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Small-scale spatial distribution of marine meiobenthos: the effects of decaying macrofauna

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Summary. To evaluate the effects of decaying animals on small-scale horizontal distribution of meiobenthos in muddy habitats, a laboratory experiment was performed at the Askö Laboratory in the northwestern Baltic Sea. A microcosm (35 × 55 × 28 cm) containing a ca. 7-cm thick layer of sieved (0.5 mm) sublittoral mud was established in June 1990. Three months later specimens of the bivalve *Macoma balthica* were collected and killed in boiling water. The sediment inside the microcosm was implanted with empty shell, empty shell and dead animal or left alone. At the end of the experiment (17 days) visual examination of the microcosm revealed black spots at the sediment surface where dead animals had been implanted. The densities of nematodes, the most abundant group (98%), were not significantly different between areas. However total non-nematode fauna was found in much lower numbers ($P < 0.01$) in the black spot areas. A multivariate analysis (detrended correspondence ordination) of nematode species abundance data separated samples from the black spot areas from the others. Of the 25 nematode species recorded in the microcosm, there was a significant difference between areas for four species. The decaying animals clearly attracted *Monhystera disjuncta* which was almost 6 times as abundant in the black spot areas compared to control and shell areas. Both the overall dominant species, *Leptolaimus elegans* and *Calomicrolaimus honestus* were found in lower numbers in the areas of dead *Macoma* than in control and shell areas. *Sabatieria pulchra* was found in lower numbers in the control areas compared to shell and dead animal areas. The overall structure of the nematode assemblage indicated a shift to lower dominance in the dead animal areas and it is speculated that decomposing animal tissue may be of primary importance regarding spatial distribution of meiobenthos.

Key words: Microcosm – Small-scale spatial distribution – Patch formation – Decaying macrofauna – Meiofauna

Spatial heterogeneity of plant and animal populations is a common phenomenon in nature. Aggregations can occur at various dimension levels, from a few millimetres to many kilometres (e.g. Jörgensen 1977; Raymont 1980). The causes of patchy distribution are not always known as a variety of biological and physical variables may account for the observed patterns.

For marine meiobenthic populations differences in physical/chemical properties like granulometry, salinity and oxygen tension are considered to be responsible for differences in assemblages between localities (see reviews by Hicks and Coull 1983; Heip et al. 1985). Variations over smaller distances (centimetres) have also been recorded (Arlt 1973; Findlay 1981; Hogue and Miller 1981; Warwick et al. 1986; Hodda 1990; Pinckney and Sandulli 1990; Fleeger et al. 1990; Ólafsson et al. 1990) and the meiofauna found to be spatially heterogenous. For example Hodda (1990) compared the variation of estuarine littoral nematode populations over three spatial scales i.e. cm, tens of m and hundreds of km. He found that the variation in the nematode population arose from several sources and estimated that about a third of the variance stemmed from small-scale variation in conditions.

Within a given habitat the macrofauna can give rise to a patchy distribution of the meiobenthos. Enhancement of meiofauna may occur in microhabitats e.g. near tubes or burrows (Reise and Ax 1979), in faecal casts (Warwick et al. 1986) and a reduction in feeding or disturbance areas (Sherman et al. 1983; Warwick et al. 1986; Palmer 1988; Ólafsson et al. 1990). Physical attributes also exhibit small-scale variation. Hogue and Miller (1981) found for example that sediment microtopography accounted for differences in nematode populations in an intertidal sand-flat.

Microfauna and flora, which constitute major food resources for meiofauna (see Heip et al. 1983; Hicks and Coull 1983 for reviews), are highly aggregated in the benthos (e.g. Arlt 1973; Jörgensen 1977; Wiackowski 1981; Fenchel 1987; Patterson et al. 1989). This has prompted attempts to assess the relationship between

meiofauna and its potential food patches in the field (Decho and Fleeger 1988; Blanchard 1990; Pinckney and Sandulli 1990). In all these studies some correlation between microphytobenthos and meiofaunal taxa was found. Manipulative experiments examining small-scale spatial heterogeneity of meiofauna are however almost completely lacking. Gerlach (1977) followed the recolonization of nematodes into sand samples with and without a small fish bait in a Bermuda beach. His results indicated that the decaying fish attracted certain nematode species but not others. Lee et al. (1977) used several different experimental approaches to examine the recruitment of benthic meiofauna to patches of selected species of algae. They found that meiofaunal species were selectively recruited to patches of some species of algae but not to others.

