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Small-scale spatial patterns of meiobenthos in the Arctic deep sea

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Abstract A variety of analytical techniques were used to quantify and describe small-scale (centimetre to decimetre) spatial patterns of meiofauna taxa, with emphasis on nematode species, at a bathyal site in the Arctic deep sea. Three cores (10-cm diameter) taken from the same multicorer were each subsampled as 12 contiguous subcores (1.2-cm diameter) for meiofauna and 16 contiguous subcores (0.9-cm diameter) for bacteria (eight subcores) and phytodetritus (chl *a* and phaeopigment concentration) (eight subcores). Coefficients of variation and the variance component from PERMANOVA were estimated to compare variability between cores (20–50 cm) versus within cores (≤10 cm). Both methods showed that spatial variation within cores contributed the main part of total heterogeneity for all parameters, while differences between cores were less important. To further investigate distribution patterns at this small scale (≤10 cm), indices of dispersion were calculated and autocorrelation analyses were performed on the complete data set. Abundances of nematodes, nauplii and 65.5% of the nematode species were significantly aggregated at the scale of subcores (2 cm). Nematode species aggregations were discordant on the small scale, suggesting that processes maintaining diversity in the deep sea can be expected to operate at scales smaller than 10 cm. Autocorrelograms suggested that nematode patch sizes were smaller than 4 cm^2, while adult harpacticoid copepods and nauplii showed aggregations of ca. 9–25 cm^2 and 64 cm^2, respectively. Significant spatial autocorrelation at the core scale was also observed for 24 nematode species. These species were grouped in ten different spatial patterns according to their scale of heterogeneity. The spatial patterns observed for the meiobenthos were neither explained by the concentration of chloroplastic pigments nor by bacterial densities. Nevertheless, observations on nematode morphology suggest that morphological characters linked to their locomotion and feeding behaviour may be involved in pattern formation. Finally, our data provide evidence that studies based on few replicates to characterise large-scale or long-term patterns of deep-sea benthic communities may be confounded by inadequate assessment of small-scale variability.

Keywords Small-scale heterogeneity · Spatial distribution · Autocorrelogram · Deep-sea diversity · Meiofauna · Nematodes

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Introduction

The spatial distribution of organisms provides information on both organism-organism and organism-habitat relationships (Findlay 1981; Underwood and Chapman 1996). If individuals or species interact, or if their environment is not homogeneously suitable, their distribution will bear some imprint of this. As such, identifying spatial distribution patterns is an essential step towards understanding the processes structuring ecological communities and the scales at which these processes act (Andrew and Mapstone 1987; Thrush 1991; Underwood and Chapman 1996). The deep-sea benthos is notoriously species-rich at small spatial

scales, and small-scale patchiness in species distributions has been the basis for hypotheses on mechanisms maintaining this high local diversity (Snelgrove and Smith 2002). However, there is a general paucity of data on species' small-scale distribution patterns, resulting in limited empirical support for any of these hypotheses. Indeed, most studies of deep-sea soft-sediment communities have mainly concentrated on mesoscale (meters and kilometres) changes in abundance and diversity, while knowledge about spatial structure at the small scale is scant (Jumars and Eckman 1983; Rice and Lambshead 1994).

The limited available data on the small-scale spatial patterns of deep-sea macrofauna (Hessler and Jumars 1974; Jumars 1975, 1976, 1978; Gage 1977; Volckaert 1987), harpacticoid copepods (Thistle 1978; Eckman and Thistle 1988) and foraminiferans (Bernstein and Meador 1979) generally suggest that abundances of sediment-dwelling macro- and meiofauna are significantly affected by processes operating at horizontal scales smaller than 10 cm. However, due to the low numerical abundances frequently encountered in the deep sea, analyses often showed little significant departures from random dispersion, significant spatial patterns having mainly been detected for a few species of polychaetes and harpacticoid copepods (Jumars 1975; Eckman and Thistle 1988). How valid generalisations based on these groups are for other deep-sea taxa is still unclear. Nematodes are at the same time the most abundant and most speciose metazoans at a local scale in deep-sea sediments (Lambshead and Boucher 2003), rendering them particularly suitable models for spatial studies (Heip 1975; Rice and Lambshead 1994) as well as for investigating processes of diversity maintenance in the deep sea (Thistle 2003). However, we know of no deep-sea studies that have investigated the small-scale horizontal distribution of nematodes.

This paper aims at a detailed analysis of the small-scale (cm-scale) spatial patterns of nematodes (at the species level), harpacticoid copepods and nauplii at a bathyal site in the Arctic deep sea. Specifically, we aimed to (1) quantify the variation in meiofauna abundances on two small spatial scales: <10 cm versus 20–50 cm. We hypothesized that if occupancy of habitat patches is primarily an outcome of behaviour on the scales on which individuals interact, the smallest sampling scale should yield a larger variation; (2) test, by means of dispersion indices, whether the distribution of meiofaunal organisms is clumped, regular or random at the smallest spatial scale; (3) analyse the form of spatial patterns (i.e. size of patches and/or presence of gradients) using spatial autocorrelation. This is important because dispersion indices may indicate that two distributions have a similar intensity of pattern (as revealed by dispersion indices), while they actually have drastically different spatial arrangements. Also, dispersion indices may indicate that distributions do not differ significantly from random, but patterns may still be represented by distinct patches or density gradients (Thrush 1991); (4) investigate whether species have concordant or discordant abundances. If any biogenic structure or biological disturbance acting at the scales of our study generates microhabitats, which are important for particular (groups of) species, then discordance in local abundances among species should result (Jumars 1976). Finally, since food is often considered a prime determinant of meiofauna distribution (Lee et al. 1977; Decho and Castenholz 1986; Blanchard 1990), we also aimed to (5) investigate the spatial distribution of potential food sources (phytodetrtitus and bacteria) and their possible relationship with abundances of meiofauna.

Material and methods

Sampling design and sample processing

Samples were taken from 1,300 m water depth at the Fram Strait, west off Spitsbergen (approximately 79°N, 4°E) using a multiple corer (MUC). Three cores (10-cm diameter) from the same MUC, arranged in a triangular form (Fig. 1), were subsampled in detail for analysis of meiofauna, particularly nematode assemblages, phytodetritus concentration (chlorophyll *a* and phaeopigments) and bacterial abundance. From each core, 12 subcores were taken for meiofauna (1.2-cm diameter up to 1-cm depth), eight for phytodetritus and eight for bacteria (0.9-cm diameter up to 1-cm sediment depth) using syringes with cut-off ends. To minimise possible sampling disturbance, all syringes were gently pushed into the sediment prior to their removal. The smallest distances between meiofauna subcores (centrepoint distance) within each core were 2 cm (*x*-axis) and 2.5 cm (*y*-axis). For phytodetritus and bacteria, the smallest distances between subcores were 3.2 cm (*x*-axis) and 4 cm (*y*-axis) (Fig. 1).

Meiofauna samples were preserved in 4% formalin and stored. At the laboratory, samples were washed through a 32-μm sieve and meiofauna extracted by flotation with Ludox TM50 (Heip et al. 1985). After staining with Rose Bengal, meiofauna was counted and all nematodes were picked out, evaporated to anhydrous glycerol and mounted on permanent slides for identification. All nematodes were identified to genus level and further separated into species or putative morphospecies. The amount of phytodetritus was assessed by measurements of sediment-bound chlorophyll *a* (chl *a*) and phaeopigment concentrations according to Shuman and Lorenzen (1975). Microbial cell number was determined by epifluorescence microscopy after staining with acridine orange (Meyer-Reil 1983; Grossmann and Reichardt 1991). For each sample 40 grids from one filter were counted.

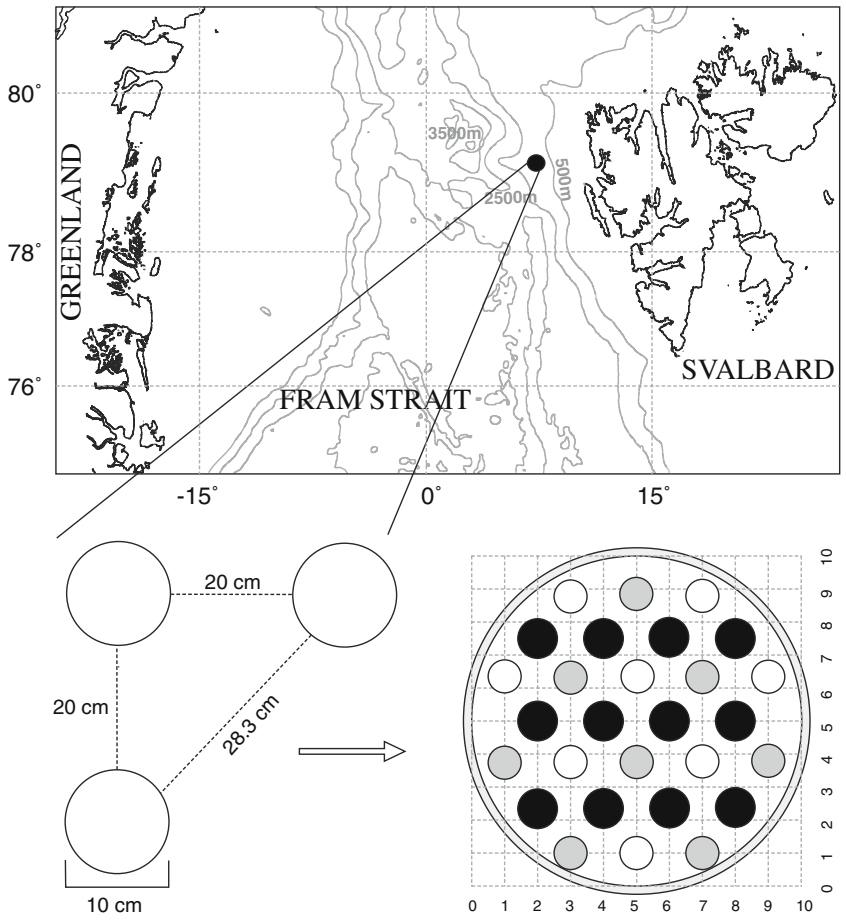


Fig. 1 Location of the sampling site and schematic of the sampling design showing the position of the three cores in relation to each other as well as the position of the subcores within one core: *black* meiofauna subcores, *grey* bacteria subcores, *white* chloroplastic pigment subcores

Data analyses

Statistical analyses of spatial patterns were performed for chloroplastic pigments (chl *a* and phaeopigments), bacterial numbers, total densities of nematodes, adult copepods and nauplii, and for densities of all nematode species which occurred in all three cores and had total abundances higher than ten individuals (as suggested by Rice and Lambshead 1994). Based on this criterion, a total of 58 nematode species out of 176 were selected for the analysis.

