

Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna

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ABSTRACT: Priapulids are potentially important in structuring soft-bottom communities in temperate and arctic regions, and this study is a first attempt to evaluate their importance in zoobenthic communities. *Halicryptus spinulosus* is an important component of the zoobenthos of the northern Baltic Sea. It is competitive in harsh environmental conditions as it can withstand hypoxia and hydrogen sulphide. The natural food selection of *H. spinulosus* consists mainly of detritus (62 to 68% of the stomach contents) and 10 infaunal categories (the amphipod *Monoporeia affinis* and other crustaceans being most frequent). The effects of *H. spinulosus* on both meio- and macrofauna were studied experimentally. Significant negative effects were found for both meiofauna (nematodes and total abundance) and macrofauna (*Manayunkia aestuarina*, oligochaetes and total abundance). The effects on recruitment (mainly larval *Macoma balthica*) were also significant. In the field, total abundance and the number of nematodes were also significantly reduced by the presence of *H. spinulosus*. The effects of *H. spinulosus* on other fauna is suggested to be a consequence of predation in combination with disturbance.

KEY WORDS: *Halicryptus spinulosus* · Priapulida · Meiofauna · Macrofauna · *Macoma balthica* · Recruitment · Predation · Disturbance

INTRODUCTION

Interactions between meiofauna and higher trophic levels have been studied since the 1980s, and meiofauna has proven to be a food source for both juvenile and small fish (Alheit & Scheibel 1982, Hicks 1984, Sogard 1984, Fitzhugh & Fleeger 1985, Gee et al. 1985, Pihl 1985, Gee 1987, Coull 1990, Aarnio & Bonsdorff 1993, Aarnio et al. 1996), and for some macrobenthic organisms (Bell & Coull 1978, Bell 1980, Hoffman et al. 1984, Pihl 1985, Gee 1987, Coull 1990). However, only a few studies have dealt with the effects of predators on meiofauna assemblages (Bell & Coull 1978, Smith & Coull 1987, Aarnio et al. 1991, Sundelin & Elmgren 1991, Nilsson et al. 1993, Ólafsson et al. 1993). Most studies have been able to distinguish only small or no effects of macrofauna on meiofauna (Reise 1979, Gee et al. 1985, Smith & Coull 1987, Mattila et al. 1990, Kennedy 1993, Ólafsson et al. 1993, Bonsdorff & Pear-

son 1997). Where found, these effects are caused mainly by predation (Hoffman et al. 1984, Ólafsson & Moore 1990), disturbance (Creed & Coull 1984, Branch & Pringle 1987, Ólafsson et al. 1990, Warwick et al. 1990) or both (Bell & Coull 1978, Bell 1980, Palmer 1988). However, most of these studies deal with the effects of epibenthic macrofauna on meiofauna, and virtually no attention has been directed towards the interactions between macroinfaunal species and meiofauna.

The phylum Priapulida consists of 8 macrobenthic and 9 meiobenthic species. They are practically restricted to cold waters, as most species are concentrated towards temperate and arctic regions. Few species live in tropical areas, and these are mainly of meiofaunal size. Priapulids live in various kinds of sediments but prefer mud or clay, and they occur from the intertidal to abyssal depths (van der Land 1970, Calloway 1988). The priapulid *Halicryptus spinulosus* (von Siebold), also called 'a living fossil', occurs in the boreal and arctic waters of the Northern Hemisphere. It is able to burrow deep into the sediment, down to 30 cm depth, and

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the burrows may have several openings to the surface (Powilleit et al. 1994). As a consequence of its sedentary life-strategy it is able to live in marginal biotopes. It can, for example, withstand conditions of hypoxia and even hydrogen sulfide for prolonged periods (van der Land 1970, Oeschger 1990, Schreiber et al. 1996). It is a weak competitor, but in harsh environmental conditions it may be the dominating species in benthic communities (van der Land 1970). In the northern Baltic Sea it is widely dispersed but occurs in relatively low abundances (50 to 150 ind. m⁻²). Here it is most common at depths below 10 m, while elsewhere it inhabits very shallow waters. Few studies have analysed the possible structuring role of priapulids in the benthic community. Ankar & Sigvaldadottir (1981) described the food composition of *H. spinulosus* in the northern Baltic Sea, but to our knowledge no previous studies have analysed the importance of the priapulids as possible regulators of other fauna.

