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## Effects of biological disturbance by *Monoporeia affinis* (Amphipoda) on small-scale migration of marine nematodes in low-energy soft sediments

Received: 24 February 2003 / Accepted: 23 May 2003 / Published online: 5 July 2003  
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**Abstract** Free-living marine, benthic nematodes quickly colonise sediments where physical forces are strong enough to suspend them into the water column. In the absence of such forces colonisation is much slower and is more likely to be affected by biological factors. The aim of the study was to investigate if nematodes disperse more readily in the presence of biological disturbance where physical disturbance is rare or non-existent. Amphipods are able to greatly rework sediments, and thereby induce disturbance to the infauna. A laboratory experiment with the amphipod *Monoporeia affinis* and nematodes from a low-energy, 30-m-deep location was conducted in mesocosms where the nematodes were given the choice to colonise azoic sediment at three amphipod densities, zero, low and high. Each area of azoic sediment in the mesocosms was divided into three equilateral sections from the nematode source, i.e. 10, 23 and 36 cm. At termination, after 7 weeks, there were no significant differences in nematode abundance and assemblage structure between treatments despite considerable biological disturbance created by the amphipods. The number of nematodes was 16%, 15% and 11% of the total numbers in the source at the three sections 10, 23 and 36 cm, respectively. There were distinct differences in the nematode community composition between distances, with the small surface-dwelling taxon *Leptolaimus* spp. being a rapid and the numerically dominant coloniser of the azoic sediments. Migration of nematodes over short distances is likely to be slow in the absence of strong physical forces. To our knowledge, this is the first paper ever that investigates the influence of macrofauna on nematode short-range migration.

### Introduction

Nematodes are found practically in every conceivable marine habitat and they are normally the major component of soft sediments, both regarding abundance and diversity (Platt and Warwick 1980; Heip et al. 1985). They are usually regarded as poor swimmers (Fegley 1985) and are considered to have limited dispersal capacity (Fleeger et al. 1984). However, numerous studies indicate that nematodes are common in, and can be dispersed via the water column (Hagerman and Rieger 1981; Mott and Harrison 1983; Palmer 1983; Fleeger et al. 1984; Fegley 1985; Armonies 1988; Bertelsen 1998; Powers 1998). They have been found in plankton samples (Hagerman and Rieger 1981; Sibert 1981) and inside the gut of pelagic planktonic fish (Schneider 1914). Hatched juveniles have been found to migrate to the flocculent layer to be dispersed by water currents (Surey-Gent 1981), and their swimming ability has been observed and recorded on several occasions (Peters 1928; Gray and Lissman 1964; Wallace and Doncaster 1964; Crofton 1966; Jensen 1981; Chandler and Fleeger 1983; Fegley 1985). Nevertheless, compared to their high sediment densities they occur in relatively low abundance in the water column (Bell 1980; Sibert 1981; Jacobs 1984; DePatra and Levin 1989; Soetaert and Van Rijswijk 1993). Nematodes are not restricted to the sediment surface layer like many other meiobenthic taxa, as many nematode species have relatively deep vertical distributions within the sediment (Hendelberg and Jensen 1993).

Recolonization experiments conducted in soft-bottom intertidal areas reveal that the density of the major meiofaunal taxa, including nematodes, rapidly recovers in defaunated areas (Sherman and Coull 1980; Kern and Taghon 1986; Billheimer and Coull 1988; Savidge and Taghon 1988). Relative abundance of nematode species in the water column and the sediment has been found to be very similar (Bell 1980; Commito and Tita 2002). This finding may explain why workers have found little

Communicated by L. Hagerman, Helsingør

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difference in relative abundance of major species colonising open intertidal habitats. If the water column transport of nematodes were decisive in intertidal areas, then one would assume that the dominant species can be found in relatively similar densities in both the overlying water and the sediment.

Subtidally, where currents are not strong enough to suspend meiofaunal animals into the water column, recolonisation into azoic sediments has been found to be much slower than in intertidal habitats (Thistle 1980; Alongi et al. 1983; Chandler and Fleeger 1983; Sherman et al. 1983; Widbom 1983; Ólafsson and Moore 1990, 1992; Aarnio and Bonsdorff 1992; Bonsdorff 1992; Vriser 1998). Furthermore, these studies emphasise the contrast between the rate of colonisation of the two major taxa, harpacticoid copepods and nematodes, whereby harpacticoid copepods are much quicker to reach ambient levels than nematodes. Indeed, three studies showed that nematode abundance never reached background levels after 18 and 8 months, respectively (Widbom 1983; Ólafsson and Moore 1990, 1992), indicating active migration through the sediment as the main dispersal mechanism.

