthica by adults of the 2 most abundant deposit-feeding amphipods, Monoporeia affinis and Pontoporeia femorata, has been considered to be a crucial factor in determining the bivalve's recruitment success. The functional response of adult M. affinis to postlarvae of the bivalve was shown in laboratory experiments to be type III-like, with no levelling off of the number of prey consumed per predator within the postlarval densities tested. Densities included were higher than the highest reported from habitats where both species occur together. In laboratory experiments, adults of P. femorata were also shown to kill M. balthica postlarvae. In neither amphipod species did adults select among sizes of newly settled M. balthica. Juvenile M. affinis were likewise found to kill M. balthica postlarvae. Our results, and a recent field study, confirm the effect of the amphipods on M. balthica postlarvae and their role in controlling bivalve recruitment in Baltic soft sediments. They also support the idea that interactions among juveniles of macrofauna may affect the recruitment success of many benthic species and therefore be important in structuring benthic communities.

KEY WORDS: Predation Juvenile-juvenile interaction Adult-juvenile interaction Monoporeia affinis Pontoporeia femorata Macoma balthica Postlarvae

INTRODUCTION

Among factors affecting the structure of benthic communities are the supply of settling larvae (Woodin et al. 1995) and factors affecting their planktonic growth and survival. After larval settlement, benthic communities are further structured by interactions among juvenile and adult macrofauna and meiofauna (Elmgren et al. 1986, Watzin 1986, Ejdung & Bonsdorff 1992, Osman et al. 1992, Osman & Whitlatch 1995, Hunt & Scheibling 1997), as visualised in conceptual models by Ankar (1977), Bell & Coull (1980), and Utito & Sarvala (1990). However, interactions within the large group of juvenile macrofauna has largely been overlooked when discussing mechanisms structuring these communities. Although juvenile macrofauna soon outgrow the threat from meiofauna, danger still remains from macrofauna, both adults and the often far more abundant juveniles.

Deposit feeders use organic material from detritus, micro-organisms and meiofauna (Lopez & Levinton 1987), and may supplement these by predation on temporary meiofauna, e.g. recently settled bivalves (Elmgren et al. 1986). Even if relatively unimportant in terms of ingested carbon, such supplementation may provide essential nutrients in short supply, e.g. polyunsaturated fatty acids (Turunen & Pekkarinen 1990). Timing, settling intensity and recruitment success varies between years (Bonsdorff et al. 1995). On occasion settling greatly increases the density of postlarvae, resulting in high abundances of potential prey, although often for a short time only (Ankar 1980, Bonsdorff et al. 1995). The number of prey consumed per predator as a function of prey density can be described as the functional response of the predator (Holling 1959). This is the first study of the functional response of early post-settlement mortality in soft-bottom habitats, more specifically for a macrofaunal deposit feeder preying on newly settled, meiofauna-sized bivalve postlarvae.

In the northwestern Baltic proper, 200 to 300 \( \mu \text{m} \) long larvae of the bivalve Macoma balthica (L.) settle in late
June to early July (Ankar 1980) on shallow to ca 40 m deep soft bottoms (Olafsson & Elmgren 1997, pers. obs.). Then, at the plantigrade stage (Baker & Mann 1997), the larvae inhabit the uppermost millimetres of the sediment (Caddy 1969). Together, the bivalve and the 6 to 12 mm long deposit-feeding pontoporeiid amphipods *Monoporeia affinis* (Lindström; see Bousfield 1989) and *Pontoporeia femorata* Kröyer make up the bulk of the macrobenthic abundance and biomass (Ankar & Elmgren 1976, Cederwall 1990). *M. affinis* is found below 9 m depth in the area (Cederwall 1990), and on deeper mud bottoms below about 30 m the amphipods co-occur. *P. femorata* tends to occupy the deeper strata, and *M. affinis* the uppermost centimetres of the sediment (Hill & Elmgren 1987). Both species feed mainly on surface sediment (Lopez & Elmgren 1989).

Young *Monoporeia affinis* are released in March/April (Sarvala 1986) and grow rapidly in June and July (Cederwall 1977, Uitto & Sarvala 1991). Lopez & Leivinton (1987) suggested that deposit feeders are food limited most of the year. This seems to hold for *M. affinis* and *Pontoporeia femorata* in our investigation area (Elmgren 1978), where food is scarce, except following the sedimentation of the spring bloom (Elmgren 1978), the period during which the amphipods grow rapidly (Cederwall 1977) and build up lipid stores for overwintering and reproduction (Hill et al. 1992). The energy used by the amphipods seems to derive mainly from detrital carbon (Uitto & Sarvala 1991, Lehtonen 1996).