The aim of this study was to investigate the diet of *Halicryptus spinulosus* in the Archipelago Sea (northern Baltic Sea, 60°N, 20°E), and to experimentally study whether *H. spinulosus* has any predation/disturbance effects on other fauna (meiofauna and settling macrofauna, such as the bivalve *Macoma balthica*).

METHODS

Food selection. 227 individuals of *Halicryptus spinulosus* were collected at 31 stations in the Archipelago Sea, from depths between 16 and 78 m, during 1994 to 1996. Sampling was done using an Ekman-Birge grab (289 cm²) or Box corer (441 cm²). The specimens were stored in 4% formalin or 70% alcohol. They were collected from 3 separate field surveys, and, despite the different preservation methods, all individuals, and their stomach contents, seemed well preserved when analysed (within 1 mo of preservation). They were weighed (accuracy 0.1 mg) and their length and breadth were measured to the nearest 1 and 0.1 mm, respectively. The intestine was removed and rinsed with water. The length and width of the intestine and of the contents of the intestine were measured to the nearest 0.1 mm, whereafter the contents were put in a drop of glycerine on a glass slide and analysed using stereo- and light microscopes (Ankar & Sigvaldadottir 1981). The prey were identified to nearest taxon or, if possible, to species. Annelids were identified by their chaeta and crustaceans by their chitinous exoskeleton parts. All unidentified material was classified as detritus. The proportion of detritus in the total contents of the intestine was estimated by eye. The frequency of occurrence of each food item was calculated according to Hynes (1950) for small (1 to 6 mm) and large

(>6 mm) *H. spinulosus* separately. These 2 size classes were chosen for comparison of the results with those of Ankar & Sigvaldadottir (1981). Also the number of individuals was most even in both size classes when using this classification.

Field enclosure experiment. In this experiment we studied the effects of *Halicryptus spinulosus* on meio- and macrofauna. The experiment was done at 9 m depth on an exposed bottom in the Åland archipelago, northern Baltic Sea (60° 17' N, 19° 49' E), during August 24 to September 20, 1994. Ten plastic cylinders (Ø 4.8 cm, height 15 cm) were pushed 10 cm deep into the sediment. Two *H. spinulosus* each (size: 9 to 12 mm) were put in 5 of the cylinders, while the other 5 served as control treatments. This density corresponds to approximately 1100 ind. m⁻² or about 10× natural density, but, as exemplified by sediment profile imaging photographs by Bonsdorff et al. (1996), specimens of *H. spinulosus* may occur just a few cm apart. All cylinders were covered with a 2 mm mesh net to ensure enclosure of *H. spinulosus*. Reference samples (Ø 2.5 cm) were taken both at the start and at the end of the experiment from the surrounding area. When terminating the experiment, 1 core sample (Ø 2.5 cm) was taken from each cylinder for the analysis of meiofauna. The remaining contents of the cylinder were taken for macrofauna. All manipulations and all sampling was done by SCUBA diving. All samples were preserved in 4% formalin and the meiofauna samples were dyed with rose bengal. In the laboratory, the meiofauna samples were sieved on 4 sieves, 0.5, 0.25, 0.125 and 0.063 mm, and the macrofauna samples were sieved on a 0.5 mm sieve. The samples were analysed by means of a stereomicroscope and the organisms identified to nearest species/taxa and counted. The effects of the treatments (*H. spinulosus*, control) on macrofauna and meiofauna abundances were statistically compared using 1-way ANOVA (Sokal & Rohlf 1981) after testing for homogeneity of variances and normality of the data. The reference samples from the beginning and the end of the experiment were also statistically compared (1-way ANOVA) to detect possible faunal changes in the area during this period. Shannon-Wiener's index of diversity (H' ; \log_2) and its evenness component (J) were calculated for each replicate according to Shannon & Weaver (1963), and to detect any structural differences between treatments these were statistically compared using Student's *t*-test (unpaired, 2-tail; Sokal & Rohlf 1981).