In only two studies of subtidal colonisation of nematodes in soft sediments have the organisms been identified to species level, both studies indicating that nematodes living deep down in the sediment are slower to colonise than nematodes at the sediment surface (Alongi et al. 1983; Ólafsson and Moore 1992). One possible explanation for this is that the surface-living animals are more susceptible to passive dispersal due to biological and physical disturbance of the sediment surface and, hence, suspension. Such disturbance has been shown to enhance nematode drift (Palmer and Gust 1985), which is probably an important factor contributing to early colonisation over short distances subtidally.

One of the most abundant and widespread macrofaunal species in subtidal soft bottoms of the Baltic Sea is the amphipod *Monoporeia affinis* (Lindström) (e.g. Segerstråle 1957; Köhn 1995). It exhibits nocturnal swimming activity (see e.g. Lindström and Lindström 1980), but remains more or less buried in the sediment during the day (Lindström and Lindström 1980). *M. affinis* is most often found in the top 5 cm of the sediment, though they are known to reach depths down to 13 cm (Hill and Elmgren 1987). Ólafsson and Elmgren (1991) found that the amphipods had a significant negative effect on the number of surface-dwelling nematodes in experimental microcosms, while assemblage structure was little affected. Due to the major sediment reworking by amphipods, it is not unlikely that they influence nematode migration. One can envisage that small nematodes may be dragged along when amphipods move around. They may also actively move away from the areas occupied by amphipods, trying to reach an area with lower disturbance rates. Another factor affecting nematodes might be the actual reworking of the sediment itself, e.g. burrows have been shown to both enhance and reduce nematode

abundance (Dobbs and Guckert 1988; DePatra and Levin 1989; Botto and Iribarne 1999).

In the present study we examined the effects of biological disturbance on short-range dispersal of free-living marine nematodes from low-energy subtidal muddy bottoms. The biological disturbance was induced by one of the dominant macrofaunal species in the Baltic Sea, the amphipod *M. affinis*. We were, particularly, interested in the two following questions:

1. Do amphipods influence movements of nematodes over short distances?
2. Do the amphipods induce more movements of small surface-dwelling species than of deeper dwelling, larger species, i.e. are there detectable differences in nematode genera composition in previously azoic areas in the presence and the absence of amphipods?

## Materials and methods

Mesocosms consisting of plastic boxes of internal dimensions 56.5×36.5×21.5 cm were established at Askö Laboratory field station in the north-western Baltic proper (58°49'N; 17°38'E). The mesocosms were divided into two sections, where one-third of the total area contained natural sediment with meiofauna and the remaining two-thirds consisted of "azoic" sediment (Fig. 1). The total sediment depth was approximately 7 cm. Brackish water was pumped from a depth of 15 m through a sand filter and then distributed to the mesocosms via small tubes at a flow rate of approximately 5 l h<sup>-1</sup>. Outflow water from the mesocosms was not recycled. Temperature and salinity were kept near field levels, i.e. 5–7°C and 6.0–6.9‰, respectively.

### Sediment handling

From several van Veen grabs (30 m depth) the overlying 5–6 cm sediment was removed and discarded to remove the bulk of the living meiofaunal organisms. The rest of the sediment was taken ashore and mechanically pressed through a 250 µm mesh and further homogenised with a paint mixer attached to an electric drill. This sediment was placed into the mesocosms to a depth of approximately 6 cm in both sections (Fig. 1).

