

Effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: a laboratory approach

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ABSTRACT: In order to evaluate the importance of biological disturbance on meiofaunal communities in muddy habitats, a laboratory experiment was performed at the Askö Laboratory in the northwestern Baltic proper. The benthic amphipod *Monoporeia affinis* (Lindström) was added to microcosms containing sublittoral mud, in quantities varying from zero up to 80 ind. 104cm⁻². After 2 mo the density of nematodes, the most abundant meiofauna taxon (97 %), was greatest in microcosms without amphipods, but they also occurred in higher numbers in microcosms containing a high density of *M. affinis*, compared to low and medium density microcosms. *M. affinis* appears to have a negative effect on surface-dwelling nematode species but a positive effect on the deeper dwelling *Daptonema* sp. However, nematode assemblage structure remained very similar in all treatments. Copepod abundances increased with increasing numbers of amphipods ($p < 0.002$) and were highest in the high density microcosms. In the microcosms without amphipods, *Macoma balthica* spat was almost twice as abundant as in the amphipod treatments. For kinorhynch and turbellarians there were also significant differences between treatments. The different responses of the major taxa to the biological disturbance may reflect the multifactorial nature of biotic perturbations.

INTRODUCTION

Abundance, composition and number of species in a given habitat is determined by an array of abiotic and biotic factors. The frequency and magnitude of disturbance have been found to be important organizing factors for assemblages of marine benthic organisms (Paine 1966, Dayton 1971, Connell 1978). How researchers define and quantify the term disturbance is not always clear. This is especially true of biological disturbance which can encompass selective and non-selective predation as well as a variety of habitat modifications resulting from feeding and bioturbation by the disturber.

The activities of the macrofauna are a source of disturbance which may influence the structure of meiofaunal assemblages (Reise & Ax 1979, Thistle 1980, Reidenauer & Thistle 1981, Sherman et al. 1983, Creed & Coull 1984, Hicks 1984, Warwick et al. 1986, Palmer 1988, Warwick et al. 1990, 'Olafsson & Moore 1990, 'Olafsson et al. 1990, Sundelin & Elmgren 1991). However, there are few reports on experiments where the intensity of biological disturbance has been graded into

more than 2 categories, i.e. disturbance or no disturbance, a refinement which may prove necessary to understanding the mechanism behind the perturbation.

The use of meiobenthos in studying changes at the community level in manipulative controlled meso- or microcosm experiments has many advantages. For the rationale behind this approach see for example Warwick et al. (1988). It may be briefly stated here that due to the life history characteristics, small size, short turnover time and direct benthic development of meiobenthic animals, community responses can be measured on realistic spatial and temporal scales in such experiments, while this is usually not the case for macrofauna.

In most of the Baltic Sea the bivalve *Macoma balthica* (L.) and the amphipod *Monoporeia affinis* (Lindström) (syn. *Pontoporeia affinis*; cf. Bousfield 1989) are the dominant macrobenthic species (Elmgren et al. 1986). *M. affinis*, in particular, is very abundant and is found in the muddy substrata in densities ranging up to several thousand per m². In the Askö-Landsort area (Sweden) *M. affinis* was the most abundant macrofaunal species, constituting 46 % of all macrobenthic

variance, all data were first $\log_{10}(x+1)$ transformed and Bartlett's test used to check the assumption of homoscedasticity. When conditions for the use of parametric tests were not fulfilled, Kruskal-Wallis tests and Spearman's rank correlation were employed.

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. *K*-dominance curves were plotted for the combined replicates of each treatment, using the method of Lamshead et al. (1983), and significance testing was carried out according to Clarke (1990) using the ANOSIM randomization test.

RESULTS

Microcosm experiment

The survival rate of the amphipods inside the microcosms was high (on average 90 %) and very similar between treatments (Table 1). The number of dead amphipods was highest in the high density treatment.