Effects of *Halicryptus spinulosus* on settling in-fauna. Aquarium experiment: The aquarium experiment was done using 35 cm high cylindrical aquaria with a diameter of 5 cm. A 4 cm thick layer of azoic (-18°C, 48 h) sediment (1/3 sand, 2/3 clay) was put in each aquarium, and the aquaria were filled with fil-

tered (0.063 mm) sea water. The aquaria were supplied with oxygen by air bubbling about 1 cm above the sediment surface. Two *H. spinulosus* each (6 to 10 mm, corresponding to 1018 ind. m⁻²) were added to 3 aquaria, while the other 3 aquaria served as predator-free controls. The potential predators were allowed to burrow into the sediment, after which approximately 200 larvae of *Macoma balthica* were added with a pipette to each aquarium. This corresponds to an abundance of 100 000 ind. m⁻² when settled, which is a naturally occurring density in this area during settling (Bonsdorff et al. 1995a). The larvae were allowed to settle in the aquaria, and after 7 d we checked the number left in the water column by sampling 50 ml from 3 aquaria and counting the number of larvae. Since about half of the larvae were still in the water column, the experiment was continued for an additional week. At the end of the experiment the water and sediment were removed and the number of larvae counted separately from these 2 media. After testing for homogeneity of variances and normality of the data, the treatments were compared using 1-way ANOVA (Sokal & Rohlf 1981).

Field experiment with sediment traps: This experiment was done in the field using 4 sediment traps, each with double sedimentation-tubes (40 cm high, Ø 6 cm). A 4 cm thick layer of azoic sediment was put in each tube and 2 *Halicryptus spinulosus* (8 to 14 mm, corresponding to 707 ind. m⁻²) added to 1 tube on each trap. The traps were placed so that the tubes were suspended vertically at 11 to 12 m depth, 3 to 4 m above the bottom. A submerged buoy held the construction in vertical position, and a surface buoy marked the position of the traps. The experimental time was 7 wk (May 24 to July 15, 1994), during which plankton samples were taken weekly to monitor the number of *Macoma balthica* larvae in the water column, in order to estimate the time of settling (Bonsdorff et al. 1995a). The experiment was ended when the number of larvae in the water decreased to near zero, and peak settling was expected. The traps were lifted, the tubes removed and both water and sediment collected from the tubes. The number of *M. balthica* larvae and other fauna found in the traps were counted. The treatments were compared using Student's *t*-test (paired, 2-tail) after testing for homogeneity of variances and normality of the data (Sokal & Rohlf 1981).

RESULTS

Food selection

The diet of *Halicryptus spinulosus* is presented in Table 1. The proportion of empty stomachs was 64 %

Table 1. Frequency of occurrence (%) of species/taxa in the guts of *Halicryptus spinulosus*

Food item	Size class		Total (n = 96)
	1–6 mm (n = 50)	>6 mm (n = 46)	
<i>Monoporeia affinis</i>	10	28	19
Amphipoda unidentified	6	11	8
Crustacea unidentified	24	33	28
Oligochaeta	20	11	16
<i>Pygospio elegans</i>	2	6	4
Polychaeta unidentified	0	4	2
Chironomidae	0	6	3
Nematoda	0	6	3
<i>Halicryptus spinulosus</i>	0	2	1
Algal remains	12	24	18
% detritus (\bar{x})	68	62	65
Total n	139	88	227
% empty guts	64	48	58

for small and 48% for large *H. spinulosus*. A large proportion of the contents found in the guts was characterised as detritus (62 to 68% of the gut contents in both size classes). The smaller *H. spinulosus* had consumed prey from 6 categories, while the larger ones had eaten prey of 10 faunal categories. The most frequently occurring prey items were Oligochaeta and Crustacea for the smaller, and Crustacea, especially *Monoporeia affinis*, for the larger ones. Other frequently occurring food components were algal remains, which were found in 12% of the small *H. spinulosus* and in 24% of the larger ones (Table 1).