First, we investigated which scale, 'within cores' (<10 cm) versus 'between cores' (20–50 cm), contributed most to the variability of our data set (chloroplastic pigments concentrations, bacterial and meiofauna abundances and multivariate structure of nematode assemblages) (see item 2 below). In a second step, we used two complementary approaches to investigate the spatial patterns of meiofauna and their potential food sources (chloroplastic pigments and bacteria) at our smaller scale (<10 cm, 'within cores'). First, we calculated the intensity of the pattern by methods such as dispersion indices based on the variance-mean ratio, sorting distributions of density estimates into clumped, regular or not significantly different from random. Then, we determined the form of the spatial pattern (i.e. size of patches or gradients) using techniques of spatial autocorrelation that utilise the information contained in the spatial arrangement of per subcore abundances of individuals (see item 3 below). Finally, we examined possible relationships between meiofauna and their potential food sources (see item 4 below).

1. General characteristics of the meiofauna and their potential food sources

To investigate how much of the total species richness was sampled within a single core and how much we gained in terms of numbers of species by sampling three distinct cores, species accumulation curves were constructed for the three cores combined (36 subcores) and for each core individually (12 subcores). Curves were constructed using the analytical method described by Ugland et al. (2003).

2. Source of variation at different scales: between cores versus within cores

Non-parametric multivariate analysis of variance (PERMANOVA, Anderson 2001) was applied to assess differences in total density of nematodes, copepods and nauplii and in number of nematode species between the cores (20–50 cm). Although PERMANOVA was designed to do

multivariate analysis on distance matrices, it can be used to do univariate ANOVA. However, PERMANOVA calculates p values using permutations, rather than relying on tabulated p values, and therefore does not have the traditional one-way ANOVA assumptions (Anderson 2005). In particular, by randomly shuffling the observational units, this analysis compensates for the fact that subcores in our study were taken systematically and do not represent a random sample from the target population. Pairwise a posteriori multiple comparisons tests were performed when significant differences were detected ($p<0.05$). The analyses were done on Euclidian distances using the FORTRAN program PERMANOVA (Anderson 2005). The test was done using unrestricted permutation of raw data (e.g. Manly 1997) with 999 random permutations. Differences in nematode assemblage structure between cores were assessed by non-metric multidimensional scaling ordination (nMDS) of fourth-root transformed nematode species abundance data using the Bray-Curtis similarity measure; the significance of these differences was assessed by the ANOSIM permutation test (Clarke and Green 1988). The variability in nematode assemblage structure among subcores was analysed using the multivariate index of dispersion (MID) (Warwick and Clarke 1993).

In a next step, two methods were used to estimate the contribution of different spatial scales ('between core' and 'within core') to the overall variability in the distribution of bacteria, chloroplastic pigments, total nematodes, nauplii, adult copepod and nematode species abundances. First, coefficients of variation (CV) [defined as (100×SD)/mean, Snedecor and Cochran 1980] were calculated to compare the dispersion of values around the mean for each parameter. There were two spatial CVs: between subcores within each core ('within core') and between adjacent cores ('between cores'). The 'within core' CVs were calculated for each core separately and then averaged. The variances obtained for each scale were fully independent estimates. Parallel to that, we used the mean square estimates from the one-way PERMANOVA to assess the contribution of the variation associated with the factor 'core' ('between core variability') and that with the residual, which represented the variation among subcores ('within core variability'), to the total data variation. These variance components were estimated by equating observed and expected mean squares (MS) (Underwood 1997; McArdle and Anderson 2001). As such, an estimate of variability between cores was simply obtained as $(MS_{cores}-MS_{residual})/n$, where n is the number of subcores within cores, and variability within cores was obtained from the $MS_{residual}$. Negative values were set to zero, under the assumption that they were sample underestimates of small or zero variances (Underwood 1996). The analyses were done on Euclidian distances for univariate measures and on Bray-Curtis distances calculated from fourth-root transformed data for the multivariate structure of nematode assemblages. The test was done using unrestricted permutation of raw data (e.g. Manly 1997) with 999 random permutations.

3. Small-scale spatial patterns

Different complementary approaches were combined to investigate small-scale spatial patterns (<10 cm). First, an exact permutation test (Clarke et al. 2006) was applied to determine whether chloroplastic pigments concentrations, as well as bacteria, total copepods, nauplii, nematodes, and individual nematode species were overdispersed (aggregated, $D>1$, $p<0.05$), underdispersed (regularly spaced, $D<1$, $p>0.095$), or randomly distributed (Poisson distribution, $D=1$, $0.05<p<0.95$) at the spatial scale of the subcores (2 cm). D was estimated as an average over the three cores (Clarke et al. 2006) using the 'Dispersion-weighting' function on Primer 6. Then, to investigate whether patches or aggregations of different nematode species tend to coincide or not, we analysed per-subcore multispecies aggregations using the dispersion chi-square statistic (Jumars 1975). This method tests for any unexpectedly large concordance or discordance in species' local abundances relative to the expected stochastic variability if their local abundances were independent. Briefly, all species in a subcore can be treated as replicates and their chi squares added together to obtain a 'total chi square', which indicates whether species on the average depart from Poisson distributions in per-subcore abundances. The chi square for the nematode species pooled together ('pooled chi square') accounts for the variability caused by differences in the total abundance of all species from subcore to subcore and determines whether the per-subcore abundances of the individual species, when summed by core, follow a Poisson distribution (as they would if the species' abundances were independent and individually Poisson distributed). The 'pooled chi square' is subtracted from the 'total chi square' to give the 'heterogeneity chi square', which is the portion of the variability resulting from discordance in species' abundances. This indicates whether the individual species tend to aggregate in the subcores at random, in concordance (i.e. tendency to aggregate in the same patches) or in discordance (i.e. tendency to aggregate in separate patches).

In a second step, to investigate the form of spatial patterns (i.e. size of patches or gradients), we used techniques of spatial autocorrelation (e.g. Cliff and Ord 1973; Jumars et al. 1977; Jumars and Eckman 1983; Eckman and Thistle 1988; Fortin and Dale 2005). All-directional Moran's I autocorrelograms were calculated using the Rookcase software (Sawada 1999). Inter-subcore distances were set as the Euclidian distance between neighbouring subcores, considering all directions, and ranged from 2 to 8 cm. Moran's I indices were calculated

separately at each of five distance classes: 2, 2.1–3.3, 3.4–5, 5.1–6.1 and 6.2–8 cm. These intervals were chosen to achieve a rough parity among intervals in the number of contributing pairs of observations. For each calculation of *I* (i.e. for each of the five distance classes), weights were set equal to 1 for subcores separated by distances falling within that class, with all others set to 0. Thus, only subcore pairs falling within that distance interval contributed to the index. Negative Moran's *I* values indicate a negative autocorrelation, and positive values denote a positive autocorrelation. The correlograms were calculated for the three cores combined, using data that had been standardised within cores (Hewitt et al. 1997; Bergström et al. 2002). The significance of all values of Moran's *I* was assessed under the randomization assumption (Cliff and Ord 1973). The null hypothesis of no autocorrelation at each distance class was tested for significance ($\alpha=0.05$) when the correlogram was globally significant. The global test of significance of each correlogram was performed by checking that at least one *I* coefficient was significant at the Bonferroni-corrected significance level $\alpha' = \alpha/n$, where n is the number of distance classes in the correlogram (Oden 1984). To aid interpretation of correlograms, plots of copepod, nematode and nauplii abundances per subcore were constructed.

Finally, we investigated (multivariate) spatial structure of the nematode assemblages, chloroplastic pigment concentrations and bacterial abundances. Non-parametric Mantel tests (RELATE), using Spearman's rank correlation between corresponding elements of resemblance matrices as the test statistic, were used to investigate relationships between matrices of intersample distances (based on Euclidian distance) and similarity matrices derived from nematode abundances (based on Bray-Curtis similarity) or chloroplastic pigments and bacterial abundances (based on normalised Euclidian distance). To examine spatial relationships, Mantel tests were used to address the hypothesis that biotic similarities between subcores a particular distance apart are higher (or lower) than similarities between subcores separated by other distances. In this procedure, biotic similarities are correlated with model matrices in which the distance of interest was coded 1, and all other distances 0. As these were all two-tailed tests (similarities may be positively or negatively correlated with distance) we considered values of $p<0.025$ and > 0.975 to be significant (Somerfield and Gage 2000).

4. Relationship between meiofauna and potential food sources

Interrelationships between copepods, nauplii, total nematodes and nematode species abundances with chloroplastic pigments (chl *a* and phaeopigments) and bacterial abundances were investigated using Pearson's correlation coefficient. Coefficients were calculated for the entire data set. Chloroplastic pigment concentrations and bacterial abundance values for the coordinates of meiofauna samples were estimated by point kriging using SURFER software. Like in the autocorrelation analysis, data from the three cores were combined after standardising within cores.

Results

General characteristics of meiofauna and their potential food sources

Chl *a* and phaeopigment concentrations varied from 0.07 to 0.28 $\mu g \cdot cm^{-2}$ and from 2.85 to 5.55 $\mu g \cdot cm^{-2}$, respectively. Bacterial densities varied from 4.82×10^7 to 10.82×10^7 $ind \cdot cm^{-3}$. The metazoan meiofauna was represented by seven higher taxa. Nematodes were the predominant taxon in all subcores (from 80 to 98% of total meiofauna per subcore), followed by harpacticoid copepods (from 0 to 10% of total meiofauna per subcore) and nauplii (from 1 to 15% of total meiofauna per subcore). Nematode abundances ranged from 407 to 1,406 ind·10 cm^{-2}. Copepods and nauplii varied from 0 to 71 and from 9 to 133 ind·10 cm^{-2} respectively.

A total of 176 nematode species belonging to 64 genera were identified in the samples. From these, four species occurred in all samples (*Microlaimus* sp.1, *Daptonema* sp.2, *Desmoscolex* sp.3 and *Desmoscolex* sp.4) and 20 species occurred in at least half of the subcores (18 subcores). Of the species, 38.6% were restricted to one (52 species) or two subcores (16 species), and 60 species occurred in singletons (only one individual per subcore). Figure 2 shows the comparison of the species accumulation curves constructed for the three cores together (total of 36 subcores) and for each core separately (12 subcores). The curves for each core and the curve considering the three cores together were similar, and did not reach the asymptote (Fig. 2a, b). The curves also evidenced that a small number of subcores coming from a single core was as representative of the total species pool as were a similar number of subcores taken from three different cores. For example, a total of five subcores contained about 50% of the total number of species (from 36 subcores) regardless of whether they were taken from a single core (area of 78.5 cm^2) or from a combination of three different cores (area of 800 cm^2). An exception was core 1, which showed a slightly lower curve (Fig. 2a, b). Each single core (12 subcores) contained approximately 75% of the total number of species recorded in the 36 subcores.