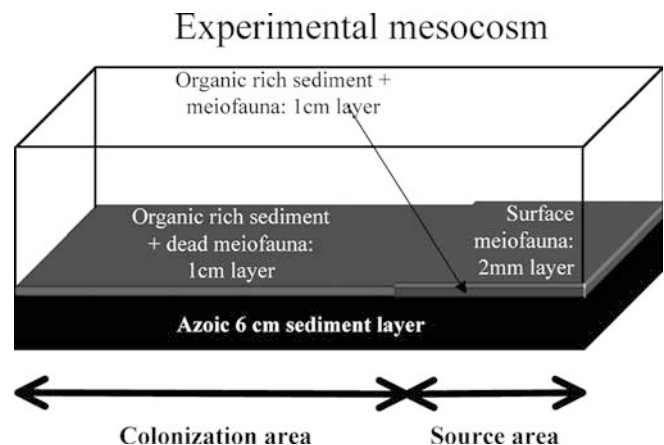


Fig. 1 Schematic representation of the experimental set-up

Organic-enriched sediment was collected with a benthic sledge with the sampling depth adjusted to 0.5–1.0 cm. This sediment was first passed through a 2 mm sieve to get rid of adult *Macoma balthica* and gravel and then mechanically pressed through a 250 µm sieve. To kill the surviving fauna, part of the sediment was heated to 70°C for at least 1 h (result checked by ocular inspection, no surviving meiofauna was found); the other, non-treated sediment, including the experimental organisms, was stored in a constant temperature room until needed. The pre-heated sediment was placed in the azoic section of the mesocosms, and the non-treated sediment was placed in the zoic part of the mesocosms (Fig. 1). An approximately 1-cm-thick layer of these two sediment types was applied on top of the 6 cm already in the mesocosms.

To increase further the nematode numbers in the source sediment, 60 Kajak-cores (8 cm inner diameter) were taken in a 200 m transect at 17–22 m depth. Only the top millimetres were taken, homogenised and carefully placed in the zoic part of the mesocosms (Fig. 1). One-year-old amphipods were collected from the same area as the sediment samples, but this time with a benthic sledge.

A total of 15 mesocosms were used to permit three treatments of five replicates each arranged in a randomised block design, with treatments as blocking factor. The treatments were: (1) no amphipods present (control), (2) low numbers of amphipods (775 m<sup>2</sup>) and (3) high numbers of amphipods (3100 m<sup>2</sup>). The amphipods were added to the mesocosms by lowering a beaker into the water mass; due to their great swimming ability the amphipods were dispersed throughout the mesocosms within the first minute and showed no preference for any particular section of the mesocosm when burying in the sediment.

The experiment was terminated after 7 weeks. The azoic sediment section of each mesocosm was transversely divided into six equal rows, and each row was subdivided into eight sampling squares. The second, fourth and sixth rows were allocated as the rows from which the samples were taken, i.e. 10, 23 and 36 cm from the source, respectively. In each row the first and last sampling squares were excluded to avoid possible edge effects. From each sampling distance three sample squares were randomly chosen. In the section that initially contained the fauna (the zoic part) samples were taken in one central row as above.

Before taking the samples, the water was siphoned off until approximately 1 cm remained. The samples were taken with a sawn-off, 60 cm<sup>3</sup> syringe, with an area of 5.5 cm<sup>2</sup>. The syringe was pushed down through the sediment until it reached the bottom of the mesocosm, while the piston was held in place just above the sediment surface. The samples were directly transferred to plastic containers holding a final concentration of 4% formalin. The remaining sediment was sieved through a 500 µm mesh to retain all macrofaunal organisms for later enumeration. The macrofauna was later placed in plastic containers holding a final concentration of 4% formalin.

Samples were sieved through a 40 µm mesh with tap water to get rid of the smaller particles and the sample was transferred into an E-flask containing Ludox silica gel (De Jonge and Bouwman 1977). The samples were suspended through rigorous stirring of the solution, holding a specific density of 1.15 g (Platt and Warwick 1988). The E-flasks were then left for 30 min whereupon the supernatant was decanted and passed through a 40 µm mesh sieve. This procedure was repeated twice. The remains in the sieve were transferred to 4% formalin in which the sample was held until enumeration.

All organisms were later enumerated and identified to major taxon in a petri dish under a stereo dissecting microscope (Wild, Heerbrugg, Switzerland). From each sample, 100 nematodes (when available) were impregnated with anhydrous glycerine (Platt and Warwick 1983) and mounted on slides for identification under a high-power microscope (Olympus).