Effects of *Halicryptus spinulosus* on meio- and macrofauna

Twenty zoobenthic species/taxa were recorded in the ambient area (Table 2). No significant differences in faunal abundances between the reference samples from August 24 and September 20 were recorded, indicating that faunal composition and abundances changed little during this period. 25 species/taxa were found in the experimental cylinders. Dominating meiofaunal taxa were: Nematoda, Turbellaria, Harpacticoida and Ostracoda (Fig. 1a), and dominating macrofaunal species/taxa were: Oligochaeta, *Macoma balthica*, *Hydrobia* sp., *Pygospio elegans* and *Manayunkia aestuarina* (Fig. 1b). The meiofaunal total abundance was significantly lower ($p < 0.05$) in the treatment with *Halicryptus spinulosus* compared to the control cylinders. At taxon level only nematodes differed significantly between the 2 treatments. Their abundance was lower ($p < 0.05$) in the treatment with *H. spinulosus* than in the controls (Fig. 1a). For macro-

Table 2. Number of individuals per meio- and macrofaunal species/taxon (ind. per 10 cm² and ind. m⁻², respectively) in the ambient area during field enclosure experiment

Species/taxon	Ambient area	
	Start	End
Meiofauna (ind. per 10 cm²)		
Ciliophora	72 ± 40	63 ± 11
<i>Protohydra leuckarti</i>	7 ± 2	5 ± 1
Turbellaria	89 ± 7	120 ± 10
Nematoda	370 ± 20	320 ± 40
Gastrotricha	–	0.4 ± 0.4
Rotifera	5 ± 3	5 ± 2
Kinorhyncha	2 ± 0	2 ± 1
Cladocera	0.7 ± 0.7	–
Ostracoda	36 ± 6	45 ± 3
Harpacticoida	75 ± 17	75 ± 10
Calanoida	–	0.4 ± 0.4
Cyclopoida	0.7 ± 0.7	–
Copepoda nauplii	31 ± 12	35 ± 3
Hydracnidae	13 ± 6	15 ± 3
Total abundance	700 ± 80	690 ± 50
Macrofauna (ind. m⁻²)		
<i>Pygospio elegans</i>	1400 ± 700	800 ± 800
<i>Manayunkia aestuarina</i>	1400 ± 1400	1200 ± 800
Oligochaeta	2700 ± 700	2900 ± 800
Chironomidae	700 ± 700	–
<i>Macoma balthica</i>	1400 ± 700	1200 ± 500
<i>Hydrobia</i> spp.	3400 ± 700	3700 ± 1500
Total abundance	10900 ± 3800	9800 ± 2200

fauna a significant difference was found for total abundance ($p < 0.05$), *M. aestuarina* ($p < 0.05$) and Oligochaeta ($p < 0.01$), all being more abundant in the controls than in the treatment with *H. spinulosus* (Fig. 1b). Macrofaunal diversity was significantly higher ($p < 0.01$) in the controls than with *H. spinulosus*, while no difference was found regarding meiofaunal diversity. Macrofaunal evenness showed no differences between the treatments, while meiofaunal evenness was significantly higher ($p < 0.05$) in the treatment with *H. spinulosus* than in the control treatments (Table 3).

