Three-dimensional spatial structure: nematodes in a sandy tidal flat

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ABSTRACT: Benthic infauna live in a three-dimensional world, and patterns of horizontal distribution may vary with depth in the sediment, as may the mechanisms that determine those patterns. This study examines how horizontal spatial structure varies with depth in a semi-exposed coarse-sand flat adjacent to St Martin's, one of the Isles of Scilly, UK. Nematode samples were collected from 3 sediment depth horizons (0 to 5, 5 to 10 and 10 to 15 cm) in a nested hierarchical design, with samples 0.1, 1 and 10 m apart. Results show that spatial patterns are strongest amongst samples of intermediate depth (5 to 10 cm), and generally insignificant amongst samples collected from 10 to 15 cm. There is short-order spatial autocorrelation in surface (0 to 5 cm) samples, with samples collected 10 cm apart being significantly more alike than samples collected further apart. We postulate that this is because spatial structure of nematodes in surface sediments is determined by patchiness induced by interactions between the water column and the physical structure of the surface layers of the sediment, which are constantly reworked by wind and tides. The deeper layers, 10 to 15 cm below the surface, are constantly reworked by a dense population of heart urchins *Echinocardium cordatum*. It is only in the intermediate horizon that relatively stable conditions allow nematode assemblages to establish spatial structure over a range of scales. It is concluded that the interaction between sediment permeability, and therefore interfacial advection, and bioturbation in controlling infaunal diversity and spatial patterns is potentially important.

KEY WORDS: Nematodes · Spatial structure · Vertical distribution · *Echinocardium* · Bioturbation · Advection

INTRODUCTION

Unlike the epifauna of hard substrata, the benthic infauna of sediments live in a three-dimensional world, and the mechanisms that determine horizontal patterns of distribution may vary with depth in the sediment. Despite this, descriptions of horizontal patterns of distribution are usually depth integrated, which masks these depth differences and, consequently, patterns may be difficult to interpret in terms of the underlying processes that determine them.

Sediment-dwelling, free-living nematodes have a range of life-history characteristics such as small body size, *in situ* feeding, a lack of a specific dispersal stage, and *in situ* reproduction followed by rapid development, which tie them closely to the sediment in which they live. One consequence is that changes in nema-

tode community structure in response to environmental changes in the sediment may be very rapid. There is a general hypothesis that in areas which we view as homogenous, such as intertidal flats, the horizontal distribution of meiofauna is patchy and unpredictable (Fleeger & Decho 1987). On the other hand, studies of the vertical distribution of meiofauna in similar habitats have shown that distribution patterns may be predictable and, in response to physical and chemical fluctuations, species-specific migrations may occur (Joint et al. 1982, Steyaert et al. 2001). A recent study (Warwick et al. 2006) suggested that spatial distributions of metazoans in a coarse-sand flat have fractal properties over certain domains and that for smaller organisms (corresponding to the meiofauna) vertical clustering is an important component of their spatial structure.

Spatial structure may be defined, and therefore detected in statistical analyses, in a large variety of ways. Many of these rely on implicit assumptions concerning the distributions of organisms in the absence of spatial structure. For example, in a univariate context a failure to detect departure from a Poisson distribution in a statistical test (such as a χ^2 test on variance:mean ratios) may be used to demonstrate a random distribution, reinforcing the idea that randomness in this context implies a lack of spatial structure. In fact the presence and absence of spatial structure are both possible even if organisms are distributed according to a Poisson process at some scale or other. Nevertheless, it is important to have some criteria against which to judge the presence and relative strength of a spatial structuring process. Here, we chose to consider spatial structure as being present when samples collected from locations closer together were significantly more (or less) similar to each other than samples collected from locations further apart, in terms of their assemblage composition. As such the general hypothesis concerns multivariate spatial autocorrelation rather than some measure of patchiness, a context within which many studies of spatial structure have been analysed and interpreted (Somerfield & Gage 2000).

Studies of spatial structure of nematodes in sediments have tended to focus on either horizontal patterns, using samples collected to a standard depth (e.g. Hogue & Miller 1981, Blome et al. 1999), or vertical structure within small areas (e.g. Platt 1977, Joint et al. 1982). We examined the extent to which horizontal structure in a free-living nematode assemblage varied at different depths within an apparently homogeneous area of coarse intertidal sand, and interpreted perceived patterns in light of the likely processes operating at various spatial scales in different depth horizons within the sediment.