Here I report on a laboratory experiment designed to assess the influence of decaying animals on the small-scale distribution of meiofauna.

Material and methods

A microcosm was established at the Askö Laboratory field station in the northwestern Baltic proper (58° 49′N, 17° 38′E) in June 1990. It consisted of a plastic box (35 × 55 × 28 cm) containing a ca. 7-cm thick mud layer. Brackish water was pumped from a depth of 16 m into a cooling tank and distributed to the microcosm through dripping needles. Outflow water from the microcosm was not recycled. Temperature and salinity were kept near field levels i.e. 5–7° C and 6.6–7.2‰.

The sediment was collected using a benthic dredge from a 34-m deep station, approximately 3 km south of the Askö Laboratory. The sediment was sieved through a 0.5-mm mesh to exclude macrofauna, homogenized by stirring and added to the box. To enrich the meiofauna in the microcosm, the top layer of a number of Kajak cores (Blomqvist and Abrahamsson 1985) were sieved as before and added to the microcosm.

Three months later specimens of the bivalve *Macoma balthica* (L.) were collected from the same station and killed in boiling water. The area inside the microcosm was divided into four arrays 6 cm apart. Along each array six points at 4-cm intervals were marked with wooden toothpicks. The area next to each toothpick was either implanted (to a depth of 1 cm) with an empty shell, an empty shell and dead animal or left alone. Eight replicates of the treatments and the control were arranged in a random block design.

After 17 days, the areas were sampled with a cut-off syringe (5.3 cm^2). The samples were fixed in 4% buffered formalin and sieved through a 40-µm mesh sieve. The animals were extracted from the sediment using Ludox (colloidal silica polymer) at a specific gravity of 1.15. The meiofauna was enumerated and identified to major taxa in a petri dish under a stereo dissecting microscope. From each sample about 100 nematodes were picked out randomly, impregnated with anhydrous glycerine (Platt and Warwick 1983) and mounted on slides for identification under a high-power microscope.

For each taxon, differences in density between the treatments were investigated by means of 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 $\log_{10}(x+1)$ transformed and Bartlett's test used to check the assumption of homoscedasticity.

Nematode species abundance data were 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 Lambshead et al. (1983) and the significance of differences between replicated dominance curves assessed using the procedures of Clarke (1990).

Results

Visual examination of the microcosm at the end of the experiment revealed black spots at the sediment surface where dead animals had been implanted. These patches were of variable size and classified as small: <2 cm^2 (3 patches), medium: 2–4 cm^2 (4 patches) and large: >4 cm^2 (1 patch). The rest of the sediment appeared homogenous, smooth and without any obvious pattern.

Major taxa

Nematodes were the most abundant group in the microcosm, composing about 98% of the meiofauna. Although they occurred in the lowest numbers within patches of dead animals the difference was not significant (Table 1). However, kinorhynchs, the second most abundant group, were found in significantly lower numbers within patches of dead animals compared with control and shell areas (Table 1). Oligochaetes (*Nais elinguis* Müller) clearly avoided the black spot areas (Table 1) and were only found (as single specimen) in two of the eight replicates. They were found in variable numbers within other areas and in some replicates within the shell areas they were relatively abundant. The harpacticoids (*Microarthridion littorale* Poppe and *Pseudobradya* sp.) were always found in low numbers within the black spot areas but showed considerable variation within other areas resulting in

Table 1. Average (AVG) number per core ($n=8$) and standard deviation (SD) of the major meiofaunal taxa in the three areas. The results from 1-way ANOVA and Tukey *a posterori* tests are also presented

	Control		Dead *Macoma*		Shell		ANOVA	
	AVG	SD	AVG	SD	AVG	SD	Sign.	Tukey
Nematoda	1941	435	1585	337	1687	318	Ns	
Kinorhyncha	22	4	9	3	25	11	***	Dead *Macoma* < Control, Shell
Copepoda	6	4	2	1	5	4	Ns	
Oligochaeta	5	4	0	1	2	2	***	Dead *Macoma* < Control, Shell
Total without Nematoda	38	6	15	7	38	13	***	Dead *Macoma* < Control, Shell