The initial densities of the major taxa, when the amphipods were introduced to the microcosms, are shown in Table 2. The initial major taxa composition reflects the findings in the field, exhibiting a very high predominance of nematodes. Compared to the field densities all taxa had lower abundances inside the microcosms, nematode and copepod numbers being only about 1/2 and 1/10 respectively of the field values. The coefficient of variation among microcosms differed between the major taxa. Copepods and nematodes showed the least variation, the coefficient being 18 % and 13 % respectively, while other taxa varied more (Table 2).

Major taxa

Comparison between the initial microcosms and microcosms without amphipods after 2 mo revealed that all the major meiofaunal taxa were in similar numbers (Mann-Whitney *U* tests, $p > 0.05$), apart from copepods which had increased with time (Mann-Whitney *U* test, $p < 0.05$).

Average numbers of the major meiofaunal taxa in each treatment are represented in Table 1 along with the results of statistical tests. There was a significant difference in the number of nematodes among experimental treatments. They were most abundant within microcosms without amphipods. Nematodes were also significantly more abundant in microcosms containing

Table 1. Abundance per microcosm (n=9) of the major meiofaunal taxa in 4 experimental treatments. Initial and final numbers of *Monoporeia affinis* in each treatment are also presented (SD: standard deviation)

Taxon	Zero (ZO)		Low (LO)		Medium (ME)		High (HI)		ANOVA Tukey test
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
<i>M. affinis</i> initial	0		20		40		80		
<i>M. affinis</i> final	0		18	2	37	2	73	4	
Nematoda	18846	1423	15027	673	14833	806	17353	977	***
Harpacticoida	127	69	143	79	151	46	262	66	*** ^a
<i>Pseudobradya</i> sp.	70	48	102	57	107	35	140	55	* ^a
<i>Microarthridion littorale</i>	28	14	9	8	32	10	74	50	***
Nauplii	28	21	32	28	12	12	47	29	NS
Ostracoda	130	27	328	45	175	103	107	66	*** ^a
<i>Macoma balthica</i>	111	22	57	25	56	47	52	35	*** ^a
Kinorhyncha	75	15	22	20	48	21	79	28	*** ^a
Turbellaria	48	26	24	12	45	17	95	39	***
<i>Halicyptus spinulosus</i>	5	4	10	9	8	9	9	6	NS
Other	22	23	10	13	12	12	7	13	

^a Variance heterogeneous, Kruskal-Wallis test employed; * $p < 0.05$, *** $p < 0.001$

lower diversity, as expressed by H' , D and J' , in the medium density microcosms compared to the initial and zero density microcosms. The K -dominance plot (Fig. 2) for combined samples from individual treatments indicates highest rank one dominance in the medium density microcosms compared to other treatments. Paired comparisons of the K -dominance curves, using ANOSIM significance testing, showed that there was a significant difference between medium density treatment and both initial control and zero density treatments ($p < 0.01$).

Natural meiofauna

Table 5 shows the composition and the depth distribution of the major meiofaunal taxa and the 10 most abundant nematode species, as determined from the Kajak core sample. As expected, nematodes were the dominant group, comprising more than 90 % of the total meiofauna. They were most abundant in the upper layers, though found in considerable numbers between 2 and 4 cm. Other taxa seem to be confined to the top 1 cm of the sediment, apart from turbellarians and kinorhynch.

Of the 18 nematode species recorded, *Calomicrolaimus honestus* and *Paracanthochus* spp. (mainly *P. caecus* Bastian) dominated the surface layer (Table 5). There was a shift in the composition in the 1–2 cm layer, where *Leptolaimus elegans* and *L. papilliger* De Man dominated along with *Microlaimus globiceps* De Man. Two species, *Sabatieria pulchra* and *Daptonema* sp. 1, were found in considerable numbers in the 2–4 cm layer. K -dominance plots of the nematode species from each depth zone indicated that the fauna from the 1–2 cm layer was the most diverse and that dominance was highest in the top layer. This was consistent with diversity indices which were highest for the