MATERIALS AND METHODS

Study site and field sampling. Samples were collected from LWST (low water spring tides) on St Martin's flats, Isles of Scilly (Fig. 1). The islands are a granite archipelago situated 40 km south-west of the English mainland. The large semi-exposed sandflat is located on the south of the island of St Martin's and consists of coarse sand (median diameter: 575 μm) with <0.1% silt/clay, a permanent water table, and no visual evidence of reducing conditions (such as a blackening of the sediment) in the upper 15 cm. Samples of sediment for the determination of free-living nematode assemblages were taken on 18 April 1999. Cores with an internal diameter of 4 cm were collected according to a nested hierarchical design, with samples 0.1, 1.0 and 10 m apart (Fig. 2). Cores were carefully inserted into the sediment, during which gentle suction was applied by mouth to reduce core compression, and sealed at the top with a rubber bung. They were then dug out and sealed from below. Each core was sliced into 3 depth horizons (0 to 5, 5 to 10 and 10 to 15 cm) by loosening the upper seal and allowing the core to slide slowly out of the bottom of the tube into sample containers (Somerfield et al. 2005). The samples were fixed in 10% formalin. Cores that were obviously disrupted at any stage during the process were discarded.

A population of *Echinocardium cordatum* inhabited the sediment, and the depths and densities at which they were living in the study area were estimated in carefully dug pits. Surface openings of *E. cordatum* respiratory shafts were counted in a 10×10 grid of 1 m² quadrats. This is likely to underestimate the densities of the animals, as this species makes single shafts (Nichols 1959), but not all are visible at the surface. However, we believe that this procedure gives an adequate indication of the population's spatial distribution.

Sample processing. Extraction and mounting of nematodes followed Somerfield & Warwick (1996) and Somerfield et al. (2005). After decanting the
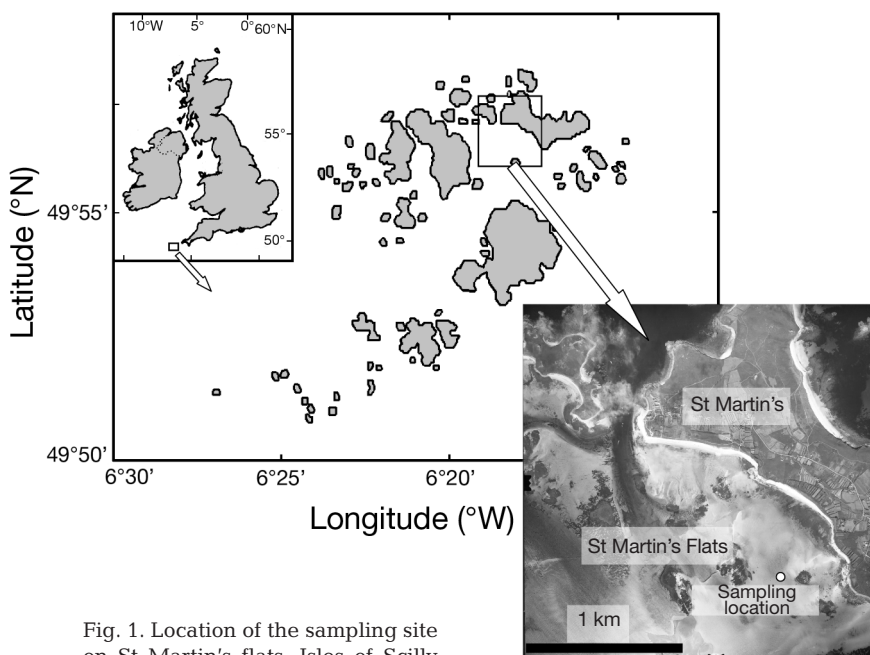

Fig. 1. Location of the sampling site on St Martin's flats, Isles of Scilly

Fig. 2. Schematic of the sampling design. Cores were collected according to a hierarchical design at distances of 0.1, 1.0 and 10 m apart and subsequently sectioned into 5 cm depth increments

samples 5 times onto a 63 μm sieve, nematodes were extracted with Ludox-TM, with a specific gravity of 1.15. The extraction was repeated 4 times, and the meiofauna were stored in 4% formalin. Prior to mounting, samples were washed into a glass cavity block with a solution of glycerol and ethanol in water. The mixture was then allowed to evaporate for 24 h on a warm hotplate, leaving the meiofauna in pure glycerol. Each sample was then mounted onto slides, and nematodes were identified under a compound microscope. Nematodes were identified to species level using Platt & Warwick (1983, 1988), Warwick et al. (1998) and taxonomic literature.

Numerical analyses. The majority of statistical analyses were carried out using the non-parametric multivariate methods (Clarke & Warwick 2001) contained in PRIMER v6 (www.primer-e.com). Bray-Curtis similarities were calculated between every pair of samples based on untransformed species abundance data. ANOSIM was used to test hypotheses concerning differences between groups of samples, and relationships between samples were visualised using non-metric multidimensional scaling (MDS). Similarity percentages breakdown (SIMPER, Clarke 1993) was used to determine species contributing to differences between groups of samples. Non-parametric Mantel tests (RELATE), using Spearman's rank correlation (ρ) between corresponding elements of resemblance matrices as the test statistic, were used to explore relationships between matrices of intersample distances and similarity matrices derived from nematode abundances. To examine spatial relationships in more detail, Mantel tests were used to address the hypothesis that biotic similarities between samples a particular distance apart are higher (or lower) than similarities between samples separated by other distances, by correlating biotic similarities with model matrices in

which the distance of interest was coded as 1, and all other distances as 0. As these were all 2-tailed tests (similarities may be positively or negatively correlated with distance) we consider values of $p < 0.025$ and > 0.975 to be significant (Somerfield & Gage 2000).

