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The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments

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A study was conducted between 1997 and 1999 to investigate meiofauna assemblages from selected inshore and offshore locations around the UK coast. The main objective was to relate the differences in meiofauna distribution patterns to a number of measured environmental variables and to establish more clearly the sensitivity of meiofauna communities to anthropogenic disturbance. Results from univariate and multivariate data analyses show that distinct spatial differences in species distribution patterns exist and that these correlate with the natural physical characteristics and concentrations of trace metals in the sediment. Abundance and diversity of meiofauna assemblages were generally higher offshore than inshore and this difference can be attributed to both natural processes and anthropogenic impacts. The inclusion of meiofauna in applied monitoring programmes offers the potential for improving the resolution of the spatial extent of anthropogenic impacts over that achievable from macrofauna investigations alone.

INTRODUCTION

The impact of disturbance on the marine environment is typically assessed by reference to changes in the structural attributes (e.g. abundance, diversity, taxonomic composition) of biological communities. The success of any study in detecting the extent and degree of biological impact is determined by a number of factors, including sampling strategy, target faunal group, biological parameters recorded and methods employed to analyse the collected data (Moore & Bett, 1989). In the late 1980s, the National Marine Monitoring Programme (NMMP) was initiated in the UK to coordinate marine monitoring between regulatory agencies (Marine Pollution Monitoring Management Group, 1998). Prior to this, monitoring in the UK had often been local, inconsistent and sometimes of dubious quality so that a comparison between sites was difficult. The main objectives of the NMMP are to establish the spatial distribution of contaminants in different areas of UK waters, to assess the current biological status of these waters and to measure long-term natural trends in physical, biological and chemical variables at selected sites (Marine Pollution Monitoring Management Group, 1998).

Soft-bottom benthic infauna are most frequently used to monitor the biological effects of environmental change in the marine system. As a group they are largely sedentary and so must withstand the extremes of their local environment or perish. For reasons of convenience, most biological investigations have traditionally targeted the larger macroinfauna (i.e. animals living within sediments that are retained on 1000 or 500 μm meshes) that can readily be counted and identified, whereas the smaller meiofauna (between 500 and 63 μm) has been largely neglected in applied sampling programmes.

As a result of their high abundance, ubiquitous distribution, rapid generation times and fast metabolic rates the meiofauna have an important role in ecosystem function. Thus the state of meiofauna assemblages may reflect the overall health of the marine benthos (Kennedy & Jacoby, 1999). The theoretical and practical advantages and disadvantages of using meiofauna in monitoring programmes are listed in Table 1 (based on Moore & Bett, 1989; Gee et al., 1992; Giere, 1993; Warwick, 1993; Moens & Vincx, 1997; Bongers & Ferris, 1999; Kennedy & Jacoby, 1999; Schratzberger & Warwick, 1999; Schratzberger et al., 2000). By virtue of their dominance, universality and robust bodies, harpacticoid copepods and nematodes are the most promising components of the meiofauna for studies assessing effects of natural and anthropogenic disturbances on the marine environment (Sandulli & De Nicola-Giudici, 1990; Sandulli & De Nicola, 1991).

Studies of marine meiofaunal taxonomy and ecology have increased considerably in the last 20 y and progress has been made in facilitating meiofaunal work by non-specialists. Somerfield & Warwick (1996) developed a laboratory manual which describes the techniques needed to process meiofauna samples and pictorial keys for the identification of meiofauna species have been published in the Synopses of the British Fauna (Platt & Warwick, 1983, 1988; Huys et al., 1996; Warwick et al., 1998). These keys have made it much easier to identify British marine nematodes and harpacticoid copepods and have stimulated interest in meiofauna studies. Meiobenthic assemblages have increasingly been used to assess the

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Table 1. *Ecological advantages and disadvantages associated with the use of meiofauna assemblages in marine impact studies.*

Advantages	Disadvantages
Small size	
Meiofauna can be maintained in relatively small volumes of sediment. Therefore, intensive repeated sampling with minor disruption to the sampling site is possible because the sample size required is small. Nematode assemblages are ideal for experiments on a small scale. Follow-up studies in the laboratory are possible under controlled and repeatable conditions.	Taxonomic problems increase with smaller body size, whereas ecological knowledge decreases. A high-power microscope is required for species identification.
Ubiquitous distribution	
Nematodes occur in any environment that provides a source of organic carbon, under all climatic conditions and in habitats that vary from pristine to extremely polluted. They can colonize virtually every moist environment that can sustain metazoan life, and in marine sediments they usually constitute the most abundant taxon.	Community responses of meiofauna to environmental perturbations are not well documented, so there is not an extensive body of literature against which particular case histories can be evaluated.
High abundance and diversity	
A generally large number of individuals and species give a high intrinsic information value to each sample and ensure statistical validity of the data. High species diversity in nematode assemblages suggests a high degree of specificity in the choice of the environment.	High abundance and diversity together with lack of taxonomic expertise make the analysis of meiofauna community structure a time-consuming and labour-intensive task.
Short generation times	
Most species have short life-cycles (one to three months) so that changes in community structure can be observed in short-term studies.	The spatial distribution of meiofauna is extremely patchy. Population density is affected by a variety of abiotic and biotic factors and consequently, meiofauna densities may fluctuate over distances of a few centimetres.
Direct benthic development, sessile habitat	
Meiofauna assemblages seem to be inherently more stable than macrofauna communities on a seasonal and year-to-year basis. Analysis of nematode assemblage structure provides information on the effects of contaminants in the sediment as the animals are in direct contact with solvents in the interstitial water through their permeable cuticle.	Separating meiofauna from the sediment matrix requires a carefully controlled laboratory protocol. Methods of elutriation must be rigorously maintained.

