



**HAL**  
open science

# MACROFAUNAL MEDIATION OF EFFECTS OF MEGAFUNAL BIOTURBATION ON NEMATODE COMMUNITY STRUCTURE

M C Austen, D M Parry, S Widdicombe, P J Somerfield, M A Kendall

► **To cite this version:**

M C Austen, D M Parry, S Widdicombe, P J Somerfield, M A Kendall. MACROFAUNAL MEDIATION OF EFFECTS OF MEGAFUNAL BIOTURBATION ON NEMATODE COMMUNITY STRUCTURE. *Vie et Milieu / Life & Environment*, 2003, pp.201-209. hal-03205271

**HAL Id: hal-03205271**

<https://hal.sorbonne-universite.fr/hal-03205271v1>

Submitted on 22 Apr 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# MACROFAUNAL MEDIATION OF EFFECTS OF MEGAFUNAL BIOTURBATION ON NEMATODE COMMUNITY STRUCTURE

M. C. AUSTEN<sup>\*1</sup>, D. M. PARRY<sup>2</sup>, S. WIDDICOMBE<sup>1</sup>, P. J. SOMERFIELD<sup>1</sup>,  
M. A. KENDALL<sup>1</sup>

<sup>1</sup> Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, PL1 3DH, UK

<sup>2</sup> School of Earth, Ocean and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK

\* Corresponding author: MCVA@mail.pml.ac.uk

SURFACE FEATURES  
BENTHIC DIVERSITY  
BIOTURBATION  
MEGAFUNAL  
MEIOFAUNA  
MACROFAUNA  
NEMATODES

**ABSTRACT.** – In a detailed field survey, spatial structure was observed in the distribution of subtidal, meiofaunal nematode communities. There were no correlations between nematode community structure and distribution of megafaunal surface features. Certain combinations of 9-11 megafaunal surface features were weakly correlated with nematode communities but only the presence of thalassinid burrow openings within a 15 cm radius of a meiofauna sample and distance to the nearest megafaunal surface feature consistently featured in these combinations (and then only for correlations with transformed nematode data). This is contrary to previous experimental and field observations that suggest such relationships should exist. Nematode and macrofaunal community structure were correlated. Since relationships also exist between macrofauna and megafauna community structure this suggests that links between meiofauna and megafauna are mediated by macrofauna.

CARACTÉRISTIQUES DE SURFACE  
DIVERSITÉ BENTHIQUE  
BIOTURBATION  
MÉGAFUNAL  
MÉIOFAUNE  
MACROFAUNE  
NÉMATODES

**RÉSUMÉ.** – Lors d'une étude détaillée, la structure spatiale de la distribution des communautés de Nématodes de la méiofaune subtidale a été observée. Aucune corrélation entre la structure de la communauté des Nématodes et la distribution des dispositifs de surface de la mégafaune n'a été décelée. Certaines combinaisons de 9 à 11 dispositifs externes de la mégafaune sont faiblement corrélées avec les communautés de Nématodes ; mais c'est uniquement le cas des ouvertures des terriers de Thalassinidés dans un rayon de 15 cm d'un échantillon de méiofaune avec la distance à la plus proche structure de surface de la mégafaune qui apparaît toujours parmi ces combinaisons (et seulement pour les corrélations obtenues à partir des données transformées sur les Nématodes). Ces résultats sont en contradiction avec les observations antérieures, expérimentales ou de terrain, qui suggéraient que de telles relations existaient. La structure des communautés de Nématodes et celle de la mégafaune sont corrélées. L'existence de relations entre la structure des communautés de Nématodes et de la mégafaune suggère que les liens entre la méiofaune et la mégafaune sont assurés par la macrofaune.

## INTRODUCTION

Correlative evidence from field surveys suggests macrofauna-meiofauna interactions are important in structuring meiofaunal communities (e.g. Bell *et al.* 1978, Thistle 1979, Reise 1981, 1987, Reidenauer 1989, Dittman 1990, Warwick *et al.* 1990, 1997). Additionally, experimental evidence indicates that at the species level, meiofauna communities in soft sediments are structured by different types and densities of large macrofauna (e.g. Bell 1980, 1985, Warwick *et al.* 1986, Olafsson & Elmgren 1991, Aarnio *et al.* 1998, Austen & Widdicombe 1998, Austen *et al.* 1998, Schratzberger & Warwick 1999, Botto & Iribane 1999, Tita *et al.* 2000). Megafauna are defined op-

erationally as those organisms large enough to be observed by a camera (Grassle *et al.* 1975), while meio- and macrofauna are defined as metazoan organisms retained on a 63 µm or 0.5 mm mesh sieve respectively. In reality, the size threshold for megafaunal species is variable because the absolute dimensions of an organism on an image depend upon camera orientation and image resolution. For practical purposes, in the present study it encompasses large epibenthic macrofauna individuals and biotic sediment structures associated with burrowing megafauna that are larger than 10 mm and can be viewed through the video camera deployed on a remotely operated vehicle (ROV) described below.

Structuring of meiofaunal communities by macrofauna and megafauna occurs through either

predation or bioturbation activities which alter sediment structure or water and oxygen flow through the sediment and at the sediment-water interface. Bioturbation may in turn affect meiofauna either directly, through alteration of the physical and chemical properties of the sedimentary habitat including direct burial of associated organisms, or indirectly, by altering microbial dynamics and hence benthic trophic structure.

Field evidence of a direct link between the activity of large macrofauna or megafauna and the structure of meiofauna communities is still rare. This is partially due to difficulties of designing and carrying out field experiments that can prove cause and effect. For example, Austen & Thrush (2001) were unable to demonstrate effects of the horse mussel *Atrina zeelandica* on nematode community structure despite strong correlative evidence from Warwick *et al.* (1997) that such effects would be likely. Possible causes for that lack of effect may have been due to problems of spatial and temporal scale of sampling.