An exact permutation test (Clarke et al. 2006) was applied to determine whether nematode species and *Echinocardium cordatum* respiratory-shaft openings were overdispersed (clumped, $D > 1$, $p < 0.05$), underdispersed (regularly spaced, $D < 1$, $p > 0.95$), or had a Poisson distribution (randomly distributed, $D = 1$, $0.05 < p < 0.95$).

RESULTS

A total of 152 species of free-living nematodes were identified in the samples, including many species and genera previously unrecorded from the UK (Tables 1 & 2). Dominant species included *Perepsilonema crassum*, *Desmodora schulzi*, *Neochromadora poecilosomoides*, *Echinotheristus teutonicus*, *D. pontica*, *Theristus denticulatus*, *Spirinia gerlachi* and *D. sanguinea*. A total of 102 species were found at 0 to 5 cm, 98 at 5 to 10 cm and 95 at 10 to 15 cm. There were small (Fig. 3) but highly significant differences in numbers of species in samples (1-way ANOVA: $F_{2,42} = 23.14$, $p < 0.0001$) among different sediment horizons. Average abundances per sample (12.6 cm^2, 63 cm^3) ranged from 400 in the surface layer, through 262 at 5 to 10 cm, to 162 at depths of 10 to 15 cm, but variability in abundance was highest at intermediate depths ($\sigma = 101$), lower in the surface layer ($\sigma = 88$) and lowest in the deepest layer ($\sigma = 49$). These differences in variance precluded a test for significance between the abundances at different depths, but the pattern is clear.

Fig. 3. Number of species in samples from 0 to 5, 5 to 10 and 10 to 15 cm depth

Table 1. Total number of individuals of species with non-Poisson spatial distributions in at least 1 depth horizon (0 to 5 cm, 5 to 10 cm, 10 to 15 cm) occurring in samples (N = 15 from each depth horizon) from St Martin's flats. +: species recorded in Linnean Society Synopses [Platt & Warwick 1983, 1988, Warwick et al. 1998]; 1: genus new to the UK; 2: species new to the UK; ~: species identification uncertain, probably new to the UK when generic identification known; D: variance:mean ratio, values >1 significant [p < 0.05] overdispersion in an exact permutation test for departure from a Poisson distribution, 1 indicates Poisson distribution

Species	UK status	0–5 cm	D	5–10 cm	D	10–15 cm	D	Total
Perepsilonema crassum	1, 2	1557	18	1170	23	402	29	3129
Desmodora schulzi	+	1342	21	1480	31	808	16	3630
Neochromadora poecilosomoides	+	326	7	8	3			334
Echinotheristus teutonicus	1, 2	311	5	18	3			329
Desmodora pontica	+	252	2	44	3	5	1	301
Theristus denticulatus	+	224	3	65	1	23	1	312
Ixonema sordidum	1, 2	184	4	137	4	7	3	328
Prochromadorella ditlevseni	+	175	4	4	2	10	1	189
Paracyatholaimus occultus	+	155	6	96	3	16	2	267
Chromadorita nana	+	143	5	45	2	5	2	193
Metachromadora suecica	+	105	3	3	1	5	5	113
Anomonema haplostoma	1, 2	101	2	46	6	1	1	148
Calomicrolaimus parahonestus	+	86	2	26	3	6	3	118
Chromadorid juvenile	~	71	3	2	2			73
Enoploides brunettii	+	61	2	4	2	2	1	67
Manunema proboscidis	1, 2	58	3	70	4	2	1	130
Rhynchonema longituba	2	55	6	118	2	85	4	258
Prochromadorella septempapillata	+	51	2	0		1	1	52
Calomicrolaimus honestus	+	50	7	3	1	28	4	81
Chromadorita tentabunda	+	47	5	6	1	2	1	55
Sabatieria celtica	+	46	1	86	3	44	4	176
Actinonema celtica	+	46	2	24	6	5	2	75
Oxystominid cf. *Paroxystomina*	1, ~	44	1	34	1	10	3	88
Microlaimus ostracion	+	35	2	4	1	11	4	50
Enoplolaimus denticulatus	+	32	3	30	2	8	1	70
Hypodontolaimus sp.	~	27	6	2	2			29
Siphonolaimus ewensis	+	26	3	40	2	24	1	90
Viscosia elegans	+	26	10	10	2	5	1	41
Neochromadora trichophora	+	25	3	2	1	1	1	28
Viscosia abyssorum	+	17	7					17
Monoposthia mirabilis	+	16	1	2	1	1	1	19
Axonolaimus orcombensis	+	15	3	39	4	106	7	160
Camacolaimus longicauda	+	13	1	23	1	16	1	52
Halaphanolaimus pellucidus	+	13	4	5	1	5	1	23
Sigmophoranema rufum	+	12	1	1	1	4	1	17
Chromaspirina multipapillata	+	11	2	18	2	19	3	48
Fenestrolaimus sp. 1	1, ~	11	2	3	1	2	1	16
Cyatholaimid juvenile	~	10	4	1	1	3	1	14
Anticoma acuminata	+	9	1	3	1			12
Paralongicyatholaimus minutus	+	8	6	1	1	13	2	22
Spirinia schneideri	+	7	2	21	3	69	8	97
Theristus sp.	~	7	1	4	1	6	1	17
Leptolaimus sp.	~	6	1	15	1	10	1	31
Mesacanthion africanthiforme	+	6	4	1	1			7
Desmodorid juvenile	~	6	3			4	2	10
Odontophora wieseri	+	5	1	26	4	45	2	76
Tarvaia angusta	+	5	1	3	1			8
Eleutherolaimus stenosoma	+	5	2	2	1			7
Atrochromadora microlaima	+	5	5					5
Rhips paraornata	+	5	3					5
Chromaspirina pellita	2	4	1	18	1	75	3	97
Eubostrichus sp.	1, ~	4	1	3	1	15	2	22
Desmodora communis	+	4	1	3	1			7
Acanthopharynx sp.	1, ~	4	1	2	1			6
Cyartonema elegans	+	4	2			5	2	9
Euchromadora sp. 1	~	4	2					4