Effects of *Halicryptus spinulosus* on settling fauna

Aquarium experiment

On termination of the experiment, no *Macoma balthica* larvae were found in the water phase in either treatment. The number of settled *M. balthica* differed significantly ($p < 0.05$) between the treatments. There was on average ($\bar{x} \pm SE$) 100 ± 6 (50759 ± 3060 ind. m⁻²) *M. balthica* in the controls and only 34 ± 14 (17316 ± 7345 ind. m⁻²) in the treatment with *Halicryptus spinulosus*.

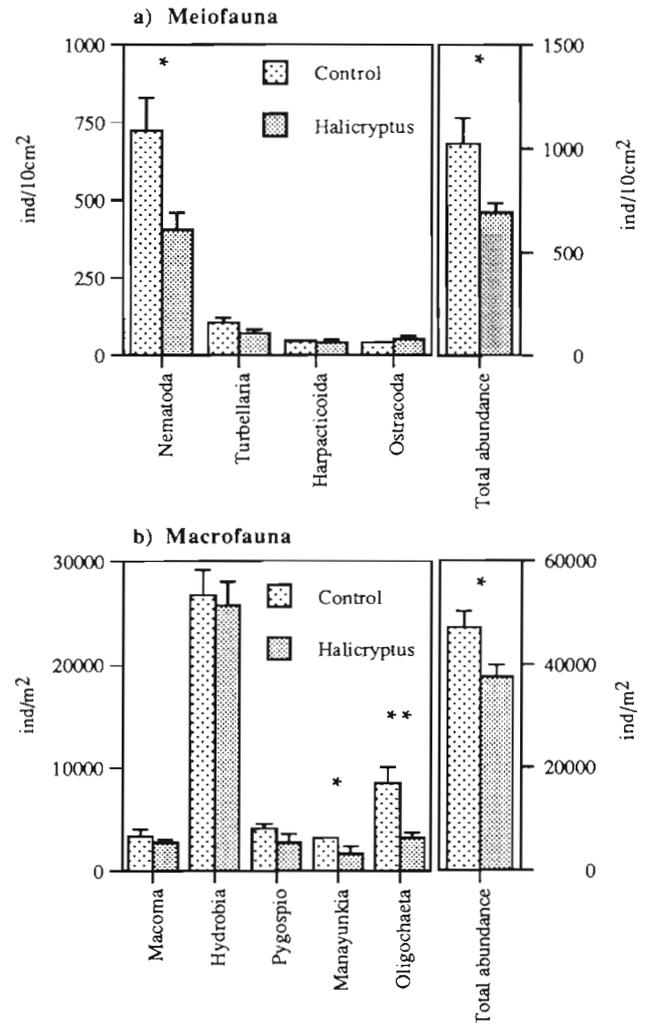


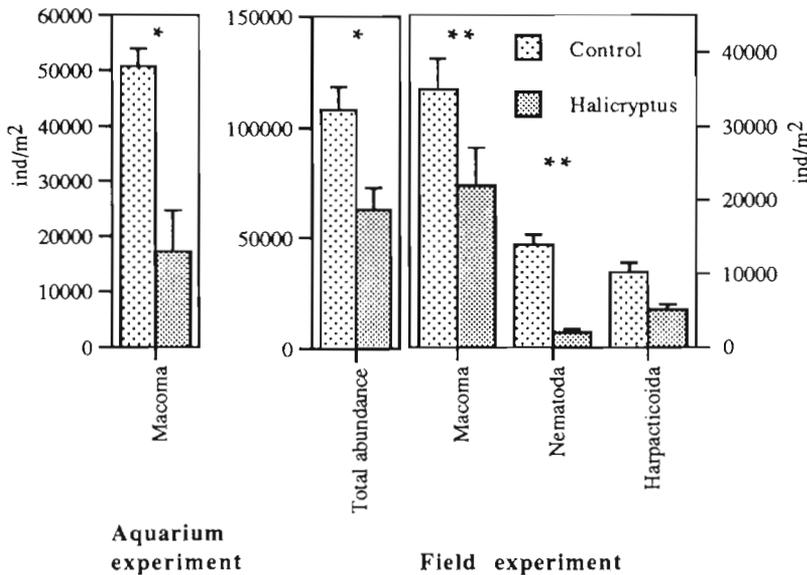
Fig. 1. Abundance of the dominating (a) meiofauna and (b) macrofauna in the field enclosure experiment. * * $p < 0.01$, * $p < 0.05$. Note the different scales on the y-axes