## Statistics

From each distance in each treatment, three samples were taken and the pooled arithmetic mean of the replicates was used to avoid the problem of pseudoreplication (Hurlbert 1984). As the result of

a Shapiro–Wilk *W*-test for normality (Shapiro and Wilk 1965) showed that our samples were non-normally distributed, all values were reciprocally transformed (1/*x*) into normality. A homogeneity of variance test was performed which showed that the variances did not differ between treatments. A two-way ANOVA was performed with treatment and distance as factors (JMP 4.0.1 and 5.0.1. for the Apple Macintosh). If a significant result occurred the Tukey–Kramer HSD-test (Kramer 1956; Tukey 1994) was used to investigate the difference(s).

The initial number of nematodes at the start of the experiment could possibly have had an influence on the results if initial differences in the treatments had been large. Therefore an ANCOVA was conducted with the initial numbers in the source as covariate (StatView 5.0.1. for Apple Macintosh).

Nematode genera abundance data were double square-root-transformed and subjected to MDS (multidimensional scaling) ordination, using the Bray–Curtis similarity index [data only shown for the 0 cm (initial fauna containing area), 10 and 36 cm], due to reduction time of the tedious labour of microscopic sorting of nematodes to genera. The significance of the MDS (differences in nematode assemblage structure) was tested for by two-way ANOSIM (analysis of similarities) (Warwick et al. 1990b). To identify the genera contributing to the differences found in the ordination analysis, the computer program SIMPER (similarity percentages) was used (Warwick et al. 1990a, 1990b), with the cut-off percentage set to 50%. All multivariate tests were performed using the multivariate statistical software package Primer 5.1 developed at the Plymouth Marine Laboratory, UK.

## Results

The ANCOVA showed that varying initial numbers of nematodes in the different treatments did not differ between treatments (row 2,  $F=0.7$ ,  $P>0.4$ ; row 4,  $F=0.8$ ,  $P>0.4$ ; row 6,  $F=1.1$ ,  $P>0.3$ ). So it is safe to assume that no difference in abundance among mesocosms prevailed at the start of the experiment.

There were large differences in abundance between different meiofaunal taxa in the mesocosms. In all, we found 13 different taxa. Due to the very low numbers of several taxa, only the six most abundant taxa are accounted for; the remaining taxa were lumped into a common group (Table 1). The six most abundant taxa were nematodes, ostracods, copepods, naupliar larvae, Turbellaria and *Macoma balthica* spat. Of the six taxa, nematodes were by far the most abundant, comprising 94.5% (8144) of the total meiofauna in the mesocosms. There were followed by ostracods (1.4%, 122), copepods (1.1%, 95), nauplii (0.95%, 81), Turbellaria (0.9%, 78) and *M. balthica* spat (0.5%, 41), from a total meiofaunal abundance of 8619 organisms. Representatives of the remaining taxa were found in lower densities (Table 1).

The two-way ANOVA (see Table 3) did not reveal any differences in nematode numbers among treatments ( $P>0.99$ ), but there was a highly significant difference in nematode numbers among distances (Table 1,  $P<0.0001$ ). The Tukey–Kramer HSD-test revealed that nematodes were in significantly different numbers at 0 cm compared to the other distances, and significantly different at 10 cm compared to 0 and 36 cm. A total of 27 nematode species/genera were recorded from our samples (Table 2). The MDS of the nematode species/genera composition data shows that

**Table 1** Average (*avg.*) number ( $n=5$ ) and standard deviation (*SD*) of major meiofaunal taxa in the experimental boxes at various distances from the meiofauna source after 2 months (*control* 0 amphipods; *low* 775 amphipods  $m^{-2}$ ; *high* 3100 amphipods  $m^{-2}$ )

Treatment	Distance (cm)	Nematoda		Copepoda		Nauplii		Ostracoda		Turbellaria		<i>Macoma balthica</i>		Others	
		Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD
Control	0	376	68	4	1	3	3	7	5	4	2	4	2	2	2
	10	68	16	2	1	0	1	0	1	1	0	0	0	1	1
	23	51	18	1	1	1	1	0	0	0	1	0	0	0	1
	36	37	19	0	0	0	0	0	0	4	7	0	1	0	0
Low	0	375	97	3	1	6	5	9	4	2	2	3	2	3	2
	10	67	33	3	1	1	1	0	0	1	1	0	0	1	1
	23	56	41	0	1	0	1	0	0	0	0	0	0	1	1
	36	45	9	0	1	0	0	0	0	0	0	0	0	0	1
High	0	398	59	4	3	3	4	6	2	3	2	2	1	2	2
	10	55	10	1	1	0	1	1	1	1	0	0	0	0	1
	23	61	37	1	1	0	1	0	0	0	0	0	0	0	1
	36	40	14	1	1	1	1	0	0	0	0	0	0	1	1