From field data, Hessle (1924) and Segerstråle (1960) concluded that recruitment of *Macoma balthica* was prevented in areas densely populated by *Monoporeia affinis* and *Pontoporeia femorata*. Segerstråle (1962) suggested that *M. affinis* (formerly *Pontoporeia affinis*) could ingest the newly settled bivalves, and tested this experimentally, using the mainly hard-bottom-living *Mytilus edulis*. He concluded that *M. affinis* may affect bivalve survival, and named this the 'Macoma-Pontoporeia theory' (Segerstråle 1965). The first experimental test of the theory actually using *M. balthica* postlarvae was performed by Elmgren et al. (1986). They demonstrated that adult *M. affinis* were able to kill and most likely also eat newly settled postlarvae of *M. balthica*, and the predicted rapid reduction after the peak in density of settling bivalves was recently confirmed in a field study (Olafsson & Elmgren 1997). The question of whether juvenile *M. affinis* and adults of the other common amphipod in the area, *P. femorata*, can also kill newly settled *M. balthica* postlarvae remained. Segerstråle (1962) believed that adult *P. femorata* had the same effect as *M. affinis* on *M. balthica* postlarvae, but doubted that amphipods of either species smaller than 6 mm could eat newly settled *M. balthica* (Segerstråle 1973).

In this study we present the first measurements of the functional response of a basically deposit-feeding amphipod feeding on a newly settled bivalve, namely of adult *Monoporeia affinis* feeding on *Macoma balthica* postlarvae. We further test whether juvenile *M. affinis* and adult *Pontoporeia femorata* also kill and presumably consume newly settled *M. balthica* postlarvae.

**MATERIAL AND METHODS**

**Study site and procedure.** This study was performed in 1990 and 1995 at the Askö Laboratory (58° 49' N, 17° 38' E), on the coast of the northwestern Baltic Sea proper. The natural abundance of the amphipods varies greatly in this area, due to differences in bottom topography (Hessle 1924). In the Askö area (22 to 54 m depth, 1972 to 1993) Elmgren & Larsson (1997) reported up to 4000 *Monoporeia affinis* m⁻², with a corresponding abundance for *Pontoporeia femorata* of up to 2000 m⁻², but more than 3000 *P. femorata* m⁻² have been recorded in the Baltic (Järvekülg 1973). The abundance of young-of-the-year (0+) *M. affinis* is high in March/April, when they leave the marsupium, and may reach over 10 000 m⁻² (Sarvala & Uitto 1991). In the Askö area settlement of *Macoma balthica* led to peak postlarval densities of 80 000 m⁻² at 10 m depth (Ankar 1980), and of 65 000 m⁻² at a 37 m deep station (Olafsson & Elmgren 1997), while densities of up to 300 000 m⁻² have been reported from the Finnish Åland archipelago (6 to 8 m depth, medium-fine sand, Bonsdorff et al. 1995). Salinity at 10 m depth in the Askö area is about 6.5, and at 45 to 50 m depth about 7.5.

Sediment and specimens were collected close to the Askö Laboratory with a benthic sled (Blomqvist & Lundgren 1996), amphipods and sediment from 30 to 40 m depth, and postlarval *Macoma balthica* from 4 to 16 m. The fine muddy sediment used was the natural sediment of the amphipods. This sediment was sieved through a 100 μm mesh, and had a loss on ignition of 5% in 1990 and of 2% in 1995. *M. balthica* that passed through a 500 μm mesh and were retained on a 100 μm mesh were concentrated according to Elmgren et al. (1986), and picked in batches of 50 in 1990 and 5 in 1995. All *M. balthica* postlarvae encountered had a maximum length of 200 μm. Amphipods were picked in batches of 10 adult *Monoporeia affinis* (1+), 20 juvenile *M. affinis* (0+) or 3 adult *Pontoporeia femorata* (1+), and kept without food for 2 d. Before the start of the experiments, amphipods and bivalves were inspected under a stereo-microscope, and damaged individuals replaced. Batches of bivalves and amphipods were randomly chosen and added to the experi-
functional aquaria in the appropriate abundances for each treatment. Bivalves were always added at least an hour before the amphipods, and not until the sediment had settled and the water above the sediment was clear.