effects of perturbations in the marine environment and in the last 25 y more than 200 meiofauna papers have been published in a pollution context (Coull & Chandler, 1992).

Information on meiofauna densities and harpacticoid copepod assemblage structure from 171 stations in the southern North Sea, sampled in 1986, was obtained during the ICES North Sea Benthos Survey (Heip et al., 1992). Steyaert et al. (1999) sampled nematode assemblages seasonally at three stations along the Belgian coast and related density, diversity and trophic structure to sediment composition, redox state and food sources. However, there is no published information on the assessment of environmental quality around the UK coast through the examination of meiofauna assemblage structure at inshore and offshore locations.

In order to improve understanding of how meiobenthic communities respond to both anthropogenic impacts and natural environmental factors, 12 locations around the UK, some of them long-term NMMP stations, were sampled for meiofauna and a number of environmental variables measured. The main objectives addressed in this study were: (1) to assess the spatial trends in meiofauna collected at selected inshore and offshore locations around the UK coast; (2) to relate the observed patterns of meiofauna species distributions to measured environmental variables; (3) to relate the differences in meiofauna distribution patterns to the concentration of trace metals in the sediment in order to refine quality assessments of the marine environment and to establish more clearly the sensitivity of meiofauna communities to anthropogenic disturbance.

MATERIALS AND METHODS

Sample collection

All locations were sampled between February and May except the station off the Thames in 1999 which was sampled in November (Figure 1, Table 2). With the exception of Cardigan Bay, the sampling depths of the offshore stations were significantly deeper than at inshore locations.

Sediment samples were taken with the Bowers and Connelly Multicorer, which is designed to take four undisturbed sediment samples (23.76 cm^2 surface area each) simultaneously. The corer was deployed four times at each site. From each deployment, one whole sediment

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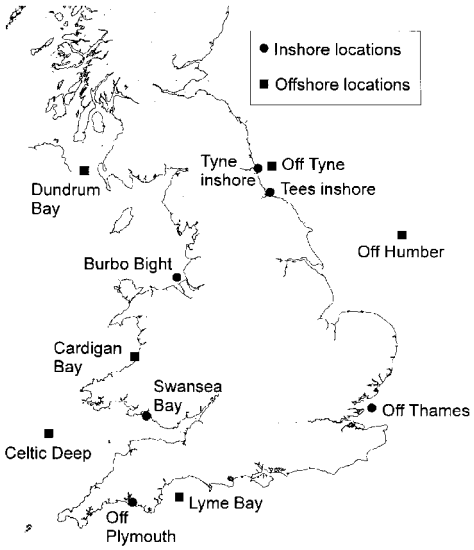

Figure 1. Inshore and offshore locations sampled between 1997 and 1999.

Table 2. *Sampling details for inshore and offshore locations.*

Location	Sampling year	Latitude	Longitude	Water depth (m)
Inshore locations				
Tyne inshore	1998	54°59.00′N	01°21.00′W	25
Tees inshore	1999	54°39.00′N	01°04.00′W	15
Off Thames	1999	51°38.16′N	01°07.63′W	<10
Off Plymouth	1999	50°20.92′N	04°07.74′W	10
Swansea Bay	1999	51°33.00′N	03°52.50′W	20
Burbo Bight	1998	53°28.29′N	03°15.58′W	13
Offshore locations				
Off Tyne	1997	55°00.50′N	01°08.00′W	72
Off Humber	1997	54°00.00′N	02°00.00′W	75
Lyme Bay	1997	50°25.80′N	03°07.30′W	53
Celtic Deep	1997	51°15.00′N	06°00.00′W	95
Cardigan Bay	1997	52°21.50′N	04°10.50′W	26
Dundrum Bay	1997	54°04.00′N	05°30.00′W	78

core was retained for meiofauna analysis and the top 5 cm of another core from the same deployment was retained for particle size and chemical analyses.