Table 1 (continued)

Species	UK status	0–5 cm	D	5–10 cm	D	10–15 cm	D	Total
Tricoma brevirostris	+	3	1	7	1	4	1	14
Paramonhystera riemanni	+	3	1	4	1	10	1	17
Theristus bastiani	+	3	3			1	1	4
Comesa sp.	~	3	3					3
Metadesmolaimus pandus	+	2	1	11	2	25	8	38
Latronema aberrans	1, 2	2	1	6	1	4	1	12
Rhabdocoma riemanni	+	2	2	2	1	2	1	6
Onyx perfectus	+	2	2	1	1	1	1	4
Sigmophoranema litorale	+	2	2	1	1			3
Odontophora exharena	+	2	2			10	3	12
Daptonema procerum	+	2	1			8	6	10
Paracanthonchus sp.	~	2	1			4	1	6
Daptonema sp.	~	2	2			3	1	5
Spirinia laevis	+	2	2					2
Stephanolaimus elegans	+	1	1	10	2	2	1	13
Metalinhomoeus sp.	~	1	1	7	1	15	2	23
Amphimonhystera anechma	+	1	1	4	1			5
Linhomoeus sp.	~	1	1	2	1	2	2	5
Spirinia gerlachi	+			13	2	140	10	153
Desmodora sanguinea	+			9	7	141	13	150
Paramesonchium belgicum	1, 2			8	1	30	2	38
Thalassomonhystera parva	+			6	3			6
Paralinhomoeous uniovarium	+			4	2	1	1	5
Metadesmolaimus gelana	+			4	1			4
Leptonemella aphanothecae	+			3	1	15	2	18
Astomonema sp.	~			3	1	5	2	8
Praeacanthonchus inglisi	+			3	3			3
Siphonolaimus cobbi	+			2	2			2
Metadesmolaimus sp. 3	~			1	1	10	3	11
Microlaimus acinaceus	+			1	1	6	2	7
Chromaspirina sp.	~					15	2	15
Paralinhomoeus tenuicaudatus	+					6	3	6
Daptonema sp. 1	~					5	3	5
Stephanolaimus bicornatus	2					3	3	3
Nannolaimus fusus	+					2	2	2

There was a clear gradient in community structure from the sediment surface to deeper sediment horizons (Tables 1 & 2, Fig. 4), reflected in a 2-way ANOSIM test for differences in assemblages collected from different depths averaged across different corners of the triangular design ($R = 0.697$, $p < 0.001$). Analysis by SIMPER showed, as might be expected, that approximately 50% of the Bray-Curtis dissimilarity between sediment horizons was contributed by decreases in abundances of dominant species (*Perepsilonema crassum*, *Neochromadora poecilosomoides*, *Echinotheristus teutonicus*, *Theristus denticulatus*, *Pseudochromadora pontica* and *Desmodora schulzi*) with increasing depth. Species with relatively more importance in the deeper sediments included *D. sanguinea* and *Spirinia gerlachi* (Table 1).