Statistics and models. Data were analysed using Statistica 5 for PC. Variance homogeneity was tested according to Cochran (balanced treatments) or Bartlett (unbalanced treatments). To obtain variance homogeneity, some data were square root transformed (number of postlarvae killed, functional response experiment) or arcsine square root transformed (for proportions). A 1-factor ANOVA ($\alpha = 0.05$) was used to test for differences between/among treatments. Significant results were followed by the Tukey test for unequal N. All values followed by a ± value are mean ± standard error of mean.

The theoretically most interesting differences between types of functional response are found at low prey densities. The functional response can be determined on the basis of the shape of the proportional mortality curve (Lipcius & Hines 1986, Eggleston 1990). The type II functional response shows proportionally higher mortality at lower prey densities, type III is characterised by proportionally lower mortality at lower densities, and type I by strictly proportional mortality (Hassell 1978). A 1-factor ANOVA was used to distinguish between these types of functional response (Eggleston 1990). In order to further characterize the type of the functional response, the type II model $y = bx/(x + c)$ and the type III model $y = bx^3/(x^3 + c)$ were fitted, where $y = \text{Macoma balthica}$ mortality, $x =$ initial density of $M.\text{balthica}$, $b =$ maximum feeding rate, $c =$ density of $M.\text{balthica}$ generating half maximum feeding, and $\beta =$ the parameter associated with the form of the response curve; $\beta = 2$ generates a type III curve (Real 1979).

Experimental conditions. The experiments with adult or juvenile Monoporeia affinis in 1990 were run for 15 d, and with adult Pontoporeia femorata in 1995 for 19 d. A faint green light gave a 17 h light:7 h dark cycle. The aquaria were supplied with sea water (ca 1.1 h$^{-1}$ aquarium$^{-1}$) from 16 m depth. During the 1990 experiments the water had a temperature of 5.4 ± 0.1°C (n = 16), and a salinity of 6.8, and in 1995 temperature and salinity were 5.0 ± 0.1°C (n = 14), and 6.2. In 1990, the 1 L glass aquaria of Elmgren et al. (1986) were filled with sieved sediment to a depth of ca 4 to 5 cm, giving a sediment area of 194 cm$^2$. The 2.1 L aquaria were placed randomly in water-filled troughs and connected to the seawater system. In 1995 sieved sediment was added to small 105 ml aquaria, to a depth of ca 2 cm, giving a sediment area of 13 cm$^2$. The aquaria were placed in a temperature-regulated room, and supplied with sea water from the seawater system.

Functional response of adult Monoporeia affinis to Macoma balthica postlarvae. This experiment assessed the feeding response of adult $M.\text{affinis}$ over a range of $M.\text{balthica}$ (length 337 ± 6 μm) densities, between 2400 and 153 000 m$^{-2}$ (25 to 1600 aquarium$^{-1}$; see Table 1). Forty $M.\text{affinis}$ (3800 m$^{-2}$, length 6.8 ± 0.1 mm) were used per aquarium. The design of the experiment was unbalanced, and only one control treatment was used (see Table 1).

Effect of small Monoporeia affinis on survival of postlarval Macoma balthica. This experiment tested whether juvenile $M.\text{affinis}$ can reduce the survival of $M.\text{balthica}$ postlarvae. There were 2 treatments, each with 400 $M.\text{balthica}$ spat per aquarium (38500 m$^{-2}$, length 334 ± 3 μm), one of which received 100 amphipods per aquarium (9600 m$^{-2}$, length 3.6 ± 0.1 mm, 6 replicates), while the other, including 4 replicates, served as a control.

Effect of adult Pontoporeia femorata on survival of postlarval Macoma balthica. This experiment tested whether adult $6.5\pm0.1$ mm long $P.\text{femorata}$ kill juvenile bivalves. Three amphipods (2300 $P.\text{femorata}$ m$^{-2}$) were added to each of 10 vials containing 25 juvenile $M.\text{balthica}$ (19 200 m$^{-2}$, length 312 ± 5 μm). Ten vials without $P.\text{femorata}$ served as controls.

Final measurements. At the termination of the experiments, the sediment was sieved through a 100 μm mesh, and recovered specimens were preserved in 4% buffered formalin, stained with Rose Bengal. The maximum shell-length of $Macoma balthica$ and amphipod length (straightened out individuals, from the tip of the rostrum to end of the last urosome segment) were measured with an image analyser.