Source of variation at different scales: Between cores vs. within core

Nauplii abundances, the total number of nematode species, and chl *a* and phaeopigment concentrations differed significantly between the cores (Fig. 3). Total nematode,

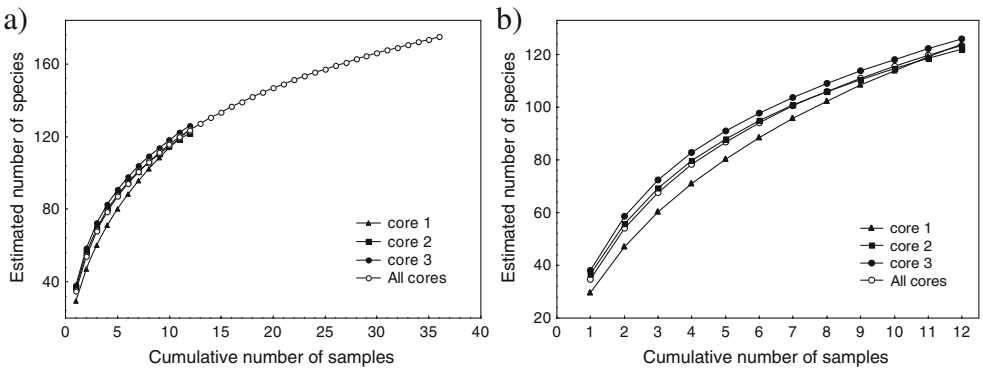


Fig. 2 Species-accumulation curves for (**a**) each core separately and for the three cores together; (**b**) detailed view of the comparison between each core and the three cores together

copepod and bacterial abundances did not differ significantly (Fig. 3). From all nematode species, a total of 58 were selected for the statistical test of between-core differences (Table 2). Together, these 58 species averaged 87% of total nematode densities. The densities of only eight species (together comprising an average of 30.8% of total nematode density) differed significantly between the cores (Table 2). To compare variability of all parameters at different scales, coefficients of variation (CV, Table 1) and the variance component from the PERMANOVA (Fig. 4) were used. Both methods yielded similar results. For all meiofauna parameters as well as for chloroplastic pigments and bacterial abundances, CVs were much higher at the smaller spatial scale ('within core') (Table 1). Accordingly, the estimation of variance components showed that spatial variations within cores contributed the main part of total heterogeneity for all parameters, while differences between cores were less important (Fig. 4). The residual variance (within-core variance) accounted for 69 to 100% of the variation of the different parameters (Fig. 4).

The multidimensional scaling ordination (nMDS) of the selected nematode species revealed a high degree of variability within cores (average MID_{cores} = 1.0) and did not show a separation between cores (Fig. 5). Subcores from one core were intermingled with subcores from other cores, and neighboring subcores were not necessarily the most similar. Indeed, dissimilarities between cores ($C_{1,2}$: 55.9, $C_{1,3}$: 57.9, $C_{2,3}$: 54.6) were similar to those within cores (C_1: 57.3, C_2: 53.0, C_3: 55.3) (PERMANOVA). Results of the ANOSIM test, however, showed a slight but significant difference (R=0.2, p=0.005) in the multivariate structure of nematode assemblages between cores 1 and 3. As for the univariate measures, the components of variation of the nematode assemblage structure (extracted from the PERMANOVA) also showed highest variability at the within-core scale (Fig. 4).

Small-scale spatial patterns

Dispersion indices (D) of both chloroplastic pigments were significantly lower than 1, indicating that they were not aggregated at the scale of subcores (Table 2). The results of Mantel tests showed a significant relationship (R=0.379, p=0.001) between inter-subcore dissimilarities of chl *a,* phaeopigment and bacteria data and distances between subcore locations, i.e. subcores located further apart were more dissimilar than those located more closely to each other. The Mantel correlogram together with plots from concentrations and abundances distribution, indicated a gradient in the distribution of chl *a* and phaeopigment concentrations as well as of bacterial abundances within the cores (Fig. 6).

The dispersion index for total nematode abundances was significantly greater than 1, indicating aggregation at the 2-cm scale of subcores (Table 2). Accordingly, the correlogram for nematode densities showed significant negative autocorrelation at the first distance class, suggesting patches on a scale smaller than the inter-subcore distances (2 cm) (Fig. 7a). The alternation of positive and negative values in the nematode correlogram indicates that small patches repeat at regular distances, as observed in the abundance plot (Fig. 7a, d). For copepods, the correlogram together with the abundance distribution plot suggest slightly larger aggregations and, indeed, small-scale heterogeneity was detected on a scale of ca. 3–5 cm (Fig. 7b, e). Nevertheless, overall harpacticoid densities did not differ significantly from the Poisson expectation of randomness (Table 2). The index of dispersion of nauplii abundances was significantly greater than 1 and according to the correlogram and the plot of abundances, they were distributed in heterogeneous patches which were larger than the core size (Fig. 7c, f).

Of the 58 nematode species analysed, 38 species showed significant departures from a random distribution; all of these were contagiously distributed (i.e. D>1; p<0.05) (Table 2). No species were significantly underdispersed. Spatial patterns, as elucidated from autocorrelograms, were apparent not only for populations which had an aggregated distribution but also for populations which did not demonstrate a distribution significantly different from random (Table 2). Of the 58 species studied, spatial patterns were indicated in 24 cases (Table 2). Of the 34 species which showed non-significant correlograms, 23 were

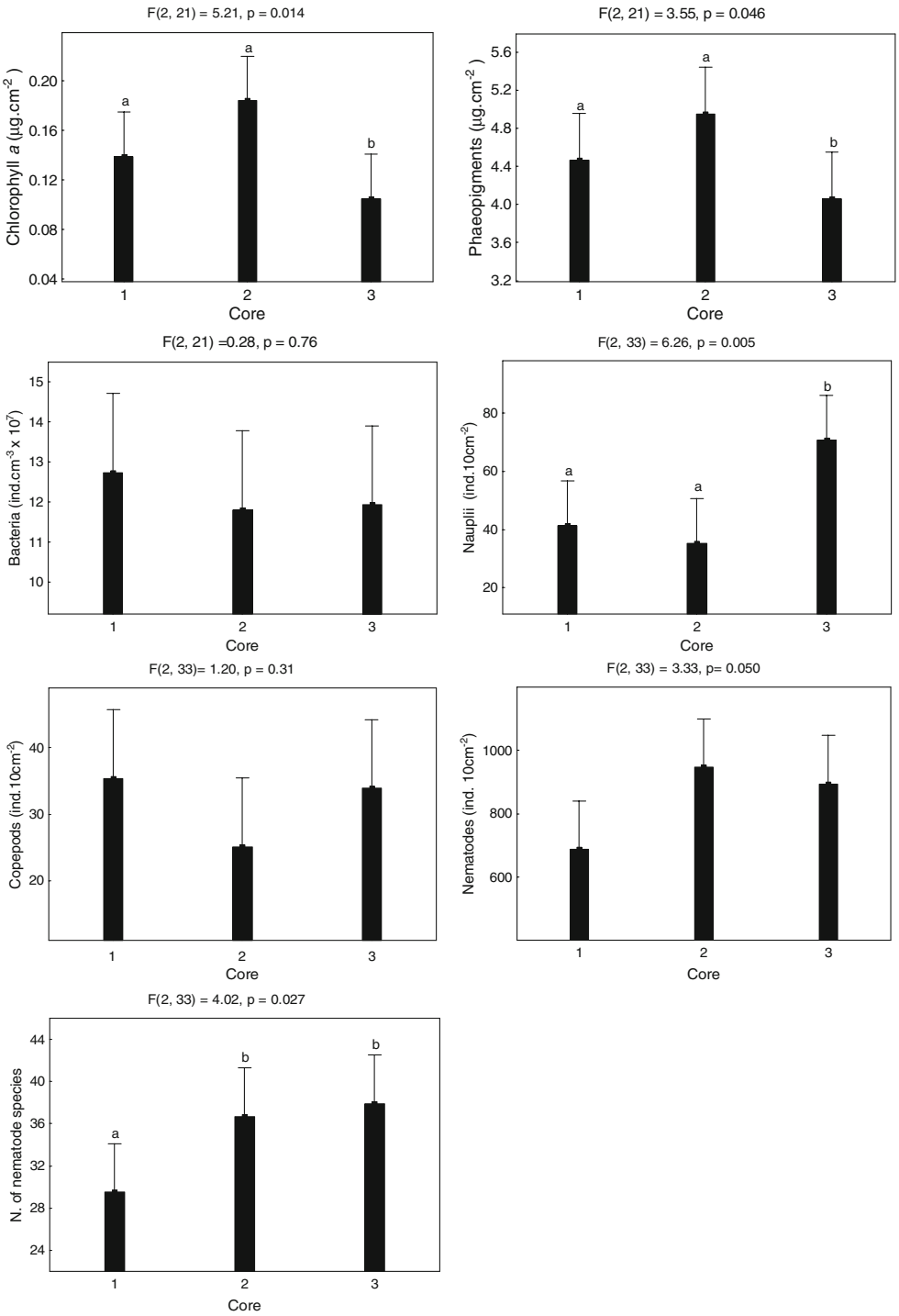


Fig. 3 Means and 95% confidence intervals for chl *a* and phaeopigment concentrations, bacterial abundances, nauplii, harpacticoid copepods and nematode abundances and total number of nematode species. *Letters above bars* indicate significant differences between cores after pair-wise a-posteriori comparisons

contagiously distributed based on *D*, indicating aggregation at a scale smaller than the sampling scale (Sokal and Wartenberg 1981).