Most experiments and surveys have tended to be carried out in intertidal areas where there is strong visual evidence of macrofaunal bioturbation activity, usually by a single dominant species (see references above). Similarly field experiments have been carried out with single macrofaunal species being manipulated. Yet, in subtidal habitats there may be several bioturbating organisms present in close proximity within the sediment (Atkinson *et al.* 1998, Parry *et al.* 2002, 2003).

Parry *et al.* (2002, 2003) indicated that megafauna can be visually enumerated by analysing seabed surface images recorded from a video camera deployed on a remotely operated vehicle (ROV). Such data describes the biologically-mediated landscape rather than megafaunal species abundance because different burrows have a variable number of surface openings. Nevertheless, the morphology of surface features may be used to infer the identity of species responsible for burrow construction (e.g. Nickell & Atkinson 1995). In an exploratory study a 3m × 3m grid was videoed and benthos were sampled within the grid to determine whether megafaunal assemblages are surrogates for benthic community structure Widdicombe *et al.* (2003, this issue) and therefore whether such video sampling can be used to develop rapid assessment techniques for macrofaunal community monitoring. The survey yielded promising results indicating a relationship between diversity of macrofauna and of surface megafauna features and between multivariate megafaunal community structure (indicated by megafaunal surface features) and macrofaunal community structure. In this study we test the hypotheses that there is a direct relationship between the field distribution of megafauna and meiofaunal nematode assemblage structure in subtidal communities. We then test the hypothesis

that there is a relationship between field distributions of subtidal macrofauna and meiofauna.

## METHODS

*Study area, sampling and faunal analysis:* Surveys and sampling were carried out on 30-31<sup>st</sup> May 2000. Study area, megafaunal surface features and core sampling are described in detail by Widdicombe *et al.* (2003, this issue) and are briefly summarised here. The study was carried out in Jennycliff Bay, a sheltered, muddy sand area at 10 m depth located in Plymouth Sound, SW England (50°21.0'N 04°07.8'W). High megafaunal bioturbation occurs patchily across this site (Parry 2002).

A 3m × 3m steel frame supported on 4 steel legs with an intersecting 0.5 m<sup>2</sup> grid constructed using polypropylene cord at 0.5 m intervals was gently placed on the seabed by SCUBA divers with the legs protruding 40 cm above the sea-bed.

A video camera deployed from an ROV was used to film megafaunal individuals and biogenic surface features greater than 1 cm in diameter within each of the 50×50 cm cells. Recorded video images were analysed and the following megafaunal surface feature categories were identified and enumerated: thalassinidean burrow openings, thalassinidean mounds, bivalves (single surface openings with visible bivalve siphon tips), *Goneplax rhomboides* burrows, circular openings about 1 cm in diameter, 3-siphoned openings and 2 openings in a common pit. The size and position of each megafaunal surface feature or individual organism was determined using *Benthic Imager* software (University of Plymouth, UK; Pilgrim *et al.* 2000).

After the grid was videoed SCUBA divers removed 61 cores (10 cm diameter) one sample at the centre of each cell and a sample at each intersection of the grid (Fig. 1). On board the dive vessel a single meiofaunal core sample was taken from each core using a 50 ml sawn off plastic syringe (internal diameter 2.6 cm) pushed into the sediment to a depth of 5 cm. Sampling was restricted to the first 5 cm of sediment because in most coastal habitats with a high proportion of fine sediments > 90% of the meiofauna are found in the surface 1-2 cm (Coull 1992). The remainder of the core was kept for macrofauna.

Within 4 hours of sample collection, macrofauna and meiofauna samples were fixed and then kept in 10% formalin for a minimum of 4 days. Macrofauna samples were washed over a 0.5 mm mesh, all animals were extracted and identified under a binocular microscope to the lowest practical taxonomic level (Widdicombe *et al.* 2003, this issue). Meiofauna were extracted from the sediment using flotation in Ludox TM colloidal silica (McIntyre & Warwick 1984) with a 63 µm sieve. Samples were placed in 10% glycerol, evaporated to anhydrous glycerol, and then mounted on slides for microscopic identification and enumeration of all nematodes to lowest practical taxonomic level. For those genera where it is difficult to distinguish species amongst juvenile or female specimens, or where only female or juvenile specimens were observed, nematodes were identified only to genus level.

**Data analysis:** The distance between each meiofauna/macrofauna core and each megafaunal surface-feature was calculated using MATLAB software (version 5.03, The MathWorks Inc.). Around each core biogenic features were quantified with progressively larger virtual quadrats of 5, 10, 15, 20, 25, 30, 35, 40, 45 and 50 cm radius. For each core, distance to the nearest feature in each megafaunal category was determined and also distance to the nearest feature regardless of identity.

Multivariate data analysis followed methods described by Clarke & Warwick (2001) and Clarke (1993) using the PRIMER version 5.2 software package (Clarke & Warwick 2001). In all statistical tests a significance level of  $p < 0.05$  was used for 1-tailed tests and for 2-tailed tests  $0.975 < p < 0.025$ . Analysis was carried out using a range of data transformations to determine the effects of the treatments on different aspects of the community: a) no transformation – sensitive to changes in the abundance of the dominant species, b)  $\sqrt{x}$  transformation – detects effects on community structure generally without being unduly influenced by either dominant or rare species, c)  $\sqrt[4]{x}$  transformation – sensitive to changes in abundance of the lower abundance and rare species. Similarity matrices for faunal data were constructed using the Bray Curtis similarity index.