The depth of the sediment core obtained at each sampling site depends on the sediment compaction and the amount of weight loaded on the multicorer. The depths of sediment cores collected at the inshore sites ranged from 3 to 13 cm, those sampled at the intermediate and offshore locations ranged from 4 to 20 cm.

Meiofauna samples were fixed in 7% formaldehyde in 63 μm filtered seawater. Samples for particle size and chemical analyses were frozen to a temperature of -20°C pending analysis.

Sediment analyses

Particle size analysis

After thawing, the sediments were wet sieved through a 500 μm sieve, and the fraction >500 μm was oven dried at 90°C for 24 h. It was then dry sieved at 0.5 ϕ intervals, down to 1 ϕ (500 μm). The fraction <500 μm was freeze dried and analysed on a Coulter LS 130 Laser sizer. The laser sizer results were combined with the dry sieve results to give the full particle size distribution (Dyer, 1986).

Analysis of organic content

The sediment fraction <63 μm was freeze-dried, and then ground in a Fritsch planetary mill. Carbonate was removed by adding sulphuric acid and the organic carbon content was then determined with a Leeman CE440 elemental analyser.

Analysis of trace metal concentrations

The sediment fraction <63 μm of the sediment samples was totally assimilated in hydrofluoric acid and aqua regia. The concentrations of a range of trace metals were analysed in the aqua regia extract using an inductively-coupled plasma mass spectrometer (ICP-MS, Jones & Laslett, 1994). Mercury concentrations in the extracts were determined by cold vapour atomic absorption spectrophotometry.

Sample processing

Meiofauna samples were initially washed onto a 63 μm sieve to remove the fine silt fraction and the formalin. After decanting the samples five times onto a 63 μm sieve in order to separate the meiofauna and lighter sediment fractions from the coarser material, meiofauna was extracted with Ludox TM 40 with a specific gravity of 1.15 (Somerfield & Warwick, 1996). The extraction process was repeated three times.

The harpacticoid copepods were picked out of each sample under a binocular microscope and identified to species or genus level in hanging-drop mounts or by dissection. The remaining samples were evaporated slowly in anhydrous glycerol and evenly spread on microscope slides for identification and counting of nematodes. All nematodes were counted and the first 200 specimens on each slide identified to genus or species level.

Data processing

Sediment variables

A correlation-based principal components analysis (PCA) was applied to ordinate results from the sediment analyses. The positions of samples are defined in relation to axes representing the full set of environmental variables measured, one axis for each variable. The first principal component axis (PC1) is then defined as the direction in which the variance of sample points projected perpendicularly onto the axis is maximized. The second principal component (PC2) is defined as the axis perpendicular to PC1 (Clarke & Warwick, 1994).

Meiofauna assemblage structure

Simple regression analysis was performed to identify any relationship between a number of univariate indices and the depth of the sediment core collected. There was no significant relationship between core depth and total

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abundance, Shannon–Wiener index (H') or evenness (J') at $P<0.05$ allowing these indices to be used as legitimate descriptors of differences in meiofauna assemblage structure between stations. Bartlett's and Cochran's tests were used to test for homogeneity of variance. One-way ANOVA was applied to test the null hypothesis that there were no significant differences between stations. The Tukey HSD multiple comparisons test was used in pairwise comparisons of samples. These analyses were performed using the software package STATGRAPHICS Plus, version 3.3.

Non-metric multidimensional scaling (MDS) ordination using the Bray–Curtis similarity measure was applied to relative species abundance data (Clarke & Warwick, 1994). Analysis of similarities (ANOSIM, Clarke, 1993) was performed to test the significance of differences in meiofauna assemblage composition between samples. The nature of the community groupings identified in the MDS ordinations was explored further by applying the similarity percentages program (SIMPER) to determine the contribution of individual species to the average dissimilarity between samples.

Following a procedure described in Somerfield et al. (1995), the RELATE program was applied to test for significant relationships between similarity matrices based on relative meiofauna abundance and measured environmental variables. The Spearman rank correlation (ρ) was computed between the corresponding elements of each pair of matrices, and the significance of the correlation determined using a permutation procedure.

Additionally, the relationships between multivariate community structure and environmental variables were assessed using the BIOENV program. In this procedure rank correlations (ρw) between a similarity matrix derived from the biotic data and matrices derived from various subsets of environmental data are calculated, thereby defining suites of environmental variables which best explain the biotic structure (Clarke & Warwick, 1994).

RESULTS

Sediment characteristics

Particle size distributions and trace metal concentrations at inshore and offshore locations are listed in Tables 3 & 4. No sediment data are available for the samples collected at the Tees inshore location in 1999.