Nematode species were grouped according to distinct patterns of the correlograms (Table 4). Group A: species were negatively autocorrelated at the 2-cm distance class, indicating aggregation at a scale smaller than the inter-subcore distance. Particularly for *Neochromadora* sp.1, the patches apparently repeated in a ca. 6– to 8-cm interval; Group B: species were distributed in heterogeneous patches at a scale smaller than 3 cm. For *Monhystrella* sp.2, patches repeated at ca. 5– to 6-cm intervals; Group C: species showed significant and positive autocorrelation at the first distance class (2 cm), i.e. neighbouring subcores usually assumed similar values. This correlogram pattern indicates that species from this group occurred in homogeneous aggregations at the 2-cm scale. Group D: species were distributed in homogeneous patches at the 2– to 3-cm scale;

Table 1 Coefficients of spatial variation (CVs) of bacteria, phytodetritus (chl *a* + phaeopigments), nauplii, copepod and nematode abundances and average from all CVs calculated for each nematode species. Within-core coefficients were calculated separately for each core and then averaged. Within core numbers indicate averages ± standard deviations

	Within core	Between core
Bacteria	13.67±6.36	3.9
Phytodetritus	14.9±3.8	10.4
Nauplii	56.3±18.7	38.6
Copepods	55.1±9.7	17.7
Nematodes	30.6±1.2	16.2
Nematode species	152±57	46±26

Group E: populations were distributed in heterogeneous patches at a scale of ca. 3 cm. Group F: distribution in homogeneous patches at scales of 3–5 cm; Group G: distribution in heterogeneous patches at scales of 3–5 cm; Group H: species were distributed in heterogeneous patches at scales of 5–6 cm; Group I: small-scale heterogeneity at the 8-cm scale, and Group J: individuals were distributed in patches larger than the sampling size, i.e. at a scale >8 cm.

Dispersion chi-square analysis also revealed strong clumping on the species level, i.e. on average, nematode species were aggregated ('total chi square' = 4,143, degrees of freedom = 1,995, $p<0.001$). The significant 'pooled chi square' ('pooled chi square' = 349, degrees of freedom =

Table 2 Total number of individuals (*n*), dispersion index (*D*) with significance at 5% probability level indicated by an *asterix*, and presence (+) or absence (–) of spatial pattern inferred from Moran's *I* correlograms (*I*) for chloroplastic pigments, bacteria, meiofauna groups and selected nematode species

	n	*D*	*I*		*n*	*D*	*I*
Bacteria		0.6					
Chl. *a*		0.01					
Phaeo		0.1*					
Nauplii	200	1.6*	-				
Harpacticoids	128	1.1	-				
Nematodes	3,381	9.0*	+				
Acantholaimus sp.1	22	1.2	+	*Halalaimus* sp.3	25	2*	-
Acantholaimus sp.2	30[a]	1.6*	+	*Halalaimus* sp.4	16	1.0	-
Aegioalalimus sp.1	52	1.4	-	*Halalaimus* sp.5	34[a]	1.1	+
Amphimonhystera sp.1	21[a]	1.0	-	*Leptolaimus* sp.1	16	1.6*	+
Amphimonhystera sp.2	16	1.8*	-	*Microlaimus* sp.1	562[a]	9.5*	-
Amphimonhystrella bullocauda	39[a]	3.1*	-	*Microlaimus* sp.2	128	5.2*	-
Anticoma sp.1	32	1.7*	+	*Molgolaimus* sp.1	22	1.4	+
Camacolaimus sp.1	36	1.5*	-	*Thalassomonhystera* sp.1	106[a]	1.7*	-
Campylaimus sp.1	41	1.9*	+	*Thalassomonhystera* sp.2	64	2.1*	-
Campylaimus sp.2	50	1.8*	-	*Thalassomonhystera* sp.3	36	1.6*	+
Chromadorita sp.1	19	1.5*	-	*Monhystrella* sp.1	10	1.0	-
Cobbia sp.1	17	1.9*	+	*Monhystrella* sp.2	18	1.5*	+
Daptonema sp.1	44	1.0	-	*Monhystrella* sp.3	14	1.1	+
Daptonema sp.2	136	1.2	-	*Monhystrella* sp.4	84	3.3*	+
Daptonema sp.3	13	2*	+	*Neochromadora* sp.1	36	1.7*	+
Daptonema sp.4	36	2*	-	*Neochromadora* sp.2	84	1.6*	-
Daptonema sp.5	14	1.5*	-	*Paracyatholaimus* sp.1	18	2*	+
Daptonema sp.6	50	2.5*	-	*Paralinhomoeus* sp.1	12	0.9	+
Daptonema sp.7	37	3.1*	+	*Pomponema* sp.1	28	1.2	-
Daptonema sp.8	30[a]	1.6*	-	*Pselionema* sp.1	14	1.0	-
Desmoscolex sp.1	17	1.5*	+	*Rhynconema* sp.1	10	1.6*	+
Desmoscolex sp.2	33	1.6*	-	*Southerniella* sp.1	65	1.2	+
Desmoscolex sp.3	250[a]	1.4	-	*Sphaerolaimus* sp.1	15	0.9	+
Desmoscolex sp.4	175	1.1	+	*Sphaerolaimus* sp.2	12	1.9*	-
Diplopeltoides sp.1	16	1.1	-	*Tricoma* sp.1	27	1.7*	-
Diplopeltoides sp.2	14	1.1	-	*Tricoma* sp.2	97	2.2*	-
Diplopeltula sp.1	20	1.5*	+	*Tricoma* sp.3	41	2.1*	-
Halalaimus sp.1	39	2*	-	*Tricoma* sp.4	30	2.6*	-
Halalaimus sp.2	10	1.2	+	*Tricoma* sp.5	10	1.4*	-

[a] Significant differences between cores (PERMANOVA)

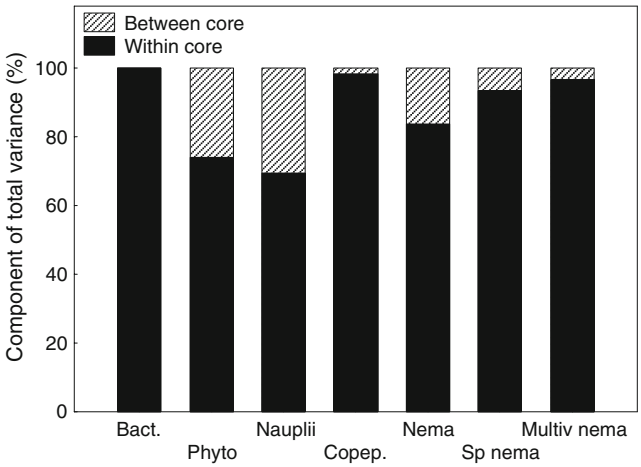


Fig. 4 Components of total variance for phytodetritus concentrations, bacterial and meiofaunal abundances and multivariate structure of nematode assemblages (after PERMANOVA). *Bact.* bacterial abundances, *Phyto* chlorophyll a + phaepigment concentrations, *Copep.* harpacticoid copepods, *Nema* total nematode densities, *Sp nema* average for all selected nematode species, *Multiv nema* multivariate structure of nematode assemblages

35, $p<0.001$) indicated that total abundances (the total number of individuals of all selected species) were aggregated within cores. Finally, the significant 'heterogeneity chi square' ('heterogeneity chi square' = 3,794, degrees of freedom = 1,960, $p<0.001$) indicated that the non-randomness detected by the 'total chi square' was not entirely caused by variance in total abundance among subcores, but resulted because abundances of different species did not vary proportionally among the subcores, i.e. species were typically discordant in their abundance patterns. The same statistics calculated after omission of the dominant species showed equal patterns.

The results of Mantel tests showed a significant relationship between inter-subcore similarities in the multivariate structure of nematode assemblages and distance between subcore locations (Table 3). There was a significant negative spatial autocorrelation between subcores 2–3.3 cm apart and even more so between subcores 6.2–8 cm apart (Table 3).

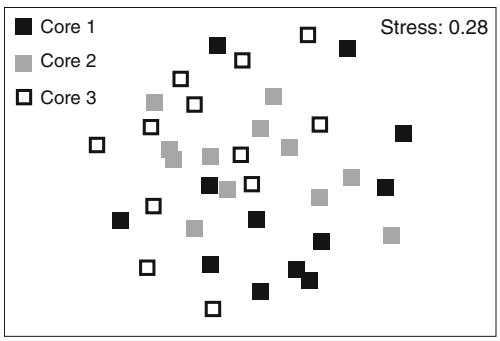


Fig. 5 nMDS ordination based on fourth-root transformed abundances of selected nematode species

Relationship between meiofauna and potential food sources

The small-scale sampling failed to reveal significant correlations between bacteria, phytodetritus and the distributions of nematode species and nauplii. Also, there were no significant correlations between pairs of nematode species. The only significant correlations were found for copepods, which were positively correlated with chl *a* (0.43, $p<0.001$) and, albeit weakly, with phaeopigments (0.23, $p<0.01$).

Discussion

Intensive sampling within less than 0.1 m^2 (ca. 800 cm^2) of deep-sea sediment revealed a total of 176 nematode species belonging to 64 genera. Only eight species occurred in more than 80% of the subcores, and 68 species were restricted to one or two subcores. On average, a single core (78.5 cm^2) contained approximately 75% of the total number of species. Most of the variability (69–100%) in abundances of meiobenthic groups was variability within cores. The same holds true for bacterial densities and chloroplastic pigment concentrations, and for the multivariate structure of the nematode assemblages. It is difficult to compare the small-scale variability identified here with other results from soft sediments, as many studies have been conducted in distinctly different habitats and have focused on different organisms. For the deep sea, 85% of the total variance of meiofauna abundances along a depth transect (400–4,000 m) was associated with subsamples within a box-corer (10 cm^2) (Coull et al. 1977). Particularly for nematodes, comparable analysis is only available from the sublittoral (30 m deep; Hogue 1982), and from intertidal (Hodda 1990) and shallow subtidal (mean of 6 m deep; Li et al. 1997) estuarine sediments. Whereas in sublittoral habitats, ca. 75% of the total variance in nematode (and nematode species) abundance was due to within-box-corer variability (10-cm scale) (Hogue 1982), small-scale variability (5-cm scale) in the intertidal (Hodda 1990) and shallow estuarine subtidal (Li et al. 1997) accounted for only 35% and 16%, respectively, of total variability, suggesting that in more energetic environments, physical disturbance possibly homogenises small-scale patchiness, thereby decreasing small-scale heterogeneity (Lambshead and Boucher 2003; Gallucci and Netto 2004).