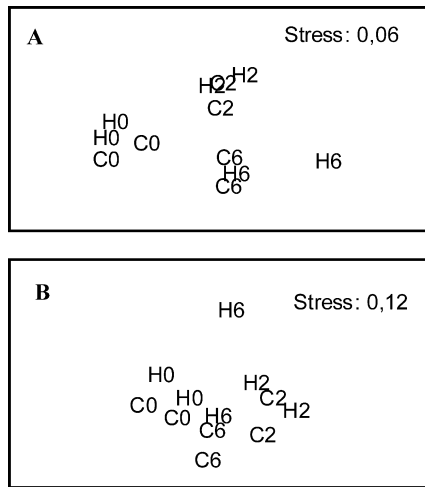
**Table 2** Average (*avg.*) number per 10  $cm^2$  of nematode species, standard deviation (*SD*,  $n=4$ ) and percentage of total at three distances in mesocosms of two treatments: control and high amphipod density

Species	Distance								
	0 cm			10 cm			36 cm		
	Avg.	SD	%	Avg.	SD	%	Avg.	SD	%
<i>Sabatieria pulchra</i>	167	63	27	49	14	29	15	4	18
<i>Daptonema</i> spp.	109	48	18	15	5	9	6	3	7
<i>Calomicrolaimus honestus</i>	81	24	13	6	3	4	5	3	6
<i>Leptolaimus</i> spp.	71	20	11	36	27	22	32	12	39
<i>Paracanthocheilus</i> spp.	56	14	9	6	5	4	4	1	5
<i>Eleutherolaimus stenosoma</i>	38	18	6	0	0	0	1	2	2
<i>Desmolaimus zeelandicus</i>	18	6	3	14	7	8	4	3	4
<i>Dichromadora</i> sp.	17	12	3	3	2	2	1	1	1
<i>Microlaimus globiceps</i>	13	14	2	4	3	2	4	4	5
<i>Campylaimus gerlachi</i>	6	2	1	2	3	1	1	0	2
<i>Paramonhystera</i>	6	12	1	1	2	1	1	1	0
<i>Sphaerolaimus</i>	5	4	1	0	0	0	1	1	2
<i>Chromadorita fennica</i>	5	8	1	5	4	3	1	1	2
<i>Eumorpholaimus</i>	5	6	1	6	4	4	0	0	0
<i>Cobbia</i> sp.	3	7	0	1	1	1	1	1	1
cf. <i>Plectus</i> sp.	3	4	0	0	0	0	0	0	0
<i>Axonolaimus spinosus</i>	3	3	0	6	2	4	1	0	2
<i>Camacolaimus</i>	1	3	0	0	0	0	0	0	0
<i>Adoncholaimus</i>	1	2	0	0	0	0	1	1	1
<i>Halalaimus</i>	1	2	0	0	0	0	0	0	0
<i>Monhystera</i>	1	2	0	2	3	1	0	1	0
<i>Anoplostoma</i>	0	0	0	1	1	0	0	1	0
<i>Ascolaimus</i>	0	0	0	2	2	1	1	3	2
<i>Enoploid</i> sp.	0	0	0	0	0	0	0	1	0
<i>Monhystereide</i> sp.	0	0	0	0	0	0	0	1	0
<i>Theristus</i>	0	0	0	2	2	1	0	1	0
<i>Viscosia</i>	0	0	0	0	1	0	0	0	0
Unidentified	6	5	1	6	4	4	1	1	2

the nematode assemblage structure differs between distances but not between treatments (Fig. 2a, b). The nematode assemblage structure was significantly different only between distances 10 and 36 cm ( $P < 0.05$ , adjusted for multiple comparisons), using ANOSIM with a stress value of 0.06 and the value for global  $R$  of 0.856. Stress can be seen as a measure of goodness of fit (Kruskal 1964; Kachigan 1991) and global  $R$  as a

multiple correlation coefficient for all variables (Kachigan 1991).