No nematode species were significantly underdispersed (Tables 1 & 2), but many species were overdispersed (Table 1) in 1 or more depth horizons, and in each horizon there was a significant relation-

ship between the variance:mean ratio (D) of species and their abundances (Fig. 5). A total of 50% of species were overdispersed in the 0 to 5 cm horizon; 35% at 5 to 10 cm; and 41% at 10 to 15 cm. The similarity in
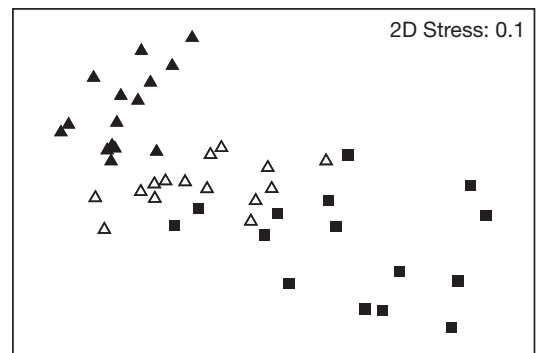

Fig. 4. MDS ordination of samples based on Bray-Curtis similarities computed from abundances of free-living nematodes (▲: 0 to 5 cm; △: 5 to 10 cm; ■: 10 to 15 cm)

Table 2. Total number of individuals of species for which an exact permuta-
tion test showed no evidence for departure from Poisson distribution in any
depth horizon (0 to 5 cm, 5 to 10 cm, 10 to 15 cm) occurring in samples (N = 15
from each depth horizon) from St Martin's flats. +: species recorded in Lin-
nean Society Synopses [Platt & Warwick 1983, 1988, Warwick et al. 1998]; 1:
genus new to the UK; 2: species new to the UK; ~: species identification
uncertain, probably new to the UK when generic identification known

Species	UK status	0–5 cm	5–10 cm	10–15 cm	Total
Gammanema rapax	+	3	2	3	8
Halalaimus sp.	~	3	1		4
Paramonhystera sp.	~	3	1		4
Leptonemella granulosa	2	3		3	6
Viscosia viscosa	+	2	1		3
Paracanthonchus longus	+	2		2	4
Araeolaimus sp.	~	2			2
Chromadora nudicapitata	+	2			2
Chromaspirina parapontica	~	2			2
Metachromadora scotlandica	+	2			2
Microlaimus conothelis	+	2			2
Pontonema vulgare	+	2			2
Rhabdocoma wrong tail	~	2			2
Paradesmodora sp.	1, ~	1		2	3
Paralinhomoeus sp. 1	~	1		2	3
Enoplolaimus propinquus	+	1		1	2
Axonolaimus spinosus	+	1			1
Belbolla sp.	~	1			1
Desmodora tenuispiculum	+	1			1
Enoploides spiculohamatus	+	1			1
Eurystomina sp.	~	1			1
Fenestrolaimus sp.	1, ~	1			1
Linhomoeus sp. 1	~	1			1
Metadasynemoides sp.	1, ~	1			1
Stylotheristus sp.	1, ~	1			1
Terschellingia longicaudata	+	1			1
Theristus sp.	~	1			1
Tricoma longirostris	+		3	1	4
Filitonchus ewensis	+		2	2	4
Odontophora villoti	+		2	2	4
Spirinia parasitifera	+		2		2
Ascolaimus elongatus	+		1	1	2
Daptonema invagiforoum	+		1	1	2
Xyala sp.	~		1	1	2
Chromadorella sp.	~		1		1
Cyartonema germanicum	+		1		1
Dasynemoides sp.	~		1		1
Enoplus quadridentatus	+		1		1
Gerlachius novusetosus	+		1		1
Mesacanthion hirsutum	+		1		1
Metoncholaimus scanicus	+		1		1
Neotochus sp.	~		1		1
Paracyatholaimoides multispiralis	+		1		1
Pontonema reducta	+		1		1
Syringolaimus sp.	1, ~		1		1
Theristus sp. 1	~		1		1
Trileptium sp.	~		1		1
Axonolaimus hexapilus	+			3	3
Neochromadora sp.	~			2	2
Calomicrolaimus acanthus	+			1	1
Enoplolaimus litoralis	+			1	1
Choniolaimus sp.	~			1	1
Halichoanolaimus/Latronema	~			1	1
Paracanthonchus longicaudatus	+			1	1
Paralinhomoeus lepturus	+			1	1
Pselionema sp.	~			1	1
Pterygonema sp.	~			1	1
Richtersia inequalis	+			1	1
Stephanolaimus sp. 1	~			1	1
Thalassironus sp.	~			1	1

D-values for individual species (Tables 1 &
2), and in the relationships between *D* and
abundance (Fig. 5), at different depths
indicate that a species' tendency to aggre-
gate is relatively constant and not marked-
ly influenced by the depth at which it oc-
curs.

The results of Mantel tests of the overall
relationships between intersample similari-
ties and distances between sample loca-
tions in different depth horizons (Table 3)
clearly show that there was a significant
relationship between distance and simi-
larity among samples taken from the 5 to
10 cm horizon, with samples collected
closer together tending to be more similar.
The relationship was weaker (and failed to
achieve significance at the p = 0.025 level)
in the 10 to 15 cm horizon and was practi-
cally non-existent ($R < 0.1$) in the surface
(0 to 5 cm) layers.