The high degree of small-scale variation may result from highly patchy occurrences of individuals (Hodda 1990). In our study, abundances of total nematodes, nauplii and 65.5% of the selected nematode species were indeed

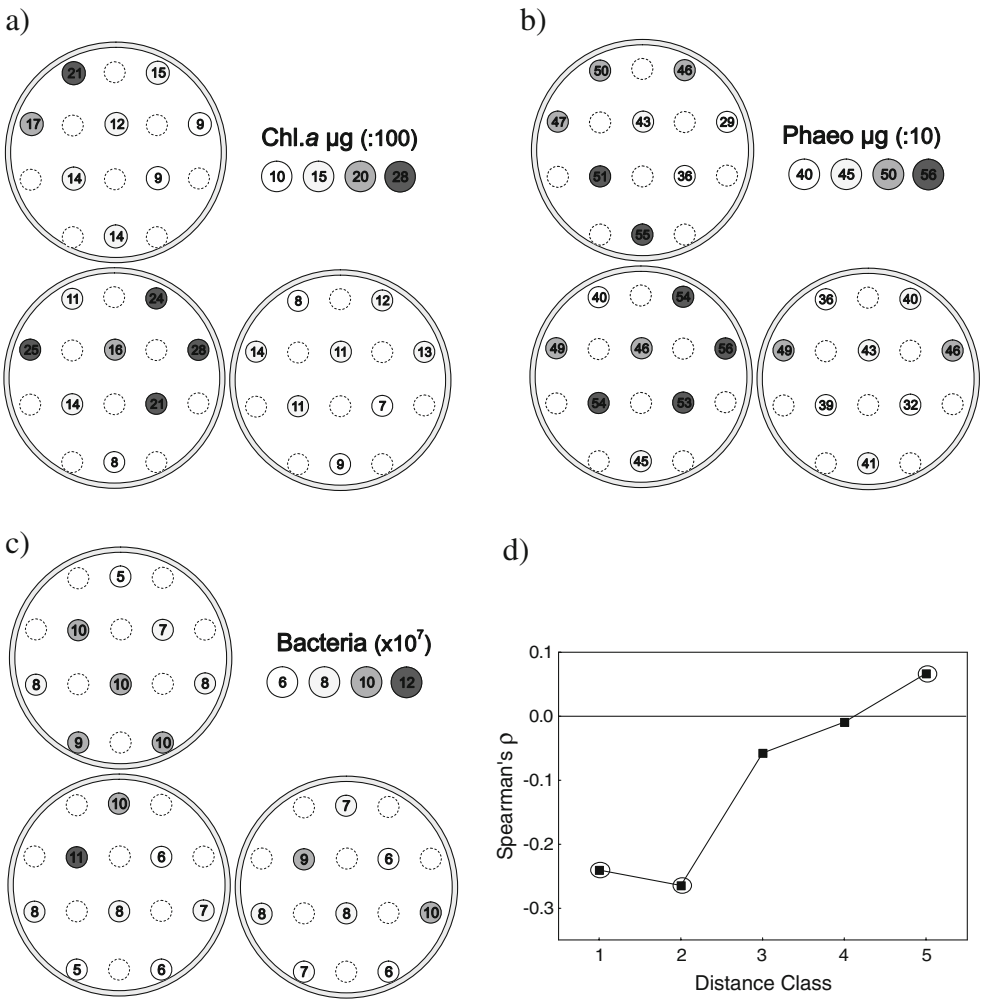


Fig. 6 Spatial distribution of concentrations of chl *a* and phaeopigments and abundance of bacteria for the three cores (**a**, **b**, **c**), and Mantel-correlogram of the Euclidian distance matrix of these three parameters with the coordinate distance matrix (**d**). Values in the legends represent the upper limits of chloroplastic pigments concentrations and bacterial densities. Distances within distance classes: *1*=2 cm, *2*=2.1–3.3 cm, *3*=3.4–5 cm, *4*=5.1–6.1 cm and *5*=6.2–8 cm. *Symbols surrounded by a circle* represent significant values ($p<0.05$) of Spearman's rank correlation coefficients

distinctly aggregated at our smallest scale of sampling, i.e. 2 cm. Non-random patterns at a scale of centimetres were also documented in harpacticoid copepods and ostracods in the San Diego Trough (Eckman and Thistle 1988), and in foraminiferans from the abyssal central North Pacific (Bernstein and Meador 1979). On the other hand, overall harpacticoid copepod densities distributions in the present study did not differ from random, in agreement with a previous study on deep-sea meiofaunal dispersion (Thistle 1978). In such cases, caution is due because the low abundances of individual taxa frequently encountered in the deep sea confer low resolving power to the statistical tests (Jumars and Eckman 1983). Likewise, low densities of copepods and some nematode species in our study render them less prone to a non-random distribution, so caution is due when interpreting these non-significant results.

According to the correlograms, nematode patch sizes were smaller than 4 cm^2, while adult copepods and nauplii showed aggregations of ca. 9–25 cm^2 and larger than 64 cm^2, respectively. The only previous deep-sea study that directly assessed meiofauna spatial patterns by means of autocorrelation showed that copepods, as a group, did not exhibit spatial autocorrelation, while individual species were distributed in 3.2- to 4.6-cm clusters and others were regularly spaced at scales from 2 to 9 cm (Eckman and Thistle 1988). Comparative studies conducted in shallow-water environments also suggested that copepods and nauplii have somewhat larger patch sizes than nematodes. For instance, Blanchard (1990) reported nematode patch sizes smaller than 4 cm^2, copepod patch sizes from 4 to 28 cm^2 and nauplii patch sizes between 28 and 113 cm^2 in an intertidal oyster pond. Findlay (1981) observed nematode patchiness in a subtidal salt marsh creek at the 5-cm^2 scale, while copepods and nauplii were patchy on a scale of 24 cm^2. There is yet other shallow-water evidence of nematode patches having less than a 5-cm radius (Hogue 1982; Hodda 1990; Blome et al. 1999), and copepod patches occurring on a decimetre scale (Sandulli and Pickney 1999; but see Fleeger et al. 1990). The consistency of the patch size of these groups across a range of marine habitats is surprising given the very different physical regimes in habitats as different as intertidal versus deep-sea soft bottoms. Constant differences in patch size between groups, in particular, probably relate to their different

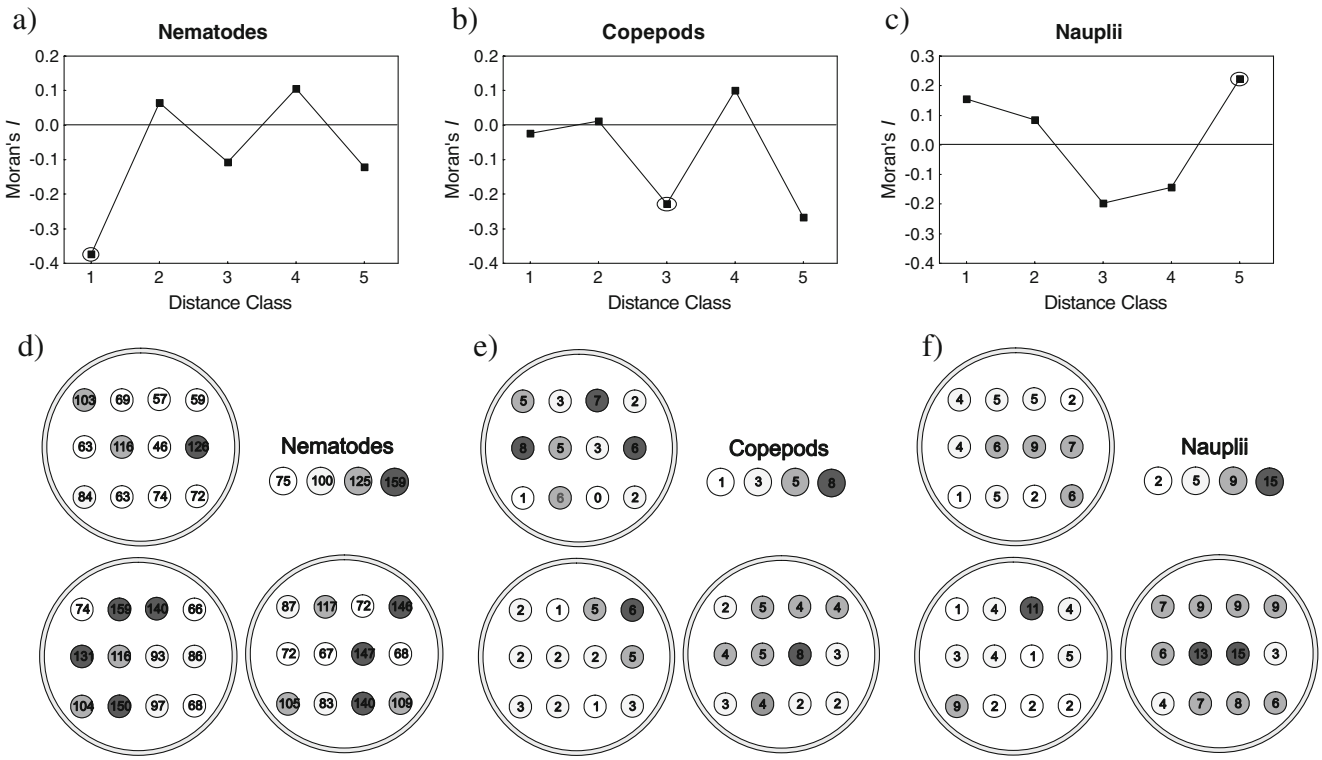


Fig. 7 Spatial autocorrelograms (**a**, **b**, **c**) and spatial distribution in single subcores (**d**, **e**, **f**) for nematode, harpacticoid copepod and naupliar abundances. Values in the legends represent the upper limits of densities. For the correlograms, data from the three cores have been combined. Distances within distance classes: *1*=2 cm, *2*=2.1–3.3 cm, *3*=3.4–5 cm, *4*=5.1–6.1 cm and *5*=6.2–8 cm. *Symbols surrounded by a circle* represent significant values ($p<0.05$) of Moran's *I* spatial autocorrelation coefficients

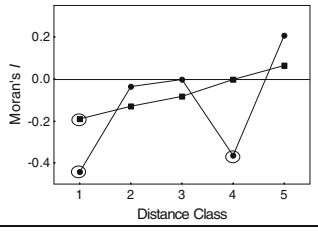
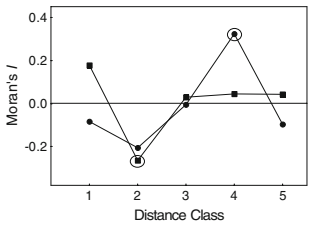
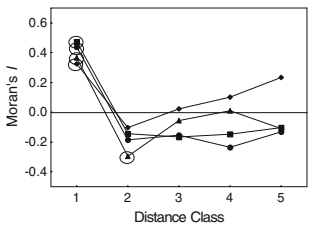
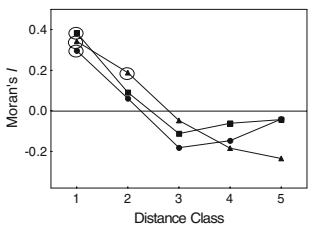
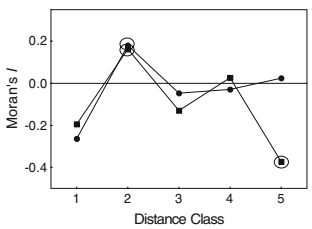
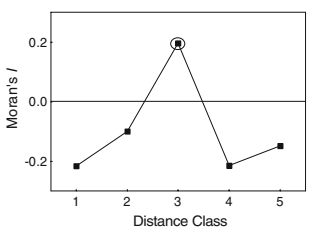
locomotory abilities: copepods and nauplii have a higher mobility and can actively emerge into the water column (Thistle et al. 2007), making use of bottom water flow for locomotion. Nematodes, on the other hand, are generally considered poor swimmers (Palmer 1984; but see Jensen 1981). Their dispersal is mainly through sinusoidal, active movements through the sediment (Giere 1993), and therefore likely restricted to a smaller area.