**Spatial autocorrelation of nematode samples:** The relationship between nematode community structure and the spatial variation in assemblage composition encompassed by the sampling design was examined using RELATE analysis to give an indication if there was any spatial autocorrelation (Somerfield & Gage 2000). Spatial distances between every pair of samples were computed and used to create a spatial distance matrix. RELATE computes a rank Spearman correlation coefficient between the faunal similarity matrix and the spatial distance matrix and the significance of this correlation is then tested by a randomisation/permutation test. To determine if samples a certain distance apart were more likely to be spatially autocorrelated and to determine what distance this might be, the RELATE analysis was repeated but this time constructing a series of 'model' matrices representing a range of distance classes. In each 'model' matrix pairs of samples that were within specified distance classes are coded as 1 and the rest of the entries are coded as 0 (Somerfield & Gage 2000).

**Relating megafaunal surface feature diversity and macrofaunal diversity to nematode diversity:** Total nematode diversity (number of species/taxa) was plotted against diversity of megafaunal surface features (number of types of features) within the surrounding quadrat with a radius of 25 cm and against macrofaunal diversity in the same core sample. To compare diversity at a larger spatial scale, total nematode (number of species/taxa) and macrofaunal diversity within a 50 cm radius quadrat was determined from 5 pooled cores located within each of nine, non overlapping 50 cm radius quadrats (Fig. 1). Nematode diversity was then plotted against megafaunal surface feature diversity and macrofaunal diversity in these nine 50 cm radius quadrats.

**Relating nematode diversity and abundance to distance of nearest megafaunal surface feature:** For each nematode core sample and for each type of megafaunal surface feature, nematode diversity (number of species) and

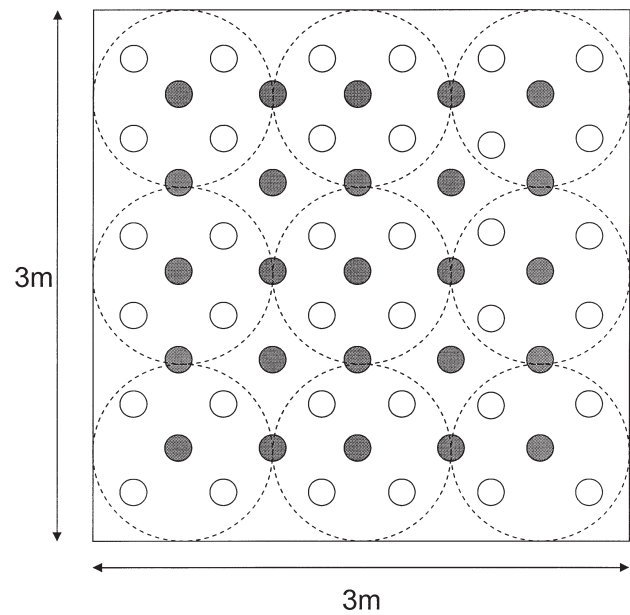


Fig. 1. – Layout of grid indicating position of 10 cm benthic cores for sampling macrofauna and meiofauna (small circles), position of large 50 cm radius virtual quadrats (large dashed circles) for megafaunal surface feature correlations with nematode data for which either 5 benthic cores wholly inside each quadrat were used to provide pooled or mean nematode data values or the central core alone in different comparative analyses. Shaded and unshaded benthic cores indicate two separate sets of cores used in RELATE analysis to correlate nematode community structure and megafaunal surface features data within 20 and 25 cm radius virtual quadrats.

abundance were plotted against distance to nearest feature. Similarly, distance to nearest feature regardless of the identity of that feature was plotted against nematode abundance and diversity. Where the distance to the nearest feature was greater than the distance to the edge of the plot the nematode sample was excluded from the plot.

**Multivariate relationships between megafaunal surface features data and nematode community structure:** For each set of virtual quadrats of the same size (15, 20, 25, 30, 35, 40, 45, 50 cm radius), pair-wise Bray-Curtis similarities were calculated between quadrats of megafaunal surface-features (untransformed and fourth root transformed data) from which similarity matrices were constructed. RELATE analysis was used to compare each of these matrices with the equivalent matrices calculated from the nematode abundance data for corresponding cores or groups of cores. For the smallest virtual quadrat size (15 cm radius) all nematode samples were used in the analysis. However, larger quadrats overlapped more than one nematode sample. Consequently, for comparisons involving quadrats greater than 15 cm radius smaller subsets of nematode samples were used to ensure sample independence. For quadrats of 20 cm and 25 cm radius 2 separate subsets of nematode cores were used (Fig. 1), for quadrats with a radius greater than 25 cm a subset of only 9 core samples was used



in the RELATE analysis (these are the nine cores at the centre of each of the 50 cm radius virtual quadrats shown in Fig. 1). In an additional analysis for the largest quadrat size (50 cm radius) surface feature similarities between each of the nine, non-overlapping, 1 m diameter surface-feature samples, were compared with nematode similarity matrices constructed using mean Bray-Curtis similarity values calculated from pair-wise analyses between the pooled meiofauna cores contained within the area of each of the 50 cm radius surface-feature quadrats.

*Correlation of different megafaunal surface features with nematode community structure:* Distance to the nearest feature, identity of the nearest feature, position of core (x or y coordinate on the grid) and abundances of each megafaunal surface feature within virtual quadrats at 5 cm radius intervals from each core up to a maximum of 50 cm radius were considered as possible explanatory variables for nematode community structure. A BVSTEP analysis was used to test whether any variable or any combination of variables, was correlated with any multivariate aspect of nematode community structure (Clarke & Warwick 2001). The nematode data was subjected to a range of transformations to construct Bray-Curtis similarity matrices which were correlated, using a Spearman rank correlation, with a distance matrix constructed from the megafaunal surface features 'variables' data using normalised Euclidean distance. Perimeter cores which were less than 50 cm from the edge of the grid were excluded from the analysis as not all of the corresponding megafaunal surface features up to 50 cm radius from these samples would have been quantified if they were outside of the grid. BVSTEP was conducted with 40 random restarts including a random 50% of the variables to determine which minimum number of variables gave the best correlation with the nematode data (Clarke & Warwick 2001).