Experiment with sediment traps

Fourteen species/taxa were found in the sediment traps. The dominant taxa were *Macoma balthica*, Calanoida, Cyclopoida, Harpacticoida and Nematoda. Total abundance was significantly higher ($p < 0.05$) in the control tubes compared to the tubes with *Halicryptus spinulosus*. The number of *M. balthica* differed significantly ($p < 0.01$) between treatments; there were on the average ($\bar{x} \pm SE$) 62 ± 15 (21928 ± 5223 ind. m⁻²) *M. balthica* in the treatment with *H. spinulosus* compared to 99 ± 12 (34925 ± 4213 ind. m⁻²) in the controls. Significantly more nematodes ($p < 0.01$) were found in the controls than in the treatment with *H. spinulosus* (Fig. 2).

Table 3. Diversity (H') and evenness (J) in meio- and macrofauna assemblages ($\bar{x} \pm SE$) in field enclosure experiment in both treatments. ** $p < 0.01$, * $p < 0.05$; ns: no significant difference

	Control		<i>Halicryptus spinulosus</i>		Levels of significance	
	H'	J	H'	J	H'	J
Meiofauna	1.41 \pm 0.08	0.44 \pm 0.02	1.74 \pm 0.15	0.54 \pm 0.04	ns	*
Macrofauna	1.89 \pm 0.06	0.68 \pm 0.03	1.57 \pm 0.05	0.58 \pm 0.03	**	ns

Fig. 2. Abundance of the dominating settled species/taxa in the aquarium and field experiments. ** $p < 0.01$, * $p < 0.05$. Note the different scales on the y-axes

DISCUSSION

Our results clearly illustrate the potential importance of *Halicryptus spinulosus* in regulating benthic meio- and settling macrofauna. The diet of *H. spinulosus* in the Archipelago Sea was similar to that reported by Ankar & Sigvaldadottir (1981) in the Askö-Landsort area in the NW Baltic proper. In their study, 41 to 44% of the guts were empty and 83 to 89% of the filled guts contained detritus. We found a somewhat higher proportion of empty guts (\bar{x} : 58%), whereas the amount of detritus recorded was correspondingly lower (62 to 68%). *H. spinulosus* is considered to be mainly carnivorous (Ankar & Sigvaldadottir 1981). The large number of empty stomachs indicates that *H. spinulosus* is able to starve for prolonged periods, which must be considered as an advantage in unpredictable environments with a varying food supply. It may also be possible that the specimens had regurgitated when preserved, but nothing like this was noted in our study.

Predation and disturbance affect infauna

In the field enclosure experiment, *H. spinulosus* had a negative effect on both meio- and macrofaunal abundances. At species/taxon level, negative effects were found for Nematoda, the polychaete *Manayunkia aestuarina*, and Oligochaeta. Other studies have shown that nematodes may be negatively affected by the macrofaunal predator/disturber (e.g. Creed & Coull 1984, Branch & Pringle 1987, Ólafsson & Elmgren 1991, Sundelin & Elmgren 1991), whereas predation/disturbance by fish has not affected nematode abundances. This may be due to nematodes having deeper vertical distribution than other meiofaunal taxa. Fish usually feed on the sediment surface and have access only to the uppermost sediment layer (Gee