The shape of the spatial pattern also differed among nematode species. Significant spatial autocorrelation at the core scale was observed for 24 out of 58 analysed species. These species were separated in ten different spatial patterns according to their correlograms (Table 4). Apart from Group B, which was composed of two *Monhystrella* species, all groups were composed of species belonging to different genera and different feeding types (Wieser 1953; Moens and Vincx 1997). We further analysed morphometry and biomass data from a previous study conducted at the same station (Gallucci et al. 2008). Plotting species biomass versus the scale of the spatial pattern (i.e. the groups from Table 4) revealed that the size of the patches can be partially explained by nematode biomass, larger species typically showing larger patch sizes (Fig. 8). Moreover, smaller nematodes with long filiform tail and minute buccal cavity tend to have smaller patch sizes (homogeneous patches at scales up to 3 cm; Groups A–D) than larger nematodes with conical/clavate tail shape and/or larger buccal cavity (Fig. 8). Based on laboratory observations on deep-sea species, Riemann (1974) suggested that nematodes with long and filiform tail shapes have a hemi-sessile lifestyle and use their tails to anchor themselves to the substratum. At the same time, nematodes with a conical tail shape would be more motile (Thistle and Sherman 1985). Biomass per se also appears to be an important factor determining nematode locomotion (Schratzberger et al. 2004; Gallucci et al. 2008), larger deep-sea nematodes,

Table 3 Results of non-parametric Mantel tests of 'no relationship' between the Bray-Curtis similarity matrix from nematode abundances and matrices representing distances between sampling locations ('all distances') or model matrices (distance classes) (ρ Spearman's rank correlation coefficient). Bold values indicate significant coefficients at $p<0.025$ or $p>0.975$

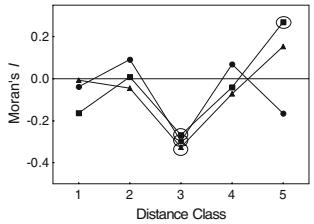
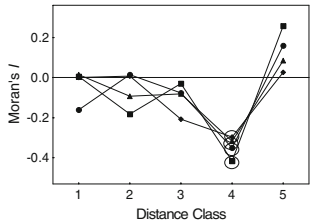
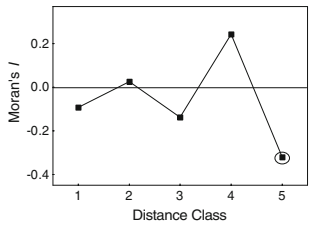
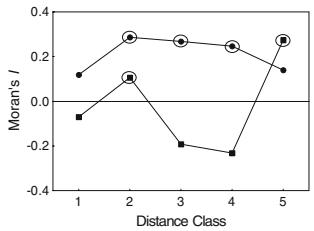
	ρ	*p*
All distances	**0.125**	**0.014**
2 cm	-0.034	0.833
2.1–3.3 cm	**-0.066**	**0.988**
3.4–5 cm	-0.031	0.813
5.1–6.1 cm	-0.059	0.924
6.2–8 cm	**-0.1**	**0.996**

Table 4 Small-scale spatial patterns of nematode species which showed significant correlograms based on Moran's *I* autocorrelation coefficients. For the correlograms, data of the three cores were combined. Symbols surrounded by a circle represent significant values ($p<0.05$) of Moran's *I* spatial autocorrelation coefficients. Distances within distance classes: 1=2 cm, 2=2.1–3.3 cm, 3=3.4–5 cm, 4=5.1–6.1 cm and 5=6.2–8 cm

	Species	Correlogram	Pattern
Group A	*Neochromad*ora sp.1 (•) *Rhynchonema* sp.1 (■)		Patches at the scale < 2cm
Group B	*Monhystrella* sp.2 (•) *Monhystrella* sp.4 (■)		Heterogeneous patches at the scale < 3 cm
Group C	*Acantholaimus* sp.2 (•) *Amphimonhystera* sp.3 (■) *Desmoscolex* sp.4 (♦) *Halalaimus* sp.2 (▲)		Homogeneous patches at the scale of 2 cm
Group D	*Leptolaimus* sp.1 (•) *Amphimonhystera* sp.1 (■) *Diplopeltula* sp.1 (▲)		Homogeneous patches at the scale of 2-3 cm
Group E	*Paralinhomoeus* sp.1 (•) *Desmoscolex* sp.1 (■)		Heterogeneous patches at the scale of 3 cm
Group F	*Campylaimus* sp.1		Homogeneous patches at the scale of 3-5 cm

for instance, being better colonizers of disturbed patches (Gallucci et al. 2008). As such, larger nematodes, particularly those with a conical tail shape, may perceive their habitat as more homogeneous ('fine-grained' sensu Jumars 1975) and therefore may be less restricted to a microhabitat, consequently occurring in larger aggregations. Moreover, their larger buccal cavity allows utilisation of a wider range of food sizes (Moens and Vincx 1997), guaranteeing a

(continued)

Group G	*Cobbia* sp.1 (•) *Acantholaimus* sp.1 (■) *Anticoma* sp.1 (▲)		Heterogeneous patches at the scale of 3-5 cm
Group H	*Daptonema* sp.4 (•) *Monhystrella* sp.3 (■) *Molgolaimus* sp.1 (▲) *Paracyatholaimus* sp.1 (♦)		Heterogeneous patches at the scale of 5- 6 cm
Group I	*Sphaerolaimus* sp.1		Heterogeneity at the scale < 8 cm
Group J	*Halalaimus* sp.5 (•) *Southerniella* sp.1 (■)		Patch larger than the sampling area

Interpretation of the correlograms according to Sokal (1979) and Legendre and Fortin (1989): Low-order (short-distance) positive autocorrelation, where neighbouring samples usually assume similar values, may arise from gradients or patches exceeding the diameter of inter-sample distances. Low-order negative autocorrelation, where neighbouring samples are different, suggests heterogeneous patches of smaller diameter than inter-sample distances. High-order (long-distance) positive autocorrelation indicates large patches or a regular arrangement of patches so that the values are approximately repeated. High-order negative autocorrelation is indicative of a gradient or a large patch with a sharp-edge boundary. The alternation of values, from positive to negative, is indicative of patch structure in the study area. The distance at which the value of autocorrelation reaches or crosses the expected value (i.e. approximately zero) is considered the 'spatial range', the 'zone of influence' or the 'patch size' of the spatial pattern under study

larger niche breadth and, therefore, wider distribution of these species. In contrast, small species with minute buccal cavity may have a narrower niche and are, therefore, spatially more constrained.

The six most abundant nematode species (*Microlaimus* sp.1, *Desmoscolex* sp.3, *Desmoscolex* sp.4, *Daptonema* sp.2, *Microlaimus* sp.2, and *Thalassomonhystera* sp.1), on the other hand, did not exhibit significant autocorrelation patterns, so patch sizes could not be determined at our sampling scale. Nevertheless, they occurred in high abundances in most (30–36 out of a total of 36) of the subcores suggesting that, if they are patchily distributed, patch sizes exceed our sampling area. Similarly, in coastal environments abundant macrobenthic species exhibit dispersion patterns on larger scales than do less abundant species (Thrush et al. 1989; Chapman and Underwood 2008), possibly because of a greater overall use of available habitat by more abundant species. Interestingly, the distribution of potential food sources such as phytodetritus and bacteria at our study area was also indicative of patches larger than our sampling scale. Therefore, on a larger scale, the distribution of the most abundant species might indeed relate to the distribution of their food. It is nevertheless important to note that *Microlaimus* sp.1 and sp.2 and *Thalassomonhystera* sp.1 had dispersion indices significantly larger than 1, suggesting that larger patches were not

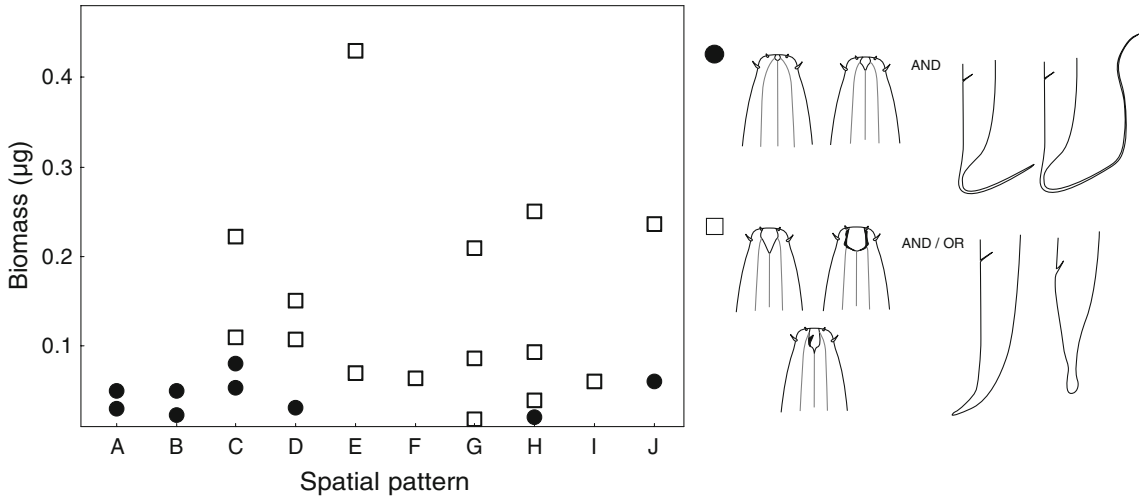


Fig. 8 Scatterplot of spatial pattern groups (Table 4) versus biomass of each species (after Gallucci et al. 2008)

homogeneous and second-order aggregations occurred on a smaller scale.