*Multivariate relationships between macrofaunal community structure and nematode community structure:* Pair-wise Bray-Curtis similarities (untransformed and fourth

root transformed data) between macrofaunal samples were calculated and similarity matrices constructed. RELATE was used to compare these matrices with the equivalent matrices calculated from the nematode abundance data. To consider the effects of macrofauna body size, all macrofauna species were allocated to one of three size classes based on a combination of geometric weight classes (Warwick 1984) and using the allocation of species in Jennycliff to each size class determined by Kendall & Widdicombe (1999). Species of geometric weight classes 10-14 were classified as small, species between 15 and 19 were classed as medium and the remaining larger animals classed as large. Again, for each size class pair-wise Bray-Curtis similarities (untransformed and fourth root transformed data) between macrofaunal samples were calculated and similarity matrices constructed and using RELATE these were compared with the equivalent matrices calculated from the nematode abundance data.

## RESULTS

A total of 113 nematode taxa (species or genera) were identified from the 3 × 3 m grid. Number of taxa per sample ranged between 20 and 54 (mean = 35, standard deviation = 8) and abundance ranged from 59 to 2495 nematodes per sample (mean = 507, standard deviation = 379). A total of 312 megafaunal surface features were identified within the grid ranging from 3 to 16 features per 0.25 m<sup>2</sup> grid cell (mean = 8.7 standard deviation = 3.81).

### *Spatial autocorrelation of nematode samples*

Results of RELATE analysis for spatial autocorrelation are shown in table I. There was a very weak but significant spatial autocorrelation

Table I. – Results of RELATE analysis for spatial autocorrelation of nematode data. Bold values indicate significant positive correlation at  $p < 5\%$  (one-tailed test) or significant negative or positive correlation correlation at  $97.5\% < p < 2.5\%$ .

		untransformed		sq root transformed		rt-rt transformed	
		rho	p(%)	rho	p(%)	rho	p(%)
whole grid		<b>0.075</b>	<b>3.62</b>	<b>0.076</b>	<b>3.9</b>	0.026	28.45
distance class	pairs in class						
0-50	200	<b>0.073</b>	<b>0.18</b>	<b>0.078</b>	<b>0.04</b>	<b>0.049</b>	<b>0.98</b>
50-100	336	0.019	21.26	0.039	6.36	0.034	9.1
100-150	474	-0.006	60.61	-0.04	92.84	<b>-0.064</b>	<b>98.86</b>
150-200	402	-0.006	59.87	-0.04	92.88	<b>-0.064</b>	<b>98.94</b>
200-250	302	-0.014	66.05	-0.007	57.43	0.013	34.85
250-300	102	-0.037	87.58	-0.036	85.74	0.005	44.87
300-360	14	-0.026	82.6	0.003	47.77	0.043	7.58
20-30	25	0.031	6.24	0.022	13.28	0.012	24.04
30-40	50	<b>0.036</b>	<b>3.38</b>	<b>0.047</b>	<b>0.84</b>	<b>0.044</b>	<b>0.96</b>
40-49	25	0.019	17.16	0.018	18.2	0.001	46.57
50-60	100	<b>0.048</b>	<b>0.84</b>	<b>0.054</b>	<b>0.36</b>	0.029	5.74
60-71	82	0.027	11.68	0.041	2.62	0.033	4.9
71-75	40	-0.001	51.97	0.01	31.57	0.02	16.76
75-80	40	-0.007	62.99	0.01	30.83	0.015	21.82

across the whole grid for untransformed and square root transformed nematode data. This autocorrelation was again weak but significant at a spatial level of 0-50 cm regardless of data transformation. RELATE analysis, to determine if there was an optimum distance apart between cores for maximum autocorrelation, indicated that cores separated by 30-40 cm and 50-60 cm were significantly but weakly autocorrelated.

#### ***Relating megafaunal surface feature diversity and macrofaunal diversity to nematode diversity***

There was no visible relationship between either megafaunal surface feature diversity within a 0.25 m radius of the meiofaunal cores and nematode diversity (Fig. 2a), macrofaunal and meiofaunal diversity from the same cores (Fig. 2b), diversity of megafaunal surface features and pooled nematode diversity in 50 cm radius quadrats (Fig. 2c), or macrofaunal diversity and nematode diversity at the same 50 cm radius quadrat spatial scale (Fig. 2d).

#### ***Relating nematode diversity and abundance to distance of nearest megafaunal surface feature***

There were clearly no visible relationships between either distance of nearest megafaunal surface feature or distance of nearest megafaunal feature in each category and either nematode diversity or abundance.

#### ***Multivariate relationships between megafaunal surface features data and nematode community structure***

In the RELATE analysis there were no significant relationships between transformed or untransformed megafaunal surface feature data and nematode data subjected to a range of transformations.