Ns = not significant, *** $P<0.001$

Table 2. Average (AVG) number per core, standard deviation (SD) and percentage ($n=8$), of nematode species in the three areas. Average species diversity (Shannon-Wiener, Simpson), evenness (Pielou) and richness (Sanders rarefaction at the 50 individual level) is also presented, and the significance of variation in abundance of the 10 most abundant species

	Control			Dead			Shell		
	AVG	SD	%	AVG	SD	%	AVG	SD	%
Leptolaimus elegans	591	111	35.0	343	120	21.6	640	182	33.0 ***
Calomicrolaimus honestus	232	104	13.8	107	61	6.7	203	83	10.4 *
Leptolaimus papilliger	206	75	12.2	205	60	12.9	222	84	11.4 ns
Daptonema sp. 1	154	97	9.1	152	50	9.6	130	50	6.7 ns
Microlaimus globiceps	136	61	8.1	86	38	5.4	108	32	5.6 ns
Sabatieria pulchra	119	38	7.0	209	82	13.2	236	106	12.2 **
Eleutherolaimus sp.	58	32	3.4	52	37	3.3	68	40	3.5 ns
Monhystera disjuncta	51	46	3.0	296	137	18.7	58	55	3.0 **
Desmolaimus sp.	45	20	2.6	49	18	3.1	123	175	6.3 ns
Paracanthonchus	24	28	1.4	13	25	0.8	39	22	2.0 ns
Paramonhystera sp.	23	22	1.4	25	17	1.5	42	58	2.2
Dichromadora sp. 1	13	20	0.8	17	17	1.1	16	22	0.8
Campylaimus sp. 1	13	12	0.7	16	17	1.0	18	14	0.9
Halalaimus sp. 3	12	18	0.7	0	0	0.0	14	12	0.7
Chromadorita fennica	6	9	0.4	2	6	0.1	8	12	0.4
Sphaerolaimus sp. b	4	11	0.2	6	8	0.4	2	5	0.1
Axonolaimus sp.	2	6	0.1	0	0	0.0	0	0	0.0
Phanodermopsis sp. 1	0	0	0.0	0	0	0.0	2	5	0.1
Oxystomina sp. 1	0	0	0.0	0	0	0.0	3	9	0.2
Anoplostoma	0	0	0.0	2	7	0.2	0	0	0.0
Aegialolaimus sp.	0	0	0.0	3	7	0.2	2	7	0.1
Bathylaimus	0	0	0.0	0	0	0.0	2	7	0.1
Enoplolaimus vulgaris	0	0	0.0	2	6	0.1	0	0	0.0
Camacolaimus sp.	0	0	0.0	2	6	0.1	3	8	0.1
Species X	0	0	0.0	0	0	0.0	3	7	0.1
Richness – S	10.53	0.83	0.62	10.71	0.70	0.68	11.28	0.67	0.58
Simpson – D	0.82	0.03	0.05	0.87	0.01	0.05	0.83	0.02	0.04 **
Shannon-Wiener – H'^{a}	2.88	0.15	0.17	3.07	0.05	0.19	3.00	0.10	0.15 **
Pielou – J'^{a}	0.80	0.03	0.05	0.86	0.03	0.05	0.79	0.03	0.04 **

[a] using $\log_2$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$, ns not significant

non-significant difference between treatments (Table 1). Total non-nematode meiofauna was found in lower numbers within the black spot areas (Table 1). There were no apparent differences in the fauna within the black spot areas, i.e. the response was similar in large and small patches.

Nematode assemblage

In total, 25 nematode species were recorded in the microcosm. The congeneric species *Leptolaimus elegans* (Schuurmans Stekhoven and De Coninck) and *L. papilliger* De Man dominated in the microcosm, comprising about 50% of individuals in the control areas (Table 2).

The detrended correspondence analysis clearly separates the samples taken from the black spot areas from the rest of the samples (Fig. 1). It is, however, more difficult to discriminate between control samples and samples from the shell areas (Fig. 1).