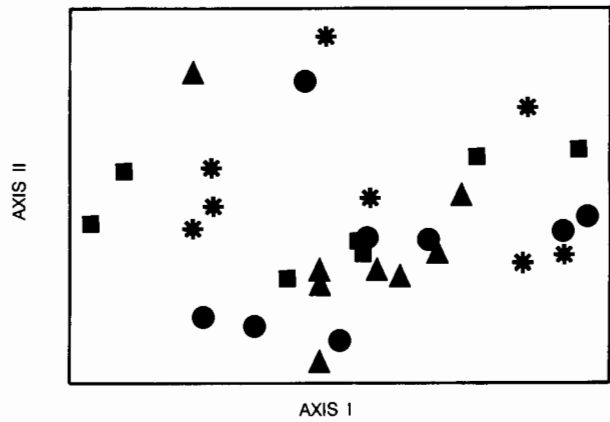


Fig. 1. Two-dimensional configuration (detrended correspondence analysis) of samples of nematode species from 3 treatments and initial control. (*) Initial control; (▲) 0 *Monoporeia affinis*; (■) 40 *M. affinis*; (●) 80 *M. affinis*

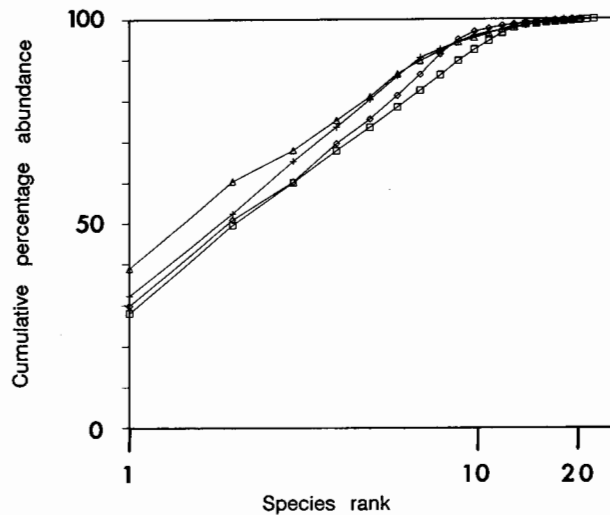


Fig. 2. K -dominance curves derived from combined replicates for 3 treatments and initial control for all nematode species. (□) Initial control; (◇) 0 *Monoporeia affinis*; (Δ) 40 *M. affinis*; (+) 80 *M. affinis*

Table 4. Mean ($n=8$) values of nematode species diversity indices (H' : Shannon-Wiener; D : Simpson), evenness (J' : Pielou) and richness (S : Sanders rarefaction at the 50 individual level) in 4 experimental treatments and from the field. Significance levels presented are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and there is no significant difference (Tukey test) between treatments where the + sign is in the same vertical position

Treatment	H'	D	J'	S
Initial control (IC)	3.00	0.84	0.82	10.91
No amphipods (ZO)	2.94	0.84	0.83	10.38
Medium amphipod density (ME)	2.66	0.78	0.75	9.87
High amphipod density (HI)	2.82	0.82	0.80	9.99
ANOVA (Significance level)	.	***	**	NS
Tukey test	ME +	+	+	
	HI +	+ +	+ +	
	ZO +	+	+	
	IC +	+	+	
Field data	3.40	0.88	0.82	12.03

very similar between treatments. This finding was quite unexpected and can be explained in one of 2 ways. Firstly, the amphipods do not affect the nematode assemblage sufficiently to alter the assemblage parameters, even at high densities. Secondly, the amphipods can affect the assemblage structure significantly, but due to experimental limitations, e.g. short experimental time (only negative effects detectable), fixed number of species due to absence of immigration, we were unable to demonstrate changes in assemblage pattern. Some studies have shown that nematodes can be quite resilient to pollution, with small or no changes in assemblage structure when perturbed (Alongi et al. 1983, Gee et al. 1985, Lamshead 1986, Warwick et al. 1988). This also applies to some studies on biological disturbance (Sherman et al. 1983, 'Olafsson et al. 1990), though in other cases significant differences have been found (Warwick et al. 1986, Warwick et al. 1990).