There was a significant positive short-
order spatial autocorrelation in surface (0
to 5 cm) samples, meaning that samples
collected 10 cm apart were significantly
more alike than samples collected further
apart (Table 3). Spatial relationships were
stronger in the 5 to 10 cm horizon. As well
as significant positive autocorrelation
among samples 10 cm apart, there was also
significant negative autocorrelation among
samples 10 m apart (samples were signifi-
cantly less similar than samples collected
closer together). Tests for spatial relation-
ships among samples from the 10 to 15 cm
horizon failed to achieve significance at the
0.025 > p > 0.975 level. Looking at broad
patterns, rather than only 'significant'
results, it can be seen that there is a switch
from a positive relationship between
similarity and distance over short distances
in the surface layers to a negative relation-
ship when samples are approximately 1 m
apart, and there is almost no relationship
($R < 0.1$) among samples taken 10 m from
each other. At intermediate depths (5 to
10 cm) a strong positive relationship be-
tween similarity and distance switches to a
negative relationship when samples are
somewhere between 1 and 10 m apart,
while deeper still there is almost no rela-
tionship ($R < 0.1$) among samples taken
10 cm from each other, but a weak positive
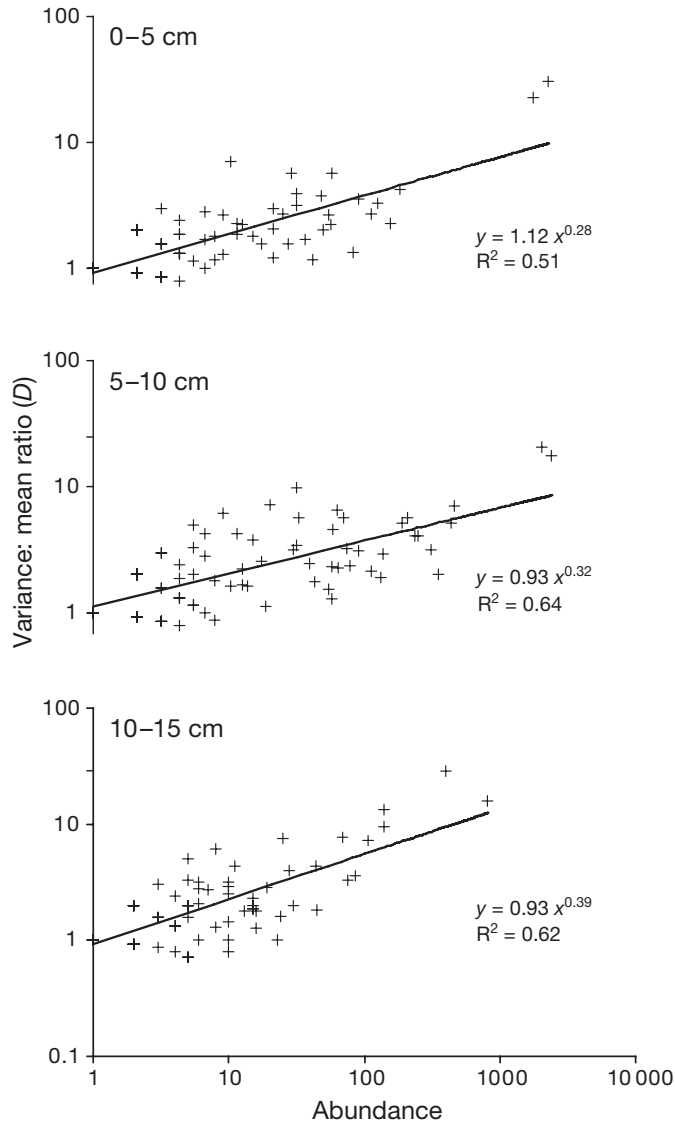relationship between similarity and dis-
tance for samples collected 1 m apart

Fig. 5. Relationship between variance:mean ratio (D) and abundance for nematode species in each depth horizon

switching to a negative one for samples collected 10 m from each other.

Most *Echinocardium cordatum* were located 10 to 15 cm below the sediment surface, at a density between 1.36 m^{-2} (the density of respiratory-shaft openings) and an estimated maximum of 10 m^{-2} observed in carefully dug pits. The respiratory shafts were significantly underdispersed (variance:mean ratio $D = 0.71$, p = 0.988), implying that the animals were spacing themselves maximally within the sediment.