RESULTS

Functional response of Monoporeia affinis to Macoma balthica postlarvae

The number of dead $Macoma balthica$ increased with increasing postlarval density in the range tested (Table 1). Considering the control mortality, an average of only 3 postlarvae were killed at the lowest density offered, as compared to 1000 at the highest density. When expressed as the proportion dying during the experiment, the average prey loss rose from 32 ± 5% at the lowest density to 62 ± 2% at the highest, as compared to 20 ± 3% in the control (Fig. 1). The proportion of postlarvae killed increased significantly with prey density (ANOVA, $F_{23} = 3.33$, $p > 0.01$), indicating a type III-like functional response. The functional response described by the type III equation $y = 3718.6x^2/(x^2 + 6.425 \times 10^{10})$ gave a better fit ($r = 0.99$) (Fig. 2), than did the type II equation $y = 1.036 \times 10^7 x/(x + 1.579 \times 10^9)$ ($r = 0.93$), and the correlation coeffi-
Table 1. Functional response of Monoporeia affinis in the presence of Macoma balthica (initial length 337 ± 6 μm). Forty M. affinis per aquarium were added initially (initial length 6.8 ± 0.1 mm). Mean ± standard error of mean values are shown.

<table>
<thead>
<tr>
<th>Treatment (no. of M. balthica added per aquarium)</th>
<th>Control, 400</th>
<th>25</th>
<th>50</th>
<th>100</th>
<th>200</th>
<th>400</th>
<th>800</th>
<th>1600</th>
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<tbody>
<tr>
<td><strong>M. balthica</strong></td>
<td></td>
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<tr>
<td>No. surviving per aquarium</td>
<td>320 ± 17</td>
<td>17 ± 1</td>
<td>31 ± 3</td>
<td>64 ± 7</td>
<td>115 ± 5</td>
<td>196 ± 22</td>
<td>375 ± 11</td>
<td>283 ± 28</td>
</tr>
<tr>
<td>% surviving</td>
<td>80</td>
<td>68</td>
<td>62</td>
<td>64</td>
<td>58</td>
<td>49</td>
<td>47</td>
<td>18</td>
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<tr>
<td>No. killed per amphipod</td>
<td>0.08 ± 0.03</td>
<td>0.24 ± 0.05</td>
<td>0.44 ± 0.17</td>
<td>1.2 ± 0.1</td>
<td>3.1 ± 0.6</td>
<td>6.9 ± 0.3</td>
<td>25 ± 1</td>
<td></td>
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<tr>
<td>Final length (μm)</td>
<td>336 ± 3</td>
<td>330 ± 4</td>
<td>350 ± 9</td>
<td>354 ± 9</td>
<td>352 ± 3</td>
<td>545 ± 4</td>
<td>948 ± 12</td>
<td>360 ± 3</td>
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<td>Length increase (μm)</td>
<td>0</td>
<td>1</td>
<td>13</td>
<td>17</td>
<td>15</td>
<td>8</td>
<td>9</td>
<td>23</td>
</tr>
<tr>
<td><strong>M. affinis</strong></td>
<td></td>
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<tr>
<td>No. surviving per aquarium</td>
<td>39 ± 1</td>
<td>39 ± 1</td>
<td>34 ± 4</td>
<td>37 ± 3</td>
<td>39 ± 1</td>
<td>40</td>
<td>40 ± 1</td>
<td></td>
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<tr>
<td>Final length (mm)</td>
<td>6.9 ± 0.1</td>
<td>6.8 ± 0.1</td>
<td>7.0 ± 0.1</td>
<td>7.0 ± 0.1</td>
<td>6.7 ± 0.1</td>
<td>6.9 ± 0.1</td>
<td>6.8 ± 0.1</td>
<td></td>
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<tr>
<td>No. of replicates per treatment</td>
<td>5</td>
<td>6</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>6</td>
<td>2</td>
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*AAverage of initial number and number of surviving amphipods

Effect of adult Pontoporeia femorata on survival of postlarval Macoma balthica

Pontoporeia femorata of 6.6 mm length significantly reduced bivalve survival, from 93 ± 3% in the control, to 78 ± 3% in the presence of P. femorata (ANOVA, $F_{8,30} = 11.4$, $p < 0.004$); the mortality rate of bivalves per amphipod (average number of amphipods calculated as above) per day was 0.10 ± 0.01. All but one amphipod survived. We assume that the increased bivalve mortality was due to predation, since pieces of crushed shell were found when sieving the amphipod treatment sediment, but not in the sieve residues from the control treatment. Surviving bivalves were significantly longer than those initially added (ANOVA,