#### ***Correlation of different megafaunal surface features with nematode community structure***

Correlation between nematode community structure and the full range of megafaunal surface features at different spatial scales was weak (Table IIa) and best correlations were with a combination of 9-11 surface feature variables. Within PRIMER v5.2 it is not possible to test for significance of these correlations. The strongest correlations were evident when the nematode data was heavily transformed (best Rho value = 0.406) and this was with a combination of 11 surface feature variables (Table IIb). For each run of BVSTEP only 1 or 3 surface feature variables were consistently among the ten best correlations and then only with nematode data that had been transformed. For square root and fourth root trans-

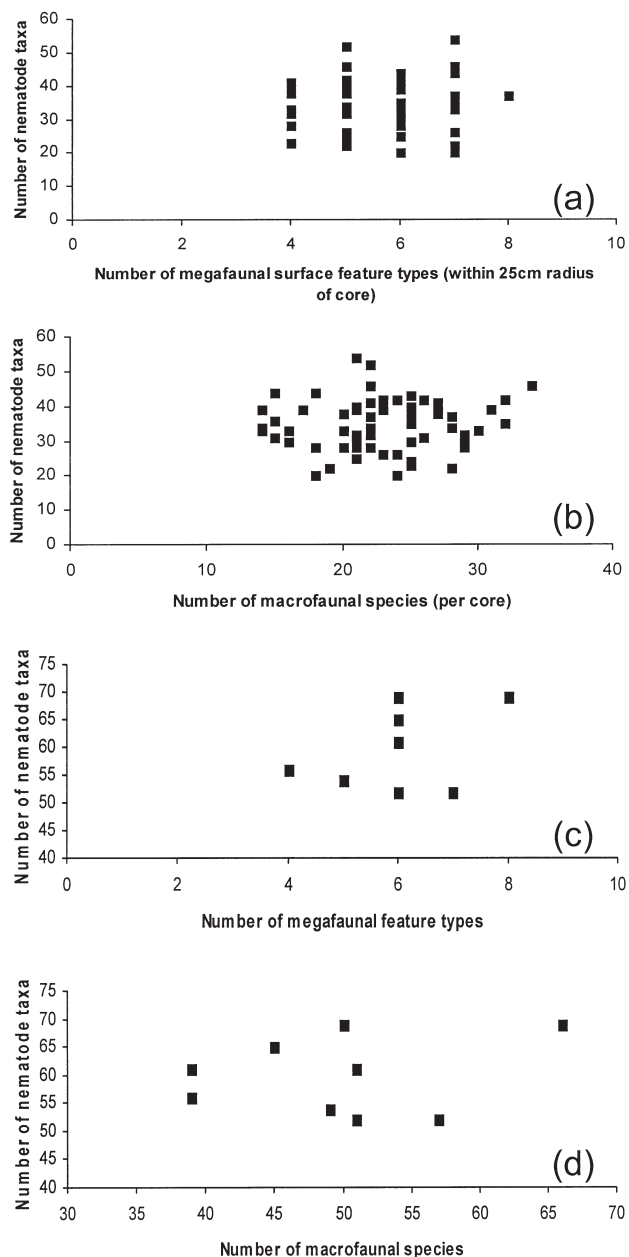


Fig. 2. – Comparison of nematode diversity (number of species/taxa) with diversity of megafaunal surface features and macrofauna (a) in 25 cm radius quadrats surrounding each nematode core sample (b) in the same core sample (c) in nine 50 cm radius quadrats where the nematode sample consists of 5 pooled core samples and (d) in 5 pooled samples within nine 50 cm radius quadrats.

formed nematode data these were thalassinid mounds within 15 cm radius, and also for fourth root transformed nematode data, 'y coordinate' (distance from one edge of the grid) and distance to the nearest surface feature.

Table II. – Results of BVSTEP analysis a, ten best correlations (rho values) under three different data transformations and the number of variables (No. vars) which give each correlation b, the combination of megafaunal surface features that gives the ten best correlations with fourth root transformed nematode community data. Key: y coordinate = distance from one edge of the grid; nearest (dist) = distance to the nearest surface feature; Thal\_opening = Thalassinidean burrow opening; Thal\_mound = Thalassinidean mound; Goneplax = *Goneplax rhomboides*; Triple\_hole = 3-siphoned opening; n-denotes radial distance (cm) from nematode core within which megafaunal surface features occur.

(a)

Nematode data transformation					
none		$\sqrt{\quad}$		$\sqrt[4]{\quad}$	
No. vars	Rho	No. vars	Rho	No. vars	Rho
9	0.219	9	0.333	11	0.406
7	0.219	9	0.333	11	0.405
7	0.219	8	0.333	10	0.405
4	0.219	8	0.333	9	0.404
4	0.219	7	0.331	9	0.404
5	0.218	9	0.33	9	0.404
7	0.217	9	0.33	9	0.403
7	0.217	9	0.329	11	0.403
7	0.217	5	0.328	11	0.402
7	0.217	5	0.328	7	0.4

(b)

No. vars	Rho	combination of megafaunal surface features that give ten best correlations with fourth root transformed nematode data										
11	0.406	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Opening	15- Thal_Mound	20- Thal_Mound	25- Triple_hole	30- Triple_hole	40- Thal_Opening	50- Thal_Opening	50- Triple_hole
11	0.405	Y_coordinate	nearest (dist)	15- Thal_Opening	Thal_Mound	15- Goneplax	20- Thal_Mound	25- Triple_hole	30- Triple_hole	40- Thal_Opening	50- Thal_Opening	50- Triple_hole
10	0.405	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Mound	15- Triple_hole	20- Thal_Mound	25- Triple_hole	30- Thal_Opening	40- Thal_Opening	50- Triple_hole	50- Triple_hole
9	0.404	Y_coordinate	nearest (dist)	15- Thal_Mound	20- Goneplax	Thal_Mound	25- Triple_hole	30- Thal_Opening	40- Thal_Opening	50- Triple_hole	50- Triple_hole	50- Triple_hole
9	0.404	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Mound	15- Triple_hole	20- Thal_Mound	25- Thal_Opening	30- Thal_Opening	40- Triple_hole	50- Triple_hole	50- Triple_hole
9	0.404	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Mound	15- Thal_Mound	20- Triple_hole	25- Thal_Opening	30- Thal_Opening	40- Triple_hole	50- Triple_hole	50- Triple_hole
9	0.403	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Opening	15- Thal_Mound	20- Triple_hole	25- Thal_Mound	30- Thal_Opening	40- Triple_hole	50- Triple_hole	50- Triple_hole
11	0.403	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Opening	15- Thal_Mound	20- Thal_Mound	25- Triple_hole	30- Triple_hole	40- Thal_Opening	45- Thal_Opening	50- Triple_hole
11	0.402	Y_coordinate	nearest (dist)	15- Goneplax	Thal_Opening	15- Thal_Mound	20- Thal_Mound	25- Triple_hole	30- Triple_hole	40- Thal_Opening	45- Thal_Opening	50- Triple_hole
7	0.4	Y_coordinate	nearest (dist)	Thal_Mound	20- Goneplax	15- Triple_hole	20- Triple_hole	25- Thal_Opening	30- Thal_Opening	40- Triple_hole	50- Triple_hole	50- Triple_hole