The SIMPER test revealed that the average dissimilarity between distances 10 and 36 cm could be attributed to nine genera at our cut-off level of 50%. The genera were, in descending order of contributing percentage difference, *Eumorpholaimus*, *Campylaimus*, *Sphaerolaimus*, *Ascolaimus*, *Paramonhystera*, *Eleutherolaimus*,



**Fig. 2** Multidimensional scaling ordination of nematode species fourth-root-transformed abundance data (A) and nematode percentage data (B) [H high amphipod density; C no amphipods; source (0), 10 cm from source (2), 36 cm from source (6)]

*Dichromadora*, *Theristus* and *Paracanthochus*. No single genus contributed disproportionately to the difference between the distances. The largest single contributing value was 10.17% (*Eumorpholaimus*), and the smallest was 3.79% (*Paracanthochus*).

All of the ten most abundant species in the source were found in lower numbers at 10 and 36 cm distance after 7 weeks (Table 2). Some species were, however, proportionally more abundant at these distances than in the zero distance, i.e. the small surface-living taxon *Leptolaimus* spp. (*Leptolaimus elegans* and *L. papilliger*) at both distances and *Desmolaimus zeelandicus* at the 10 cm distance (Table 2). The large deep-dwelling nematode *Sabatieria pulchra* was proportionally similar to the source at 10 cm, but in much fewer numbers at 36 cm. The relatively abundant nematode species at the zero distance, *Eleutherolaimus stenosoma*, was practically absent at both distances 10 and 36 cm. The two small surface-living Microaimidae species, *Calomicrolaimus honestus* and *Microlaimus globiceps*, showed different colonisation patterns, *C. honestus* being relatively slow and *M. globiceps* fast (Table 2).

## Discussion

In the present study, results indicate that *Monoporeia affinis* do not affect migration of nematodes over short distances. This came as a surprise because the amphipods, intimately associated with the nematodes, are much larger (about three orders of magnitude heavier) and show diel migration patterns over considerable distances (m to km). It is possible that the amphipods have evolved an antifouling mechanism(s) making their surface inaccessible to hitchhiking organisms like nematodes. In terrestrial systems passive dispersal by an active agent is quite common, e.g. mites clinging on

beetles to go from one dung to another (Begon et al. 1996), while in marine environments we are not aware of data that convincingly show the presence of such mechanisms for invertebrate dispersal. It has however been speculated that birds may be active dispersal agents for, e.g., aquatic nematodes, oligochaetes and foraminiferans (Abebe and Coomans 1995; Patterson et al. 1997; Milbrink and Timm 2001).

When visually inspecting the mesocosms at the termination of the experiment there was a clear difference in sediment surface texture between treatments (nil, low and high concentrations of amphipods). During the length of the experiment the sediment surface in treatments with high numbers of amphipods had become almost entirely smooth compared to the nil amphipod treatments, and compared to how the surface looked at the time of initiation of the experiment. This shows that substantial reworking of the surface sediments by the amphipods had occurred, as no other macrofauna were present. Despite this, we found little effect by amphipods on the nematode assemblage structure, which is in accordance with the experimental results of Ólafsson and Elmgren (1991). Most studies on the effects of biological disturbance by a variety of functionally different macrofauna species on nematode communities show little or no effects (Austen and Widdicombe 1998, and references therein). This is also true for another important species in the Baltic Sea, the clam *Macoma balthica*, which had no effect on the nematode community structure in a laboratory experiment (Ólafsson et al. 1993). Perhaps physical disturbance is much more important than biological when it comes to nematode dispersal in low-energy areas such as ours? Suspension of the sediment during autumn and winter storms is likely to carry nematodes much further than active dispersal through the sediment, whether induced by biological disturbance or not. However, one cannot rule out the effects of macrofauna in other parts of the world, as some species such as the polychaete *Nereis virens* have been shown to affect nematode communities (Reise 1979; Tita et al. 2000).

In some disturbance studies researchers have found significant numerical responses by nematodes (Bell 1980; Warwick et al. 1990a, 1997; Aarnio et al. 1998; Austen et al. 1998), while in others there have only been community-shift responses (Heip et al. 1985; Austen and Widdicombe 1998). In our study there were no significant differences in nematode numbers among treatments (Table 3,  $P > 0.9948$ ), but there was a highly significant difference in nematode numbers among distances. A Tukey–Kramer HSD-test revealed that 0 cm differed significantly from both the 10 and 23 cm distances and the 36 cm. The 10 and 23 cm distances were not different from each other, but differed from both distances 0 and 36. That only distances differ, and not treatments, is also supported by the multivariate statistics (see “Results” section). There was a difference in nematode community composition between the distances 10 and 36 cm, irrespective of amphipod density.