![Fig. 1 Macoma balthica. Proportional mortality due to predation by Monoporeia affinis at 7 different postlarval densities over the entire experiment (15 d). (*) Mean proportional mortality at each density. (□) Mean proportional mortality in the control. Error bars represent the standard error of the mean. (---) Assumed mean proportional control mortality for the entire experiment.](image-url)
Furthermore, the proportion of bivalves dying increased with postlarval density. Although there was a control for survivorship in the absence of amphipods only at one density, it seems unlikely that the increased mortality at high prey densities was caused by negative intraspecific interactions. The postlarvae of *M. balthica* have no means of causing each other direct harm, so any negative interspecific interaction would have to be caused by exploitative competition for resources or chemical changes caused by high densities. The highest density of *M. balthica* postlarvae used represents less than 0.8 g wet weight biomass m⁻², far below the normal biomass of either meiofauna or macrofauna in the sediment, and thus could neither have materially increased competition for resources nor, given that flow-through aquaria were used, could it have caused oxygen deficiency or accumulation of harmful excretory products. In reported experiments, control mortality of *M. balthica* postlarvae was less than 10% (Elmgren et al. 1986, this study), except in the functional response experiment, in which it was 20% (this study). In their review, Hunt & Scheibling (1997) reported no case in which competition for food was important as a cause of early post-settlement mortality in sedimantary environments. We therefore conclude that the significantly lower proportional mortality at low prey densities indicates a positively density-dependent (type III-like) functional response on the part of the amphipod predator.

In our study the 2 highest densities of *Macoma balthica* offered were higher than recorded from deeper habitats in the study area, where both species involved are found together (Olafsson & Elmgren 1997). However, the response curve still did not flatten out and, as we assume that *Monoporeia affinis* do eat *M. balthica*, this indicated that the capacity of *Monoporeia affinis* to consume *M. balthica* was not yet saturated. Estimated consumption in the treatment with the highest *M. balthica* density was ca 300 times higher than in the lowest, and consumption rates (estimated after correction for control mortality) ranged from 0.005 to 1.66 *M. balthica* amphipod⁻¹ d⁻¹. With 15 gut fillings a day and with a gut volume of 0.23 mm³ (Elmgren et al. 1986), an 8 mm *M. affinis* has the gut capacity to eat an estimated ca 500 *M. balthica* postlarvae of 330 μm length, with an estimated volume of 0.005 mm³ (extrapolated from length-weight regressions in Ankar & Elmgren 1976), not considering ingestion of other particles. Thus, assuming a consumption of 1.66 bivalves d⁻¹ at the highest density of *M. balthica* offered (which is equal to the mortality rate at the highest density), the
Amphipod abundance was estimated to be ca 2000 m\(^{-2}\) (of recorded items; Sarvala 1971). The prawn Macoma balthica, just like adult (1+) M. affinis (Elmgren et al. 1986). The surviving M. balthica in the juvenile amphipod treatment were significantly longer than both those initially added and the survivors in the control treatment. No significant change in M. balthica length was found in the adult amphipod treatment in the functional response experiment. The increase in mean length of M. balthica in the juvenile amphipod treatment can be due either to enhanced growth in the presence of juvenile M. affinis or to size-selective predation. Juvenile and adult M. affinis mix and disturb the surface sediment (Elmgren et al. 1986, van de Bund et al. 1994), and may thus affect the growth rate of juvenile M. balthica living there. The largest postlarvae found in both treatments were, however, similar in size. Our results cannot clearly differentiate between the 2 possible explanations, which are not mutually exclusive.

The size at which Macoma balthica becomes too large for juvenile Monoporeia affinis to handle effectively is not accurately known, but M. balthica >1 mm are no longer susceptible to predation from adult M. affinis (Segerstråle 1962). In the Gulf of Finland, eastern Baltic, M. balthica grows faster in shallow water, reaching a length of 1 mm in 6 mo at 3 m depth, and after 3 yr at 35 m (Segerstråle 1960). At 10 m depth in the study area, a size of 1 mm is reached in less than 6 mo after settling (Ankar 1980), but Elmgren et al. (1983) suggested that at 30 m depth the postlarvae reached a size of 1 mm only 1.5 to 2 yr after settling.