Table III. – Results from RELATE analysis for correlation between macrofaunal and nematode community structure under a range of different data transformations. Bold values indicate significant positive correlation at  $p < 5\%$ .

	Untransformed		$\sqrt{\quad}$ transformed		$\sqrt[4]{\quad}$ transformed	
	nematodes		nematodes		nematodes	
	Rho	Significance (%)	Rho	Significance (%)	Rho	Significance (%)
Untransformed macrofauna	0.352	<b>0.02</b>	0.366	<b>0.02</b>	0.311	<b>0.02</b>
$\sqrt[4]{\quad}$ transformed macro	0.219	<b>0.02</b>	0.268	<b>0.02</b>	0.257	<b>0.02</b>
Small untransformed macrofauna	0.195	<b>0.06</b>	0.230	<b>0.02</b>	0.206	<b>0.08</b>
Small $\sqrt[4]{\quad}$ transformed macro	0.119	<b>2.52</b>	0.155	<b>0.96</b>	0.150	<b>1.62</b>
Medium untransformed macrofauna	0.363	<b>0.02</b>	0.363	<b>0.02</b>	0.302	<b>0.02</b>
Medium $\sqrt[4]{\quad}$ transformed macro	0.261	<b>0.02</b>	0.312	<b>0.02</b>	0.301	<b>0.02</b>
Large untransformed macrofauna	0.064	12.04	0.019	34.41	-0.025	64.47
Large $\sqrt[4]{\quad}$ transformed macro	0.055	14.46	0.006	43.31	-0.040	74.35

### *Multivariate relationships between macrofaunal community structure and nematode community structure*

Nematode community structure correlated significantly with total macrofauna, small macrofauna and medium macrofauna regardless of data transformation of each set of community data (Table III). Nematode community structure and large macrofaunal community structure were not significantly correlated. Twelve samples were excluded from the analysis as large macrofauna were absent from them.

## DISCUSSION

The detailed survey of a 3 m × 3 m grid revealed weak but significant, spatially-related structure within the nematode community. Patches appeared to occur at a scale of 0-50 cm and further analysis suggested that patches were occurring at intervals of 30-70 cm with possible negative correlations between patches of lower abundance nematode species at scales of 100-200 cm. Distribution of bioturbators causing patchy disturbance seemed to be the most likely cause but analysis failed to reveal any strong relationship between megafaunal surface features and nematode community structure. Weak correlations from BVSTEP suggest that certain features, such as the presence of thalassinid burrow openings within a 15 cm radius, may be of some importance, mostly for the rarer and low abundance nematode species where the correlations were strongest. Yet, the combination of low Rho values, small differences in Rho values within the ten best correlations and the large number and varying nature of best correlating variables suggests that these correlations may not be particularly significant. Initially this seems surprising given the strong experimental evidence of the effects of bioturbating macrofaunal organisms observed in mesocosm experiments on subtidal meiofauna communities similar to those

found in the study area. In mesocosm experiments with subtidal sediment (Austen *et al.* 1998, Austen & Widdicombe 1998) a range of macrofaunal species in different functional groups had significant effects on nematode diversity and nematode species distribution. As pointed out by Widdicombe *et al.* (2003, this issue) many species, including those used in the subtidal fauna experiments, do not create conspicuous surface features. Visual mapping of the sediment surface provides information on the identity and distribution of many key bioturbating species but the lack of information on “invisible” species may confound the search for a relationship between bioturbating macro and megafauna and meiofaunal groups such as nematodes. Experimental and field effects have been observed for single species treatments or where there are clear differences in distribution of a single species. In the field situation the combined effects of several different bioturbators might act to homogenise the sediment at the spatial ambit of meiofaunal organisms or at the scale at which nematode samples were taken. There were between 3 and 16 megafaunal surface features in each cell. The distribution of each feature was contagious where there were sufficient occurrences for a reasonable test and otherwise random across the grid (Table IV). This would suggest that the overall effect of bioturbation across the grid should not be homogeneity. Subtle relationships might be evident if the grid survey could be repeated over different spatial scales, combined with fine scale sampling over large spatial areas but this would require a huge amount of effort and is practically difficult in the field, particularly subtidally. In a mesocosm, using fine-scale sampling Warwick *et al.* (1986) found very localised patchy nematode communities around feeding mounds of the large polychaete *Streblosoma bairdi* (Malmgren) with nematode patches occurring at a scale of approximately 20-40 cm.

The spacing of core samples was more appropriate to look at macrofauna–megafauna interactions rather than meiofauna–megafauna interactions. The

Table IV. – Abundance and distribution of megafaunal surface features across the 3×3m grid.