1987, Ellis & Coull 1989). Nematodes, which are particularly tolerant to hypoxia, are able to burrow deep into the sediment (Jensen 1983). Macroinfauna live in the same vertical habitats as meiofauna, and their activities constitute a potentially significant source of disturbance (Creed & Coull 1984, Ólafsson et al. 1990, Ólafsson & Elmgren 1991). The negative effects that *H. spinulosus* has on Nematoda are probably caused by its burrowing activity, since few nematodes were found in its gut. It is possible, though, that *H. spinulosus* had consumed the nematodes, as these are digested rapidly (Scholz et al. 1991). Palmer (1988), when separating effects of predation from predator-induced disturbance, found that disturbance was responsible for the reduction in nematode abundances. Other meiofauna was not affected in our study. Macrofaunal burrows may enhance the presence of smaller infauna by providing suitable habitats in deeper sediments, such as refuge from predators or improved oxygen conditions (Woodin 1978, Reise 1985, Dittman 1996). Thus the sediment near *H. spinulosus* burrows

may allow meiofauna to exhibit a deeper vertical distribution and thus possibly mask some effects of the predator/disturber. The effects on *M. aestuarina* were probably caused by disturbance since no specimen has been found in the gut of *H. spinulosus* (Ankar & Sigvaldadottir 1981, this study). Bonsdorff et al. (1995b) and Gee et al. (1985) found negative predation effects by crustacean predators on *M. aestuarina*. Gee et al. (1985) also showed that *M. aestuarina* does not withdraw into its tube in response to vibration disturbance caused by a predator, making it more vulnerable to predation. Oligochaeta, on the other hand, is a preferred food item of *H. spinulosus*, and the negative effects on them can be attributed to direct predation, but additional disturbance effects cannot be excluded.

It is not always possible to separate the effects of disturbance from those of predation (Menge & Sutherland 1987). Predation may increase stability in zoobenthic communities and lead to a higher diversity as it reduces competition (Caswell 1978, Peterson 1979, Bonsdorff et al. 1986, Menge & Sutherland 1987, Sandberg & Bonsdorff 1990). On the other hand, disturbance can alter the outcome of biotic interactions, as it may counteract the strength of some biotic interactions such as competition and predation (Menge & Sutherland 1987). The diversity analysis showed that *H. spinulosus* had a negative effect on the macrofaunal community structure, whereas meiofaunal assemblage diversity was not affected. However, a significant increase in meiofaunal evenness was detected in the presence of *H. spinulosus*. This was due to its negative effects on the dominant meiofaunal taxon (i.e. nematodes; Fig. 2). Our diversity and evenness analyses were calculated on both the number of species and taxa (for those that were not determined to species level), but they are still comparable with each other.

Effects on settling and recruitment

Halicryptus spinulosus had a negative effect on the settling of *Macoma balthica* in both aquarium and field experiments. Also, direct negative effects were found on nematodes and the total abundance of fauna in the field experiment (Fig. 2). The bivalve *M. balthica* is one of the most important species of the Baltic benthic ecosystem (Segerstråle 1962) and it has a key position in many energy pathways both in terms of feeding and as a prey organism (Ankar 1977, Bonsdorff & Blomqvist 1993, Bonsdorff et al. 1995a, b). The pelagic larvae settle on soft bottoms at depths of about 10 m and are temporary members of the meiofauna until reaching macrofaunal size. The massive recruitment, during which *M. balthica* may reach densities of 300 000 ind. m⁻², compensates for a variety of factors