Our experiments demonstrated that also Pontoporeia femorata can kill postlarval Macoma balthica. The postlarval mortality rate in the presence of P. femorata was 0.10 amphipod\(^{-1}\) d\(^{-1}\). A similar postlarval mortality rate was found in the presence of adult Monoporeia affinis (0.08 amphipod\(^{-1}\) d\(^{-1}\)) at the same prey density, in spite of adult M. affinis having a shorter gut turnover time (mean = 1.5 h) than adult P. femorata (mean = 2.8 h) and thus almost twice as many gut fillings per day (Lopez & Elmgren 1989).

Olausson & Elmgren (1997) estimated the settling cohort of Macoma balthica spat to ca 65 000 m\(^{-2}\) at a 37 m deep station in the Asko area in July 1989, and by October it had decreased to ca 5000 m\(^{-2}\) (Fig. 3). Amphipod abundance was estimated to be ca 2000 m\(^{-2}\) in October 1989 (C. Hill pers. comm.). Assuming that there was no other mortality, a loss of 60 000 M. balthica m\(^{-2}\) over 90 d (July to October) corresponds to a mortality rate of 0.34 M. balthica amphipod\(^{-1}\) d\(^{-1}\), a mortality rate in between the rates from the 400 M. balthica + 40 Monoporeia affinis and 800 M. balthica + 40 Monoporeia affinis treatments of the functional response experiment. Elmgren et al. (1986), using the 40 400 abundances of M. affinis and M. balthica, respectively, and similar sediment, temperature and salinity (their first test), found a mortality rate of 0.22 M. balthica amphipod\(^{-1}\) d\(^{-1}\), which approximately equals the rate obtained in the functional response experiment 400 M. balthica + 40 M. affinis treatment (0.21 M. balthica amphipod\(^{-1}\) d\(^{-1}\)).

Our experiments thus confirm the potential for amphipods to control Macoma balthica recruitment in the field. There were 4 species of macrofauna, other than the amphipods, at the studied station (data from C. Hill pers. comm.). Adult M. balthica affect the recruitment of their own offspring at high densities (Bonsdorff et al. 1986), but not at low densities (Olausson 1989). The abundance of adult M. balthica, at the 37 m station, was lower than reported by Bonsdorff et al. (1986), and therefore it seems likely that the influence of adult M. balthica on small conspecifics was minor. Of the predators, only the isopod Saduria entomon had a significant biomass (about 10 g wet weight m\(^{-2}\)), but this was predominantly of individuals of a size that in other experiments did not eat M. balthica postlarvae (Ej dung & Bonsdorff 1992). The polynoid polychaete Harmothoe sarsi had insignificant biomass (<1 g wet weight m\(^{-2}\)), but was at times present in considerable numbers of very small individuals, most small enough to pass through a 1 mm sieve. H. sarsi is known to eat M. balthica, but only as a minor food item (1% of recorded items; Sarvala 1971). The pria-
pulid Halicryptus spinulosus had low numbers and insignificant biomass, and is not known to feed on M. balthica (Ankar & Sigvaldadottir 1981), but may negatively affect the survival of small M. balthica (Aarnio et al. 1998) at H. spinulosus densities 100-fold larger than discussed here. There are also predators within the meiofauna (Watzin 1983) and other causes of mortality, e.g. loose-lying algal mats (Bonsdorff 1992). Nevertheless, it seems clear that, while other mortality factors may have made contributions, amphipod predation was the major factor restricting M. balthica recruitment at this site, and, by inference, over large areas of the Baltic Sea, as first proposed by Hessle (1924) and Segerstråle (1960). Furthermore, prey populations may be stabilised below a certain prey density threshold in the density-dependent sigmoid functional response (Hassell et al. 1977). Thus, at low density, postlarval M. balthica seem to experience a refuge from predation as the predatory mortality risk is much lower than at high density. Although the area studied has low diversity, and some information about interactions among its inhabitants exists (Elmgren et al. 1986, Hill & Elmgren 1987), physical and biological factors acting over larger areas must be known before large-scale generalisations for Baltic soft bottoms can be made and trusted.

Meiofauna may also affect the diversity and density of recruiting macrofauna, and a conceptual model including juvenile macrofauna-permanent meiofauna interactions was proposed by Bell & Coull (1980). Further, Watzin (1986) suggested that meiofaunal interactions with juvenile macrofauna should be considered in modelling benthic community organisation. Our experiments indicate that interactions among juvenile macrofauna and temporary meiofauna should also be taken into consideration, as they may affect the structure of benthic communities.

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