Megafaunal feature	Total abundance	Mean per 0.25m <sup>2</sup> grid cell	Variance	Variance:Mean ratio	$\chi^2$	Distribution
Thalassinidean Burrow Openings	180	5	13.2	2.64	92.4	contagious
Thalassinidean Mounds	14	0.39	0.36	0.92	32.29	random
<i>Goneplax rhomboides</i> bivalves	11	0.31	0.5	1.65	57.73	contagious
Circular opening about 1cm diameter	95	2.64	5.04	1.91	66.81	contagious
3-siphoned opening	5	0.14	0.18	1.3	45.4	random
2 openings in common pit	2	0.06	0.05	0.97	34	random
	5	0.14	0.12	0.89	31	random
<b>Total Features</b>	<b>312</b>	<b>8.7</b>	<b>14.51</b>	<b>1.67</b>	<b>58.62</b>	<b>contagious</b>



significant relationship between nematode community structure and community structure of total macrofauna and also small and medium macrofauna may therefore be of key importance. In RELATE analysis macrofauna were significantly correlated with megafaunal surface features and at the scale of 50 cm radius quadrats macrofauna diversity and megafaunal surface features were significantly correlated (Widdicombe *et al.* 2003, this issue). The significant relationship between macrofauna and meiofaunal community structure might indicate that megafaunal effects on meiofauna are mediated indirectly through the effects of megafauna on macrofauna. Megafauna might have more direct impact on the spatial ambit of macrofaunal organisms. Similarly the ambit of smaller macrofauna might overlap more with that of meiofauna. The 10 cm core sample was large enough to capture a reasonable number of macrofaunal species for statistical analysis but such a sample size might homogenise the small scale patterns occurring in the meiofauna. Small scale landscapes created by megafauna bioturbation at a < 30 cm scale will be modified at much smaller scale (< 5 cm) by macrofauna. This patchiness isn't seen in a 10 cm macrofauna core but would be very evident at the scale of a meiofauna core.

The lack of significant relationship of meiofaunal and large macrofaunal community structure could be a sampling artefact as larger macrofauna are not sampled well with a 10 cm core and their abundance was low and variable between cores. The relationship between macrofauna and meiofauna community structure was also not observed for diversity but diversity is rarely as sensitive a measure of community structure as multivariate aspects of community structure (Clarke & Warwick 1994).

Temporal scale effect was not considered in this snapshot survey. However it could be considered that again macrofauna have a closer temporal ambit to meiofauna than relatively long-lived megafauna. The lifecycle of nematodes is in the order of weeks or months and reproduction is considered to be continuous (Heip *et al.* 1985) whilst megafauna lifecycles are in the order of years (e.g. Witbaard & Duineveld 1989, Rowden & Jones 1994, Strasser 1999, Kinoshita *et al.* 2003). Some megafauna such as the large bivalves are relatively immobile (Holme 1959) and it is unlikely that once thalassinids have established burrows that they will readily leave them. The megafaunal surface features are relatively persistent and their temporal variability is unlikely to be the cause of a lack of strong interaction between megafauna and meiofauna. Macrofauna turnover is slower than meiofauna but many species do have an annual turnover and are likely to be more temporally variable and this again may have been reflected in the stronger relationship between nematodes and macrofauna.

Our results suggest that observations in mesocosms in carefully controlled conditions may not transfer directly to field observations, or if they do, the effects might be lost at the scale we sample at.

This is not an argument against experimentation. To the contrary, further controlled experiments are required such as field experiments to determine if the results observed in mesocosm experiments can be extended to the natural habitat and also more complex multispecies experiments within the mesocosm. Once such experiments have been done it might be easier to determine the spatial scale of sampling required to differentiate the complex effects on nematode community structure from 'noise' in the megafaunal surface features data.

Similarly, increased effort is required to understand the mechanism by which experimentally observed bioturbating macrofauna and megafauna affect meiofauna. Is it indirectly through alteration of macrofaunal communities, in which case are the larger components of the macrofauna as important as the small and medium size fractions? Or is the effect of megafauna on meiofauna mediated indirectly through changes in physical and chemical properties of the sediment that impact on the meiofauna directly and/or on trophically linked sedimentary microbiota?

ACKNOWLEDGEMENTS. – The work contained in this paper was funded by grants from UK DEFRA (project nos. AE1137 and CDEP 84/5/295) and by the UK Natural Environment Research Council through the Plymouth Marine Laboratory research program. We would like to thank Dr A Guarino for identifying the nematodes and Dr M Burrows, Dr L Nickell, Dr D Pilgrim, R Wood, and the Crew aboard RV Squilla and RV Sepia, for providing valuable contributions to aspects of this study.

## REFERENCES

- Aarnio K, Bonsdorff E, Norkko A 1998. Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. *Mar Ecol Prog Ser* 163: 145-153.
- Atkinson RJA, Froglija C, Arneri E, Antolini B 1998. Observations on the burrows and burrowing behaviour of *Brachynotus gemmellari* and the burrows of several other species occurring on the *Squilla* grounds off Ancona, central Adriatic. *Sci Mar* 62: 91-100.
- Austen MC, Widdicombe S 1998. Experimental evidence of effects of the heart urchin *Brissopsis lyrifera* on associated subtidal meiobenthic nematode communities. *J Exp Mar Biol Ecol* 222: 219-238.
- Austen MC, Widdicombe S, Villano-Pitacco N 1998. Effects of biological disturbance on diversity and structure of meiobenthic nematode communities. *Mar Ecol Prog Ser* 174: 233-246.
- Austen MC, Thrush SF 2001. Experimental evidence suggesting slow or weak response of nematode community structure to a large suspension-feeder. *J Sea Res* 46: 69-84.
- Bell SS 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol Monogr* 50: 487-505.