DISCUSSION

Warwick et al. (2006) found 207 species of nematodes in a collection of samples totalling nearly 112 l in volume, but sieved on a range of mesh sizes, collected from a nearby site on St Martin's flats. The 152 species of nematodes reported here were extracted from only 2.8 l of sand. Warwick et al. (2006) reported that spatial separation of samples had little or no effect on clustering patterns of the total fauna, and that among species in the meiofaunal size range <30% showed significant (non-Poisson) spatial clustering. They collected cores to 20 cm, and concluded that the vertical component of species' spatial distribution could be driving observed differences in clustering among smaller-sized organisms. In this study the proportions of nematode species with significantly overdispersed distributions in 5 cm sections of core ranged from 35 to 50%. Interestingly, the strongest overdispersion and highest abundances occurred in the surface layers (0 to 5 cm), but the strongest overall spatial pattern, based on analyses of untransformed abundances of all species, was found in the intermediate (5 to 10 cm) horizon, where the proportion of individual species with overdispersed distributions was lowest (35%). This reinforces the statement made in the introduction that whether spatial pattern is observed or not depends critically on how it is defined.

Although a few studies have examined synchronous vertical and horizontal spatial patterns of nematodes (e.g. Platt 1977, Steyaert et al. 2003), the horizontal component of these studies has been confounded by the choice of sites known to differ in terms of their position on the shore, granulometry and sediment environmental conditions. We believe that ours is the first study to examine horizontal and vertical distributions synchronously within a homogeneous intertidal sediment. Fleeger & Decho (1987) outline some of the difficulties involved in

Table 3. Results of non-parametric Mantel tests of 'no relationship' between Bray-Curtis similarity matrices derived from untransformed nematode abundances in different depth horizons and matrices representing distances between sampling locations ('all distances'), and model matrices to test whether similarities between samples a certain distance apart are greater (or less) than samples separated by other distances (ρ: Spearman's rank correlation coefficient between corresponding elements of the 2 matrices; p: significance level estimated from 5000 permutations; bold print indicates p < 0.025 or > 0.0975)

	0–5 cm		5–10 cm		10–15 cm	
	ρ	p	ρ	p	ρ	p
All distances	0.079	0.128	**0.287**	**0.005**	0.189	0.041
0.1 m vs. remainder	**0.282**	**0.003**	**0.259**	**0.009**	0.076	0.205
1.0 m vs. remainder	−0.160	0.968	0.120	0.081	0.167	0.057
10 m vs. remainder	−0.033	0.699	**−0.267**	**0.990**	−0.195	0.969

separating out various factors potentially affecting meiofaunal spatial distributions within sands, especially the fact that many of them are inter-related. Spatial patterns may appear as a result of aggregation or dispersion of organisms, or as a result of *in situ* reproduction, in the absence of environmental heterogeneity. Such patterns may be broken down by physical and biological processes. Conversely, responses by organisms to variation in such processes may create spatial patterns, and this has been the focus of most explanations of observed spatial patterns of meiofauna. Spatial patterns do not always reflect processes that are occurring concurrently with sample collection (Hogue & Miller 1981), and caution must be exercised when attempts are made to explain spatial distributions of animals from physical or biological conditions measured at a single point in time. We believe, however, that our findings that horizontal spatial patterns in the surface 5 cm of sediment are significant over short distances, are strongest in the intermediate 5 to 10 cm, and are weak and generally insignificant at 10 to 15 cm give clues to the processes that may be important in their generation and maintenance.

Processes considered to be capable of generating small-scale spatial aggregation among meiofauna include attraction to patchily distributed food (e.g. Hogue & Miller 1981), association with biogenic sediment structures (Ólafsson 2003), small-scale variation in sediment composition (Nichols 1980), biotic interactions with macrofauna (Ólafsson 2003) and with other meiofauna (Moens et al. 2000), and differences in species' ecophysiology (Wieser & Scheimer 1977). Platt (1977) concluded that horizontal distributions largely result from responses of species to specific combinations of the degree of environmental stability, the nature of the available food and the particle size composition of the sediment. Hogue & Miller (1981) found increased abundances of nematodes beneath the crests of sand ripples in the surface layers of an intertidal sand, and proposed a mechanism whereby the observed aggregation of nematodes was a consequence of their attraction to a food resource that was itself spatially structured by physical processes. In a study of spatial distributions of nematodes in relation to wave-generated sediment disturbance in sands at 18 to 32 m on an exposed coast, Hogue (1982) concluded that aggregation of nematodes was reduced by sediment mixing by storm activity in the winter, whereas a reduction in physical disruption allowed biological factors (food and reproduction) to lead to aggregation in summer. Recent work (e.g. de Beer et al. 2005, Røy et al. 2005) has highlighted the importance of the interplay between water-column hydrodynamics, interstitial water flows and biogeochemical processes in permeable sediments. Variations in surface topography,

be they of biogenic (mounds, pits) or hydrodynamic (ripples, sandwaves) origin, induce spatial heterogeneity at and beneath the sediment surface through the induction of alternating pressure gradients, which drive water into, and draw water out of, interstitial spaces in the sediment. This interfacial advection carries particles, oxygen and nutrients into the sediment, where they encounter microbial communities on the surfaces of sediment particles. Such physico-biological processes must be important determinants of meiofaunal distributions. Processes resulting from interfacial advection almost certainly played a role in producing the patterns observed by Hogue & Miller (1981) and Hogue (1982), and we believe that they probably play a major role in influencing both horizontal and vertical differences in nematode community structure among the sediment horizons observed in this study. Such small-scale effects of hydrodynamics on spatial structure are likely to be dynamic and short-lived, changing with every tidal cycle, or possibly in some cases with the passage of individual waves.