Of the ten most abundant species, there was a significant difference between treatments for four species. The most abundant species, *L. elegans*, was found in lower numbers within the areas of dead *Macoma* compared both to control and shell areas (ANOVA, Tukey test, $P<0.001$). *L. elegans* was nevertheless the most abundant species in the black spot areas. Numbers of *Calomicrolaimus honestus* De Man were likewise reduced in the black spot areas (ANOVA, Tukey test, $P<0.05$). For *Sabatieria pulchra* G. Schneider there were significantly fewer individuals in the control areas compared with the other areas (ANOVA, Tukey $P<0.01$). *Monhystera disjuncta* Bastian was the second most abundant species in

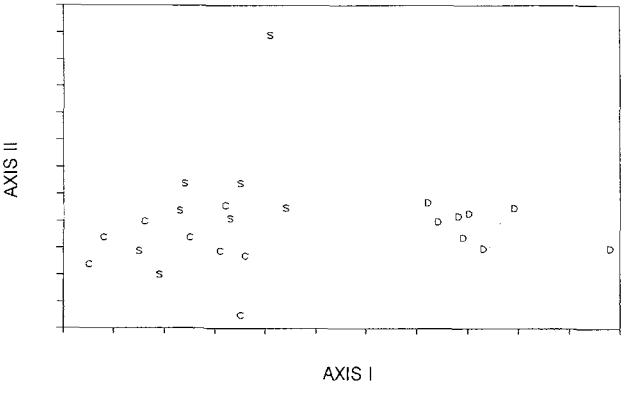

Fig. 1. Two-dimensional configuration (detrended correspondence analysis) of nematode species from the three areas. *C*, control; *S*, shell; *D*, dead animal

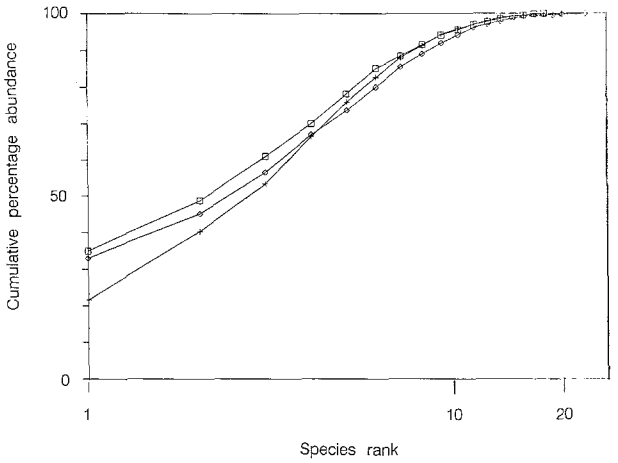

Fig. 2. *K*-dominance curves derived from combined treatment replicates for each area for all nematode species

the dead *Macoma* areas where it was present in much higher numbers than in the other areas (ANOVA, Tukey $P<0.01$).

The *K*-dominance plot (Fig. 2) for the combined replicates from individual treatments indicates that dominance was lowest within the dead *Macoma* areas. Paired comparisons of the *K*-dominance curves, using ANOSIM significance testing (Clarke 1990), showed that the curve from the dead animal treatment was significantly different from the others ($P<0.001$). This was reflected in higher diversity, as expressed by H', D and J', in the black spot areas compared with control and shell areas (ANOVA, Tukey, $P<0.01$ for D and J', $P<0.05$ for H').

Discussion

From this experiment it is quite evident that the presence of decaying dead animals greatly affects the meiofaunal community in a laboratory microcosm.

The taxa dwelling at or near the surface were all reduced in abundance within the dead animal areas. In oxic sediments, bacterial sulfate reduction can occur within in faecal pellets and detrital particles (Jörgensen 1977). This may have occurred within in the dead animal areas producing an accumulation of H_2S and a bacterial community similar to that of the RPD layer – features that may be unattractive to surface taxa. Although the presence of sulfate-reducing bacteria was not determined, the dark colour of the sediment above the implanted dead animals is indicative of a reducing environment.

For the nematodes a response at the major taxon level (phylum) was clearly masked by a concurrent decrease in numbers of the most abundant species and an increase in an opportunistic species in the black spot areas. This finding demonstrates the importance of identifying individuals to lower taxonomic levels when assessing meiofaunal community responses. This is in an agreement with Heip et al. (1988) and Warwick et al. (1988) who found that at taxonomic levels above the family rank meiofaunal community response to environmental change was difficult to detect.

Decomposing animal tissue may attract bacterial feeders as well as scavengers *sensu* Jensen (1987). A specialized ciliate fauna can be associated with the initial stages of decomposition of plant or animal tissue (Fenchel 1968). The importance of Protozoa in the nematode diet has, however, not yet been evaluated but could be of considerable importance. In Gerlach's (1977) study only one nematode species (*Sabatieria migrans* Jensen and Gerlach) was attracted to the decaying fish. The structure of the buccal cavity of this nematode indicates deposit feeding habits (Wieser 1953; Jensen 1987) so it appears this species was attracted by associated microflora or protozoa. Scavengers were absent from the control and experimental samples (Gerlach 1977).