- Bell SS 1985. Habitat complexity of polychaete tube caps – influence of architecture on dynamics of a meioepibenthic assemblage. *J Mar Res* 43: 647-671.
- Bell SS, Watzin MC, Coull BC 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *J Exp Mar Biol Ecol* 35: 99-107.
- Botto F, Iribane O 1999. Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. *J Exp Mar Biol Ecol* 241: 263-284.
- Clarke KR 1993. Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18: 117-143.
- Clarke KR, Warwick RM 2001. Changes in marine communities: an approach to statistical analysis and interpretation, 2<sup>nd</sup> Ed PRIMER-E, Plymouth.
- Coull BC 1992. Ecology of the marine meiofauna. In Higgins RP, Thiel H eds, Introduction to the study of meiofauna. Smithsonian Institution, Washington, USA: 18-38.
- Dittman S 1990. Mussel beds – amelioration or amelioration for intertidal fauna. *Helgol Meeresunters* 44: 335-352.
- Grassle JF, Sanders HL, Hessler RR, Rowe GT, McLellan T 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. *Deep Sea Research* 22: 457-481.
- Heip C, Vincx M, Vranken G 1985. The ecology of marine nematodes. *Oceanog Mar Biol Ann Rev* 23: 399-489.
- Holme NA 1959. The British species of *Lutraria* (Lamellibranchia), with a description of *L. angustior* Philippi. *J Mar Biol Assoc UK* 38: 557-568.
- Kendall MA, Widdicombe S 1999. Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediment. *J Exp Mar Biol Ecol* 237: 127-140.
- Kinoshita K, Nakayama S, Furota T 2003. Life cycle characteristics of the deep-burrowing mud shrimp *Upogebia major* (Thalassinidea: Upogebiidae) on a tidal flat along the northern coast of Tokyo Bay. *J Crustacean Biol* 23: 318-327.
- McIntyre AD, Warwick RM 1984. Meiofauna techniques. In Holme NA, McIntyre AD eds, Methods for the study of marine benthos. IBP handbook no 16 (2<sup>nd</sup> ed). Blackwell, Oxford, UK: 217-244.
- Nickell LA, Atkinson RJA 1995. Functional morphology and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Mar Ecol Prog Ser* 128: 181-197.
- Olafsson E, Elmgren R 1991. Effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: a laboratory approach. *Mar Ecol Prog Ser* 74: 99-107.
- Parry DM 2002. Quantification of marine megafaunal distribution patterns using a remotely operated vehicle. PhD Thesis, Univ Plymouth: 233p.
- Parry DM, Nickell LA, Kendall MA, Burrows MT, Pilgrim DA, Jones MB 2002. Comparison of abundance and spatial distribution of burrowing megafauna from diver and Remotely Operated Vehicle observations. *Mar Ecol Prog Ser* 244: 89-93.
- Parry DM, Kendall MA, Pilgrim DA, Jones MB 2003. Identification of patch structure within marine benthic landscapes using a Remotely Operated Vehicle. *J Exp Mar Biol Ecol* 285-286: 497-511.
- Pilgrim DA, Parry DM, Jones MB, Kendall MA 2000. ROV image scaling with laser spot patterns. *Underwater Technology* 24: 93-103.
- Reidenauer JA 1989. Sand-dollar *Mellita quinquesperforata* (Leske) burrow trails: sites of harpacticoid disturbance and nematode attraction. *J Exp Mar Biol Ecol* 130: 223-235.
- Reise K 1981. High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. *Helgol Meeresunters* 34: 413-425.
- Reise K 1987. Spatial niches and long term performance in meiobenthic plathelminthes of an intertidal lugworm flat. *Mar Ecol Prog Ser* 38: 1-11.
- Rowden AA, Jones MB 1994. A contribution to the biology of the burrowing mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea). *J Mar Biol Ass UK* 74: 623-635.
- Schratzberger M, Warwick RM 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. *J Exp Mar Biol Ecol* 235: 255-271.
- Somerfield PJ, Gage JD 2000. Community structure of the benthos in Scottish Sea-lochs. IV. Multivariate spatial pattern. *Mar Biol* 136: 1133-1145.
- Strasser M 1999. *Mya arenaria* – an ancient invader of the North Sea coast. *Helgol Meeresunters* 52: 309-324.
- Thistle D 1979. Deep-sea harpacticoid copepod diversity maintenance: the role of polychaetes. *Mar Biol* 52: 371-376.
- Tita G, Desrosiers G, Vincx M, Nozais C 2000. Predation and sediment disturbance effects of the intertidal polychaete *Nereis virens* (Sars) on associated meiofaunal assemblages. *J Exp Mar Biol Ecol* 243: 261-282.
- Warwick RM 1984. Species size distributions in marine benthic communities. *Oecologia* 61: 32-41.
- Warwick RM, Clarke KR, Gee JM 1990. The effect of disturbance by soldier crabs *Mictyris platycheles* H. Milne Edwards on meiobenthic community structure. *J Exp Mar Biol Ecol* 135: 19-33.
- Warwick RM, Gee JM, Berge JA, Ambrose W Jr 1986. Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. *Sarsia* 71: 11-16.
- Warwick RM, McEvoy AJ, Thrush SF 1997. The influence of *Atrina zelandica* Gray on meiobenthic nematode diversity and community structure. *J Exp Mar Biol Ecol* 214: 231-247.
- Widdicombe S, Austen M 2003. Using the surface-features created by bioturbating organisms as surrogates for macrofaunal diversity and community structure. *Vie Milieu* 53(4): 163-170.
- Widdicombe S, Kendall MA, Parry DM 2003. Using the surface-features created by bioturbating organisms as surrogates for macrofaunal diversity and community structure. *Vie Milieu* 53(4): 179-186.
- Witbaard R, Duineveld GCA 1989. Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidea) from the southern North Sea. *Sarsia* 74: 209-219.

Reçu le 22 septembre 2003; received September 22, 2003  
 Accepté le 18 novembre 2003; accepted November 18, 2003