Among the temporary meiofauna, *Macoma balthica* spat were negatively affected by the presence of the amphipods, which is in accordance with Elmgren et al. (1986), who found the spat being crushed and probably eaten by the amphipods. Sundelin & Elmgren (1991) found that both *M. balthica* spat and ostracods were reduced in a long-term amphipod treatment.

The copepod assemblage consisted solely of 2 species, *Microarthridion littorale* and *Pseudobradia* sp., both in the field and the microcosms. These 2 species seem to be the only representatives of the harpacticoid fauna found in an extensive area of the Baltic proper, below 20 to 30 m, where they can occur in high densities [Sarvala 1971, Ankar & Elmgren 1976 (*Pseudobradia* sp. was then identified as *Halectinosoma abrau*)].

Numbers of copepods increased on average with increasing numbers of amphipods. It seems that the bioturbating activity of the amphipods enhances the reproductive potential of the harpacticoids. How this is brought about remains speculative. *Pseudobradia* sp. showed a considerable increase in density in all treatments during the course of the experiment and its abundance was 2 times greater in the high amphipod density microcosms compared to other treatments, whereas *Microarthridion littorale* was only found in elevated numbers in the high amphipod density microcosms. Both of these species live in the top cm of the sediment. As the generation time of *M. littorale* is highly temperature dependent, of the order of 70 d at 15 °C (Palmer & Coull 1980), one would expect it to be considerably longer in the microcosms (5 °C) and not to be completed within the experimental period. However, post-embryonic development rates of harpacticoid copepods are strongly affected by quantity and quality of food resources (see Hicks & Coull 1983 for review). It is possible that increased sediment rework-

ing in the microcosms improved the available food resources, resulting in shorter generation times and therefore higher density. Alongi (1985) found, for example, that an epibenthic harpacticoid copepod became more abundant in cultures where the surface sediments were regularly disturbed, compared with no disturbance. The increasing number of dead amphipods associated with increasing numbers of amphipods may however have enhanced the food resources, thereby stimulating harpacticoid growth rate. Sundelin & Elmgren (1991) also found enhanced levels of harpacticoids and turbellarians in high amphipod treatments and suggested that the presence of dead amphipods might stimulate scavenging turbellarians.

The nematode assemblage from the field station represents species that are typically found in brackish water environments (Heip et al. 1985). Species composition was similar to that found by Elmgren (1976) at a nearby station of similar bottom type and depth, the 6 most abundant species being the same. The dominance of *Sabatieria pulchra* in the microcosms and the different ranking of the most abundant species from the field can best be explained by the sampling technique. The bulk of the sediment was collected with a benthic dredge which inevitably results in considerable loss of surface material. *S. pulchra* is known to prefer anoxic or very low dissolved oxygen conditions which is often reflected in a deep vertical distribution (Bouwman 1983, Jensen 1984). Although we tried to compensate by enriching the microcosms with surface meiofauna, we were not entirely successful. However, exact duplication of the field species assemblage was not anticipated as modifications of environmental parameters inside the microcosms were bound to occur. Merely sieving the sediment can have drastic effects on the microbial biomass, growth rate and metabolic activity (Findlay et al. 1990) and may therefore affect the meiobenthos. Although some workers have been able to keep relatively rich meiofaunal assemblages in the laboratory (Hockin 1981, Warwick et al. 1988, Austen 1989) they usually do differ from observed field assemblages (McIntyre et al. 1970, Heip 1973, Gee et al. 1985), with a tendency for opportunistic species to become dominant.

While it is clear that biological disturbance may be important in structuring meiobenthic communities, it remains difficult to make general predictions concerning how soft-bottom communities will react to biotic perturbations. This is because biological disturbance is species specific, variable within and between habitats and difficult to scale according to intensity and frequency. Similarities between our results and the longer experiments of Sundelin & Elmgren (1991) still suggest that the effects tend to be reproducible and therefore amenable to experimental investigation.

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