affecting the chances for survival. The settling is affected by both abiotic and biotic factors, among which predation and sediment disturbance are important (Thistle 1981, Bonsdorff et al. 1995a). Since no *M. balthica* have been found in the digestive tracts of *H. spinulosus*, the effects are probably due to disturbance. *H. spinulosus* has a bioturbative effect on the newly settled *M. balthica*, as the juveniles are situated at the sediment surface and will be immediately affected by sediment disturbance (Bonsdorff et al. 1995a). Powilleit et al. (1994) showed that the burrowing of *H. spinulosus* causes direct transport of particles into the sediment, and that this activity was at least in the same order of magnitude as has been reported for other burrowing invertebrates. Other macrobenthic organisms have also been shown to inhibit recruitment of juvenile clams by bioturbative effects (Peterson 1977, Probert 1984, Elmgren et al. 1986, Hall 1994, Ólafsson et al. 1994 and references therein). Nematodes had probably ended up in the traps with drifting algal material, which was found in small amounts in all tubes. They could possibly also have entered the tubes from the bottom, with suspended material, but as the tubes were placed at about 4 m above the sea floor, this seems unlikely. Harpacticoids could have swum to the traps, or they could have ended up in the traps passively, like the nematodes. No negative effects on harpacticoids were recorded in this study. In previous studies by Ólafsson & Elmgren (1991), Ólafsson et al. (1993) and Alongi (1985), harpacticoids were not negatively affected by physical disturbance. In fact the disturbance seemed to have some positive effects on the copepods, possibly due to improved available food resources caused by the sediment reworking by the disturbers (Ólafsson & Elmgren 1991).

Role of eutrophication

One main threat to the Baltic ecosystem today is eutrophication, as discharges of nutrients and deposition of organic matter have increased during the 20th century (Elmgren 1989, Bonsdorff et al. 1991, Wulff et al. 1994). As a consequence the oxygen saturation in bottom-near waters has decreased. Ecologically there is no other abiotic factor that has changed so drastically in such a short period as dissolved oxygen (Diaz & Rosenberg 1995). This has affected important biotic interactions in zoobenthic communities, and several species have been forced to emigrate from such areas (Elmgren 1989, Sandberg 1994, 1996, Norkko & Bonsdorff 1996). Changes in predator-prey relationships due to hypoxia can have crucial effects on population and community structure (Suthers & Gee 1986, Pihl et al. 1992, Sandberg 1996, 1997). Negative environmen-

tal conditions, such as hypoxia, may benefit some species, such as *Halicryptus spinulosus*. Its high tolerance to hypoxia/anoxia and its ability to starve for prolonged periods make *H. spinulosus* a strong competitor in sediments subject to intermittent periods of anoxia/hypoxia. But, when conditions improve, the role of *H. spinulosus* decreases again, and other competitors, such as amphipods or polychaetes, increase in abundance (Weigelt 1991, Laine et al. 1997).

Predation and biological disturbance (bioturbation) are some of the main factors influencing zoobenthic population dynamics and community structure in soft-bottom systems (Peterson 1979, Reise 1985, Sih et al. 1985, Wilson 1990, Hall 1994). The 3-dimensional structure of soft sediments offers refuge to infaunal benthos from epibenthic predation and sediment disturbance, and the refuge value is directly linked to the burrowing depth into the sediment (Norkko 1997). However, an infaunal predator/disturber may have a greater effect on fauna, as they affect both the surface-near sediments and the deeper sediment layers. Few predation/disturbance studies have demonstrated clear structuring effects at the community level, and enclosure/exclosure experiments have been criticised for their artefacts (Ólafsson et al. 1994, Raffaelli & Hawkins 1996). Manipulative field experiments are important in order to increase our knowledge of the functioning of marine benthic systems, but the scale of the experiments should fit the dynamics of the system being studied (Thrush et al. 1994). Enclosure experiments have been criticised for inducing abnormal behaviour in predators, particularly mobile epibenthic predators. *Halicryptus spinulosus* is sedentary and therefore not restricted by the enclosures. It moves primarily in the vertical direction and as a consequence it has local effects, which may be more easily detected than effects of more mobile predators.

In conclusion, this study has shown that *Halicryptus spinulosus* has negative effects on some meio- and macrobenthic species. The settling and recruitment of animals were also negatively affected by *H. spinulosus*. The significant role of *H. spinulosus* in controlling the zoobenthic assemblage (both meio- and macrofauna) was somewhat unexpected. As the macrofaunal priapulids are sedentary and have similar life styles, we believe that the results from this study may possibly be applied for other areas with other priapulid species as well. Yet more research in this area should be conducted, to elucidate the overall importance of priapulids in marine soft-bottom systems.

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