Evidence of aggregation and distinct patterns in many nematode species in the present study raises the question as to whether different species have concordant spatial patterns. Our data indicate that nematode species tended to have discordant abundance peaks. Spatial scales at which species' distribution patterns are discordant are relevant scales at which processes maintaining diversity can be expected to operate (Jumars 1976). Thus, our study suggests that processes shaping nematode assemblages operate at a scale smaller than 10 cm, in accordance with previous studies on deep-sea macrobenthos, harpacticoid copepods and foraminiferans (Jumars 1975, 1976, 1978; Thistle 1978, 1979; Bernstein and Meador 1979). The mechanisms causing discordance in local abundances among species are unclear but potentially include avoidance of competition or simply differential responses to their environment (Rice and Lambshead 1994). In the first case, discordance could be a consequence of either habitat partitioning or of dynamic but asynchronous local successions (Jumars and Eckman 1983). In a food-limited environment, potential competitors are unlikely to partition feeding time (Schoener 1974) or food type (Hairston 1973), and (spatial) habitat partitioning is much more likely (Jumars 1976). If, by contrast, disturbance and/or predation limit populations, then a spatial mosaic of successional sequences is expected (Grassle and Sanders 1973). Either extreme would result in patchiness, and species' abundance patterns would be expected to be discordant. On the other hand, differential responses to environmental variability (e.g. food sources or particular biogenic structures) also provide a plausible explanation for discordant species distributions. Local variations in the nature and frequency of biogenic structures on the centimetre scale are likely sources of heterogeneity (Jumars 1975; Thistle 1978; Eckman and Thistle 1988). Structures created by macrofauna (e.g. agglutinating foraminiferans, polychaete tubes, mudballs, etc.), for example, have already been related to microscale changes in abundance of foraminifera (Bernstein et al. 1978), nematodes (Bell et al. 1978; Hasemann 2006) and harpacticoid copepods (Thistle 1978), indicating they may be important for creating habitat heterogeneity for meiofauna (Thistle 1979; Thistle et al. 1993). Biogenic structures such as polychaete tubes, faecal casts and tracks, were also observed in our cores.

Patchy distribution of food sources may also explain small-scale patterns of nematode species (Rice and Lambshead 1994). In our study, however, we had no evidence that heterogeneity in potential food sources, like phytodetritus and bacterial abundances, drives small-scale variability and aggregation patterns of nematode species. Chloroplastic pigment concentrations and bacterial abundances were more homogeneously distributed in the cores than were nematodes as a group and individual nematode species. Besides, no significant correlations between chloroplastic pigments, bacteria and nematodes were observed. Although food supply influences large-scale distribution patterns in a relatively predictable manner along a gradient of food availability, at increasingly finer scale its influence is modified by small-scale heterogeneities, stochastic events and biotic interactions (Thrush 1991). At this small-scale, species might simply aggregate for reproduction (particularly the less abundant ones), and their distribution may not necessarily relate to environmental changes (Heip 1975). One must bear in mind, however, that sampling of meiofauna and food sources here was from adjacent sediment parcels. Close coupling of nematodes with food

sources might be identified if the same cores were used to establish spatial correspondence by more closely matching spatial scales.

Ecological significance aside, the high small-scale variability reported in this study also has potentially important implications for sampling designs in future deep-sea studies on meiofauna. Adequate replication of sampling units must ensure that small-scale variance in densities is representatively sampled (Chapman and Underwood 2008). Deep-sea studies typically use less than five samples from within a site to represent relatively large geographical areas, such as bathymetric and latitudinal zones (e.g. Vanaverbeke et al. 1997; Lambshead et al. 2002; Muthumbi et al. 2004; Fonseca and Soltwedel 2007), and less emphasis has been placed on the number of within-site samples and on their spatial arrangement. When sites are not well replicated, spatial variation caused by aggregated distribution patterns can markedly affect estimated variability at larger scales (Somerfield and Gage 2000) or at different points in time (Thrush et al. 1994). Consequently, any observed variability at larger scales can be due to small-scale variation rather than large-scale processes (Chapman and Underwood 2008). For example, the present study found a higher variability in nematode densities within a 0.1-m^2 area than a study at the same site but covering a bathymetric gradient (1,200–5,500 m) and a 4-year time series (Hoste et al. 2007). Besides, our study showed that a random subset of five subcores (irrespective of whether they were taken from the same core or from different cores), contained less than 50% of the species, suggesting that studies which normally take a small number of samples (three to five replicates) to characterise larger areas may underestimate deep-sea nematode species richness. This will of course also depend on the size of the corers, and especially on the number of individuals analysed from those corers. In general, three replicate cores with 2- to 4-cm diameter (as commonly used to take meiofauna samples in the deep sea) would sample an area roughly equivalent to five of our subcores (ca. 5.65 cm^2). Although in the past detailed sampling in the deep sea was a technological challenge, today effort may best be spent on obtaining accurate density estimates at each depth, latitude or time interval to prevent small-scale spatial variation from confounding large-scale patterns or temporal sequences. One alternative would be to use a multiscale approach and replicate the small scale within cores, between cores and between multicorers when larger areas are being compared (Rose et al. 2005).

It should be noted that the above conclusions rest on a single data set on the scale of a single multicore. Extensive further investigation including larger scales and other localities are definitely required before generalisations can be made. The sampling efficiency of our design also deserves closer investigation. While multicores are known to be very efficient in taking virtually undisturbed samples (due to minimal wave pressure when inserted in the sediment; Barnett et al. 1984, Bett et al. 1994), their transport to the surface and sampling may disturb the uppermost millimetres of sediment, eventually erasing in-situ patterns. Nonetheless, our cores showed no indication of disturbance after recovery and the microtopograpy of the sediment appeared well preserved. More importantly, the lack of co-variability between the spatial patterns of nematode species and environmental variables, as well as the array of specifies-specific distribution patterns we observed, goes strongly against the idea that the sampling procedure had an overriding impact on natural in-situ small-scale spatial patterns. If anything, sediment disturbance imposed by the retrieval of multicore samples should have partly homogenised small-scale patchiness, implying that the patterns and high degree of within-core patchiness we report here would even underestimate true natural patchiness. We are, therefore, confident that the patterns we found are representative of in-situ patterns, implying that future studies should include small-scale spatial variation in their sampling design if patterns, and ultimately processes, are to be fully understood.

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References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46 doi:10.1046/j.1442-9993.2001.01070.x

Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand

Andrew NL, Mapstone BD (1987) Sampling and the description of spatial patterns in marine ecology. Oceanogr Mar Biol Ann Rev 25:39–90

Barnett PRO, Watson J, Conelly D (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol Acta 7:399–408

Bell SS, Watzin MC, Coull BC (1978) Biogenic structure and its effects on the spatial heterogeneity of meiofauna in a salt marsh. J Exp Mar Biol Ecol 35:99–107 doi:10.1016/0022-0981(78)90069-2

Bergström U, Englund G, Bonsdorff E (2002) Small-scale spatial structure of Baltic Sea zoobenthos – inferring processes from