**Table 3** Summary of the two-way ANOVA

Source	df	Sum of squares	Mean square	F-ratio	Probability
Model	11	0.01802361	0.001639	9.9315	
Error	48	0.00791911	0.000165		
C. total	59	0.02594273			
Treatment	2	0.00000172		0.005	0.99
Distance	3	0.01764400		35.65	< 0.0001
Interaction (Treatm.×Dist.)	6	0.00037789		0.38	0.9

The numerical differences in abundance between distances are undoubtedly only a result of temporal variation in nematode dispersal inclination. If the study had been terminated at a later date, after sufficient time had been allowed to elapse, the difference would most certainly have ceased. Furthermore, at a later date, slower, more stationary species would have had time to reach the sampling distances furthest away.

The difference in community composition is also likely to be due to similar factors. For example, surface sediments are much more likely to be exposed to disturbance events, for example, macrofaunal movements or sediment reworking, macrofaunal feeding events, or wave or current action. Therefore, nematode species living preferentially closer to the sediment surface would benefit if they were more agile than deeper dwelling nematode genera. In that way, they would be able to respond and react faster to various disturbance events. This might be an evolutionary response towards higher levels of competence for coping with disturbance events, as surface-dwelling nematodes are much more likely to be caught in disturbance events than nematodes deeper down in the sediments. This seems to be supported by our results. The surface-living nematodes *Leptolaimus elegans* and *L. papilliger* were found to be proportionally more abundant at the 10 and 36 cm distances than at the zero distance. It could also be that the extensive reworking of the surface sediments alters the quality of the available food resources. By sediment reworking, a vertical shift in food composition can take place when food formerly situated at the surface is now found much deeper. In areas of elevated amphipod densities it has been found that differences in the vertical position of viable *Eurytemora affinis* (Copepoda) eggs are evened out (Albertsson and Leonardsson 2000). The distribution of *Sabatieria pulchra* is most likely explained as a time-dependent phenomenon. This species lives deep in the sediment (Heip et al. 1985; Olafsson and Elmgren 1991, 1997; Austen et al. 1998) and has been found to be the most abundant species below the redox potential discontinuity layer, where it also can have its maximum population number (Hendelberg and Jensen 1993). That they, then, are found in larger numbers closer to the origin than further away is most likely due to the fact that they live so deep down in the sediments, where the conditions are likely to be much more stable than at the sediment surface. Hence, there is no need to be very agile. This means that the encountered distribution in *S. pulchra* only reflects that

not enough time has passed to even out their numbers between distances. In contrast to our study, it has been shown that for vertical dispersal in nematodes as a response to depositional disturbance, nematodes are affected by the intensity and magnitude of the disturbance event. A large amount of sediment applied once had a much greater impact on the nematodes' ability to disperse upwards in the sediments than the same amount of sediment applied in successive doses (Schratzberger et al. 2000a, 2000b).

For nematodes living in high-energy environments, their most likely mode of dispersal is first resuspension by currents or wave movements, and then horizontal transport in the water column. Wave-induced resuspension can, on very exposed coastlines, extend down to 200 m (Grant et al. 1984). In very shallow areas, resuspended nematodes can also be advected by wind forcing as long as they are relatively close to the surface. In subtidal, deep habitats there are different hydrodynamic regimes, and therefore a different mode of dispersal that governs nematode movements over larger areas. Here the most common mode of dispersal is likely to consist of sinusoidal, active movement in the interstitial spaces, or through the sediment if the sediment is fine grained. In this study we have also pointed out that there seem to exist differences between surface-dwelling nematodes and nematodes living deeper down in the sediments. Nematode genera living near the surface seem faster in their horizontal migration rate than genera deeper down.

**Acknowledgements** Thanks to the staff at Askö field station, Trosa archipelago. G. Malmberg provided indispensable help with nematode measurements in the image analysis laboratory, and K. Ullberg helped to improve the language. We also thank two referees for useful comments that aided in improving the manuscript. We also acknowledge financial support from Helge Ax:son Johnsons Stiftelse to J.U.

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