When present, scavengers (Oncholaimidae and Thoracostomopsidae), have been observed eating the remains of dead animals including polychaetes, bivalves, shrimps and gastropods (Jensen 1987; Lorenzen et al. 1987 and references therein). In the soft bottoms of the inner Flensburg and Kiel fjords, Lorenzen et al. (1987) found mass aggregations of *Pontonema vulgare* (Bastian 1865) (Oncholaimidae) on dead and moribund macrofaunal animals. They also found high densities of *Monhystera disjuncta* together with the oncholaimid in the sediment.

The nematode assemblage in the microcosm is derived from an area where deposit and epistrate feeding nematodes are in majority (Elmgren 1976; Ólafsson and Elmgren 1991) and where oncholaimids and thoracostomopsids appear to be rare (personal observations). Accumulation of scavengers in the area of dead *Macoma* was therefore not expected.

It is clear that only one species responded by density enhancement in the area of dead animals i.e. *Monhystera disjuncta*. This species has a worldwide distribution, occurring from the subarctic (Spitzbergen) to subtropical shores (Gerlach and Schrage 1971). It has been isolated from decaying algae (Chitwood and Murphy 1964; Vranken et al. 1984) and found abundantly in organically enriched sediments (see Vranken et al. 1984; Lorenzen et al. 1987). It has been successfully cultured by numerous investigators (Chitwood and Murphy 1964; Gerlach and Schrage 1971; Romeyn and Bouwman 1983; Vranken et al. 1984; Vranken and Heip 1986; Herman and Vranken 1988; Vranken et al. 1988). The buccal cavity lacks armature and it can be classified as a non-selective deposit feeder eating a variety of microflora and fauna (Romeyn and Bouwman 1983). Generation time is short but highly temperature dependent and is of the order of 20–25 days at 5–7° C (Gerlach and Schrage 1971; Vranken and Heip 1986; Vranken et al. 1988).

Even though I found *M. disjuncta* in considerably higher numbers in the areas of decaying bivalves compared to other areas I suspect that only the initial phase of patch formation had occurred within the 17 days; the experimental period lasted less than the expected generation time of *M. disjuncta* at this temperature. The six-fold increase in the density of *M. disjuncta* in the dead animal areas can be explained by two processes. First it is plausi-

ble that substances emanating from the decaying animals prompted immigration from the surrounding area (Rieman and Schrage 1988). Among the early colonists it is very likely that there would have been gravid females. These may have deposited eggs within the first 10 days and hence contributed to the massive increase in the population, as the development time for eggs at this temperature is very short i.e. 2–8 days (Gerlach and Schrage 1971).

The reduction in the density of *Calomicrolaimus honestus* was probably caused by the same factors that reduced the numbers of surface taxa, as this species has been found almost exclusively in the top centimetre in the field (Ólafsson and Elmgren 1991). It is however more difficult to explain the reduction of the dominant species, *Leptolaimus elegans,* especially as its congener *L. papilliger* was unaffected and these two species have very similar distributions in the field (Ólafsson and Elmgren 1991). The enhanced density of *Sabatieria pulchra* in the dead animal areas was expected. This species is known to prefer anoxic or very low dissolved oxygen conditions which is often reflected in its deep vertical distribution (Bouwman 1983; Jensen 1984; Ólafsson and Elmgren 1991). However elevated numbers of this species in the shell areas was not expected. One plausible explanation is that the shells blocked the diffusion of oxygen into the sediment and therefore created a patch of enhanced bacterial sulfate reduction below the shells which attracted *S. pulchra.*

The models of Johnson (1970) and Grassle and Sanders (1973) state that natural disturbances create a mosaic of patches that have different species compositions depending on their states of recovery. The early successional stages would involve species characterized by rapid dispersal and high reproductive rates, followed by better resource competitors which displace the opportunistic species (Grassle and Sanders 1973). Similar conclusions were reached by Hodda (1990) who emphasized that only a given suite of species may find any particular patch attractive. The *in situ* decay of dead animals must be regarded as a very common phenomenon in nature. As demonstrated in this experiment it will clearly influence the meiofaunal community and may explain to some extent the well-documented patchiness of the meiofauna.

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