patterns. J Exp Mar Biol Ecol 281:123–136 doi:10.1016/S0022-0981(02)00440-9
Bernstein BB, Meador JP (1979) Temporal persistence of biological patch structure in an abyssal benthic community. Mar Biol (Berl) 51:179–183 doi:10.1007/BF00555197
Bernstein BB, Hessler RR, Smith R, Jumars PA (1978) Spatial dispersion of benthic Foraminifera in the abyssal Central Pacific. Limnol Oceanogr 23:401–416
Bett BJ, Vanreusel A, Vincx M, Soltwedel T, Pfannkuche O, Lambshead JPD, Gooday AJ, Ferrero T, Dinet A (1994) Sampler bias in the quantitative study of deep-sea meiobenthos. Mar Ecol Prog Ser 104:197–203 doi:10.3354/meps104197
Blanchard GF (1990) Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. Mar Ecol Prog Ser 68:101–111 doi:10.3354/meps068101
Blome D, Schleier U, Bernem KHV (1999) Analysis of the small-scale spatial patterns of free-living marine nematodes from tidal flats in the East Frisian Wadden Sea. Mar Biol (Berl) 133:717–726 doi:10.1007/s002270050513
Chapman MG, Underwood AJ (2008) Scales of variation of gastropod densities over multiple spatial scales: comparison of common and rare species. Mar Ecol Prog Ser 354:147–160 doi:10.3354/meps07205
Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. Mar Ecol Prog Ser 46:213–226 doi:10.3354/meps046213
Clarke KR, Chapman MG, Somerfield PJ, Needham HR (2006) Disperson-based weighting of species counts in assemblage analyses. Mar Ecol Prog Ser 320:11–27 doi:10.3354/meps320011
Cliff AD, Ord JK (1973) Spatial autocorrelation. Pion, London
Coull BC, Ellison RL, Fleeger JW, Higgins RP, Hope WD, Hummon WD, Rieger RM, Sterrer WE, Thiel H, Tietjen JH (1977) Quantitative estimates of the meiofauna from the deep sea off North Carolina, USA. Mar Biol (Berl) 39:233–240 doi:10.1007/BF00390997
Decho AW, Castenholz RW (1986) Spatial patterns and feeding of meiobenthic harpacticoid copepods in relation to resident microbial flora. Hydrobiol 131:87–96 doi:10.1007/BF00008327
Eckman J, Thistle D (1988) Small-scale spatial pattern in meiobenthos in the San Diego Trough. Deep-Sea Res 35:1565–1578 doi:10.1016/0198-0149(88)90103-3
Findlay SEG (1981) Small-scale spatial distribution of meiofauna on a mud- and sandflat. Estuar Coast Shelf Sci 12:471–484 doi:10.1016/S0302-3524(81)80006-0
Fleeger JW, Palmer MA, Moser EB (1990) On the scale of aggregation of meio-benthic copepods on a tidal mudflat. Marine Ecology 11:227–237
Fonseca G, Soltwedel T (2007) Deep-sea meiobenthic communities underneath the marginal ice zone off Eastern Greenland. Polar Biol 57:137–145
Fortin MJ, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge
Gage JD (1977) Structure of the abyssal macrobenthic community in the Rockall Trough. In: Keegan BF, Ceidigh PO, Boaden PJS (eds) Biology of benthic organisms. Pergamon Press, Oxford
Gallucci F, Netto SA (2004) Effects of the passage of cold fronts over a coastal site: an ecosystem approach. Mar Ecol Prog Ser 281:79–92 doi:10.3354/meps281079
Gallucci F, Moens T, Vanreusel A, Fonseca G (2008) Active colonization of disturbed sediments by deep-sea nematodes: Evidence for the patch mosaic model. Mar Ecol Prog Ser 367:173–183 doi:10.3354/meps07537
Giere O (1993) Meiobenthology: the microscopic fauna in aquatic sediments. Springer, Berlin
Grassle JF, Sanders HL (1973) Life histories and the role of disturbance. Deep-Sea Res 20:643–659
Grossmann S, Reichardt W (1991) Impact of *Arenicola marina* on bacteria in intertidal sediments. Mar Ecol Prog Ser 77:85–93 doi:10.3354/meps077085
Hairston NG (1973) Ecology, selection and systematics. Breviora 414:1–21
Hasemann C (2006) Kleinskalige Heterogentität in der arktischen Tiefsee: Einfluss kleiner Kaltwasser-Schwämme auf die Diversität benthischer Nematoden-Gemeinschaften. Ber Pol- Meeresforsch 527:1–323
Heip C (1975) On the significance of aggregation in some benthic marine invertebrates. In: Harold Barnes (ed) Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, pp 527–538
Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Ann Rev 23:399–489
Hessler RR, Jumars PA (1974) Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Res 21:185–209
Hewitt JE, Legendre P, McArdle BH, Thrush SF, Bellehumeur C, Lawrie SM (1997) Identifying relationships between adult and juvenile bivalves at different spatial scales. J Exp Mar Biol Ecol 216:77–98 doi:10.1016/S0022-0981(97)00091-9
Hodda M (1990) Variation in estuarine littoral nematode populations over three spatial scales. Estuar Coast Shelf Sci 30:325–340 doi:10.1016/0272-7714(90)90001-8
Hogue EW (1982) Sediment disturbance and the spatial distributions of shallow water meiobenthic nematodes on the open Oregon coast. J Mar Res 40:551–573
Hoste E, Vanhove S, Schewe I, Soltwedel T, Vanreusel A (2007) Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. Deep Sea Res Part I Oceanogr Res Pap 54:109–129 doi:10.1016/j.dsr.2006.09.007
Jensen P (1981) Phyto-chemical sensitivity and swimming behaviour of the free-living marine nematode *Chromadorita tenuis*. Mar Ecol Prog Ser 4:203–206 doi:10.3354/meps004203
Jumars PA (1975) Environmental grain and polychaete species diversity in a bathyal benthic community. Mar Biol (Berl) 30:253–266 doi:10.1007/BF00390748
Jumars PA (1976) Deep-sea species diversity: does it have a characteristic scale? J Mar Res 34:217–246
Jumars PA (1978) Spatial autocorrelation with RUM (remote underwater manipulator): vertical and horizontal structure of a bathyal benthic community. Deep-Sea Res 25:589–604 doi:10.1016/0146-6291(78)90615-X
Jumars PA, Eckman JE (1983) Spatial structure within deep-sea benthic communities. In: Rowe GT (ed) The sea. Wiley, New York, pp 399–452
Jumars PA, Thistle D, Jones ML (1977) Detecting two-dimensional spatial structure in biological data. Oecologia 28:109–123 doi:10.1007/BF00345246
Lambshead PJD, Boucher G (2003) Marine nematode deep-sea biodiversity—hyperdiverse or hype? J Biogeogr 30:475–485
Lambshead PJD, Brown CJ, Ferrero TJ, Mitchell NJ, Smith CR, Hawkins LE, Tietjen J (2002) Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific. Mar Ecol Prog Ser 236:129–135 doi:10.3354/meps236129
Lee JJ, Tietjen JH, Mastropaolo C, Rubin H (1977) Food quality and the heterogeneous spatial distribution of meiofauna. Helgol Wiss Meeresunters 30:272–282 doi:10.1007/BF02207841
Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. Vegetatio 80:107–138 doi:10.1007/BF00048036

Li J, Vincx M, Herman PMJ, Heip C (1997) Monitoring meiobenthos using cm-, m- and km-scales in the Southern Bight of the North Sea. Mar Environ Res 43:265–278 doi:10.1016/S0141-1136(96)00089-X

Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

Meyer-Reil LA (1983) Benthic response to sedimentation events during autumn to spring at a shallow water station in the Western Kiel Bight. Mar Biol (Berl) 77:247–256 doi:10.1007/BF00395813

Moens T, Vincx M (1997) Observations on the feeding ecology of estuarine nematodes. J Mar Biol Assoc U K 77:211–227

Muthumbi AW, Vanreusel A, Duineveld G, Soetaert K, Vincx M (2004) Nematode community structure along the continental slope off the Kenyan coast, Western Indian Ocean. Intern Rev Hydrobiol 89:188–205 doi:10.1002/iroh.200310689

Oden NL (1984) Assessing the significance of a spatial correlogram. Geogr Anal 16:1–16

Palmer MA (1984) Invertebrate drift: behavioural experiments with intertidal meiobenthos. Mar Behav Physiol 10:235–253

Rice AL, Lambshead PJD (1994) Patch dynamics in the deep-sea benthos: the role of a heterogeneous supply of organic matter. In: Giller PS, Hildrew AG, Raffaelli DG (eds) Aquatic ecology: scale, pattern and process. 34th Symposium of the British Ecological Society, Blackwell, Oxford, pp 469–499

Riemann F (1974) On hemisessile nematodes with flagelliform tails living in marine soft bottoms and on microtubes found in deep sea sediments. Mikrofauna Meeresb 40:1–15

Rose A, Seifried S, Willen E, George KH, Veit-Köhler G, Bröhldick K, Drewes J, Moura G, Martinez Arbizu P, Schminke HK (2005) A method for comparing within-core alpha diversity values from repeated multicorer samplings, shown for abyssal Harpacticoida (Crustacea: Copepoda) from the Angola Basin. Org Divers Evol 5:3–17 doi:10.1016/j.ode.2004.10.001

Sandulli R, Pickney J (1999) Patch sizes and spatial patterns of meiobenthic copepods and benthic microalgae in sandy sediments: a microscale approach. J Sea Res 41:179–187 doi:10.1016/S1385-1101(98)00048-3

Sawada M (1999) ROOKCASE: an Excel 97/2000 Visual basic (VB) add-in for exploring global and local spatial autocorrelation. Bull Ecol Soc Am 80:231–234 doi:10.1890/0012-9623(1999)080[0231:TT]2.0.CO;2

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39 doi:10.1126/science.185.4145.27

Schratzberger M, Whomersley P, Warr K, Bolam SG, Rees HL (2004) Colonisation of various types of sediment by estuarine nematodes via lateral infaunal migration: a laboratory study. Mar Biol (Berl) 145:69–78 doi:10.1007/s00227-004-1302-1

Shuman FR, Lorenzen CF (1975) Quantitative degradation of chlorophyll by a marine herbivore. Limnol Oceanogr 20:580–586

Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. Iowa State University Press, Ames

Snelgrove PVR, Smith CR (2002) A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanogr Mar Biol Ann Rev 40:322–342

Sokal RR (1979) Ecological parameters inferred from spatial correlograms. In: Patil GP, Rosenzweig ML (eds) Contemporary quantitative ecology and related ecometrics. Statistical Ecology Series, vol. 12. International Co-operative Publishing House, Fairland, pp 167–196

Sokal RR, Wartenberg D (1981) Space and population structure. In: Griffith D, Mckinnon R (eds) Dynamic spatial models. Sijthoff and Noordhoff, Alphen aan den Rijn, pp 186–213

Somerfield PJ, Gage JD (2000) Community structure of the benthos in the Scottish Sea-lochs. IV. Multivariate spatial pattern. Mar Biol (Berl) 136:1133–1145 doi:10.1007/s002270000311

Thistle D (1978) Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. J Mar Res 36:377–397

Thistle D (1979) Harpacticoid copepods and biogenic structures: Implications for deep-sea diversity maintenance. In: Livingstone RJ (ed) Ecological processes in coastal and marine systems. Plenum, New York, pp 217–231

Thistle D (2003) On the utility of metazoan meiofauna for studying the soft-bottom deep sea. Vie Milieu 53:97–101

Thistle D, Sherman KM (1985) The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep-Sea Res 32:1077–1088 doi:10.1016/0198-0149(85)90063-9

Thistle D, Hilbig B, Eckman JE (1993) Are polychaetes sources of habitat heterogeneity for harpacticoid copepods in the deep-sea? Deep Sea Res Part I Oceanogr Res Pap 40:151–157 doi:10.1016/0967-0637(93)90058-B

Thistle D, Sedlacek L, Carman KR, Fleeger JW, Barry JP (2007) Emergence in the deep sea: evidence from harpacticoid copepods. Deep Sea Res Part I Oceanogr Res Pap 54:1008–1014 doi:10.1016/j.dsr.2007.03.002

Thrush SF (1991) Spatial patterns in soft-bottom communities. Trends Ecol Evol 6:75–79 doi:10.1016/0169-5347(91)90178-Z

Thrush SF, Hewitt JE, Pridmore RD (1989) Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. Mar Biol (Berl) 102:529–536 doi:10.1007/BF00438355

Thrush SF, Pridmore RD, Hewitt JE (1994) Impacts on soft-sediment macrofauna: the effects of spatial variation on temporal trends. Ecol Appl 4:31–41 doi:10.2307/1942112

Ugland KI, Gray JS, Ellingsen KE (2003) The species-accumulation curve and estimation of species richness. J Anim Ecol 72:888–897 doi:10.1046/j.1365-2656.2003.00748.x

Underwood AJ (1996) Spatial patterns of variability in density of intertidal populations. In: Floyd RB, Sheppard AW, De Barro PJ (eds) Frontiers of population ecology. CSIRO Publishing, Melbourne, pp 369–389

Underwood AJ (1997) Ecological experiments: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107:212–224 doi:10.1007/BF00327905

Vanaverbeke J, Martinez-Arbizu P, Dahms HU, Schminke HK (1997) The metazoan meiobenthos along a depth gradient in the Arctic Laptev Sea with special attention to nematode communities. Polar Biol 18:391–401 doi:10.1007/s003000050205

Volckaert F (1987) Spatial pattern of soft-bottom Polychaeta off Nova Scotia, Canada. Mar Biol (Berl) 93:627–639 doi:10.1007/BF00392800

Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. J Exp Mar Biol Ecol 172:215–226 doi:10.1016/0022-0981(93)90098-9

Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arch Z 4:439–484