In the upper 1 cm of a sandy estuarine tidal flat Blome et al. (1999) found a difference in aggregation patterns between 'diatom feeders' (a diverse assemblage containing epistrate and non-selective deposit feeders, sensu Wieser 1953) and relatively long and slender nematodes with thin smooth cuticles, which may be capable of transepidermal uptake of dissolved organic matter (Jensen 1987), termed DOM-users. A similar division in morphotypes has been interpreted as evidence of adaptation to physical stress (Ward 1975, Hogue 1982), as shallow, wave-disturbed sediments tended to be inhabited by short (<1100 µm) species with annulations, spines, or other ornamentation. In the present study, some of the species that decreased in abundance with increasing depth are small and possess long setae or spines (*Perepsilonema crassum*, *Echinotheristus teutonicus*, *Theristus denticulatus*), while others have heavily annulated cuticles (*Neochromadora poecilosomoides*, *Pseudochromadora pontica*, *Desmodora schulzi*). Species with more importance in the deeper sediments (*Desmodora sanguinea* and *Spirinia gerlachi*) are relatively long with very sluggish movement and presumably low metabolic requirements, and are more typical of the DOM-user group. Naturally there is a relationship between hydrodynamic forces and sediment structure, so the extent to which the relationship between sediment structure and the community structure of the nematodes within those sediments is determined by the same forces, or reflects physiological or ecological responses to environmental conditions within the sediments, is still an open question.

Echinocardium cordatum were underdispersed, perhaps to reduce competition and maximise the use of

spatially distributed resources. Densities (1.36 to 10 m^{-2}) and depth distribution (10 to 15 cm) are entirely consistent with observations of intertidal UK populations made previously (Buchanan 1966). Animals move through the sediment at 6 to 8 cm h^{-1} (Buchanan 1966) and are typically 3 cm in length (Buchanan 1966), with a corresponding cross-sectional area of 6 to 7 cm^2 (Lohrer et al. 2005), although the functional cross-sectional area is probably greater, owing to the action of tube-feet and spines (Nichols 1959, Buchanan 1966). Thus, at a density of 10 m^2, a population can rework >10 l d^{-1} of sand, or all the sand in a 5 cm deep horizon at least once every 5 d. Lohrer et al. (2005) calculate that a subtidal New Zealand *Echinocardium* population is also capable of reworking a 5 cm thick layer of sediment every 3 to 5 d, although subtidal populations tend to be denser, but slower moving (Buchanan 1966). The absence of strong spatial structure in the nematode assemblages in this sediment horizon could, therefore, be a result of environmental homogenisation by this population of bioturbators. The majority of studies examining relationships between bioturbators and meiofaunal community structure (see Ólafsson 2003) have focused on the role of bioturbators in increasing environmental heterogeneity, leading to statements that bioturbators are 'critical' to the maintenance of infaunal diversity (Widdicombe & Austen 1998). While there is no doubt that some larger organisms modify the environment to produce microhabitats that support particular populations of meiofaunal organisms, our results remind us that larger organisms may also act to break down environmental heterogeneity and therefore, presumably, to reduce infaunal diversity.

Echinocardium cordatum is considered to be a non-selective deposit feeder. It is entirely possible that these animals contribute to nematode spatial patterns by digestion of nematodes in the sediment and by competition for food which could, in part, explain the decrease in nematode abundance with depth in the sediment. However, the volume of sediment reworked by a related echinoid, *Brissopsis lyrifera*, while burrowing exceeded the volume ingested by 60 to 150 times (Hollertz & Duchêne 2001), and we believe, therefore, that the primary interaction between the urchins and the nematodes results from the reworking activities of the former.

In conclusion, different processes operate to generate or remove spatial patchiness in each depth horizon. In the surface layers, physical disturbance homogenises the nematode assemblage at larger spatial scales, while short-term, smaller-scale features such as ripples and buried algal debris introduce small-scale patchiness, at least in part as a result of advective processes. A dense population of *Echinocardium corda-*

tum inhabits the sand, concentrated between 10 and 15 cm deep, and the activities of these bioturbators are likely to homogenise the sediment at this depth, removing patchiness. The strongest spatial pattern was found at intermediate depths (5 to 10 cm). Between the dynamic surface layer, which is likely to be disturbed and to some extent redistributed each tidal cycle, and a deeper layer, which is likely to be disturbed daily by burrowing urchins, is an intermediate region where environmental heterogeneity, when created, may last long enough for spatial patterns to become established. Our study highlights the potential importance of the interaction between sediment permeability, and therefore interfacial advection, and bioturbation in controlling infaunal diversity and spatial patterns.

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