The sediments collected at inshore locations in 1998/1999 were generally poorly sorted, with mean particle size diameters between 2.70 ϕ off the Thames and 4.85 ϕ in Swansea Bay (Table 3). The total organic carbon content was highest at the Tyne inshore location (probably largely natural in origin, due to higher burdens of coal particles in surface sediment, Buchanan & Longbottom, 1984) and in the Burbo Bight (probably largely anthropogenic in origin; Norton et al., 1984), and lowest off Plymouth. Concentrations of most trace metals were highest in the Burbo Bight, off Plymouth and at the Tyne inshore location. Lowest concentrations occurred off the Thames (Table 3).

The sediments collected at offshore locations all fell within the category of muddy sands or sandy muds and were generally poorly sorted, with sorting coefficients between 1.74 and 2.30, and poor in organic content, with the highest values being found off the Tyne (Table 4). Sediments collected in Lyme Bay were coarser than those collected at other offshore locations. The concentrations of trace metals were generally lower than at inshore locations. Concentrations of some metals were highest in the northern Irish Sea (Dundrum Bay) and lowest in the English Channel (Lyme Bay). Mercury concentrations off the Tyne were twice as high as any other sampled offshore location but substantially lower than at most inshore locations (Table 4).

Though generally low, the concentrations of most trace metals, in particular copper and mercury, were higher at

Table 3. *Sediment characteristics at inshore locations.*

	Tyne inshore	Off Thames	Off Plymouth	Swansea Bay	Burbo Bight
Particle size distribution					
Mean (ϕ)	3.41	2.70	4.22	4.85	3.12
Sorting	1.27	2.33	1.94	2.13	2.48
Skewness	2.72	0.31	0.94	0.65	0.98
Kurtosis	15.02	6.23	4.98	3.84	3.92
Gravel (%)	0.06	7.80	0.36	0.28	1.54
Sand (%)	82.91	73.45	53.23	33.85	67.19
Mud (%)	17.02	18.75	46.41	65.88	31.28
C (%)	2.7	1.9	1.3	1.4	2.5
Concentration of trace metals					
Cr (ppm)	50	43	27	30	67
Ni (ppm)	36	18	23	27	35
Cu (ppm)	49	15	61	20	37
Zn (ppm)	105	58	99	116	168
As (ppm)	19	7	23	12	14
Cd (ppm)	0.31	0.07	0.19	0.33	0.38
Pb (ppm)	49	29	81	42	91
Hg (ppm)	0.12	0.18	0.53	0.24	0.84

Table 4. *Sediment characteristics at offshore locations.*

	Off Tyne	Off Humber	Lyme Bay	Celtic Deep	Cardigan Bay	Dundrum Bay
Particle size distribution						
Mean (ϕ)	4.63	3.76	3.21	4.11	4.82	5.77
Sorting	1.74	1.89	2.05	1.79	2.30	2.00
Skewness	1.45	1.69	1.53	1.53	0.65	0.36
Kurtosis	5.43	5.73	5.53	5.84	3.25	3.71
Gravel (%)	0.03	0.10	0.30	0.04	0.15	0.08
Sand (%)	48.19	71.87	76.07	63.63	41.15	13.33
Mud (%)	51.78	28.03	23.63	36.33	58.70	86.59
C (%)	3.2	2.0	1.7	1.5	1.3	1.5
Concentration of trace metals						
Cr (ppm)	52	51	27	36	44	56
Ni (ppm)	32	29	16	24	31	35
Cu (ppm)	18	16	8	21	19	21
Zn (ppm)	103	80	45	89	71	119
As (ppm)	10	12	8	12	13	7
Cd (ppm)	0.24	0.24	0.07	0.25	0.22	0.24
Pb (ppm)	48	31	18	25	41	47
Hg (ppm)	0.14	0.06	0.04	0.07	0.06	0.08

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inshore than at offshore locations. This might indicate anthropogenic impacts in the inshore environment.

The ordinations of sediment data by PCA in Figure 2 show that there is no clear separation of sediments collected inshore in 1998/1999 and offshore in 1997. In terms of particle size distribution, sediment collected at the Tyne inshore location, characterized by highest sand content and lowest percentage of silt/clay and sorting coefficient, clusters separately from other locations (Figure 2A). The similarity of sediments collected in Cardigan Bay, Dundrum Bay and Swansea Bay is mainly due to their high mud content (>50%).

Three groups emerge in the PCA ordination based on results from the chemical analyses (Figure 2B). The inshore stations off Plymouth and in the Burbo Bight, where concentrations of most trace metals were highest, are separated from those with lowest (Lyme Bay and off the Thames) and intermediate values (off the Humber, off the Tyne, Celtic Deep, Cardigan Bay, Dundrum Bay, Swansea Bay, Tyne inshore location).

Between 80 and 82% of the total variation is explained by the first two principal components, indicating that the two-dimensional ordination gives an appropriate representation of the similarity between sediments.

Meiofauna assemblage structure

A total of 158 species was identified at inshore locations (129 nematode species and 29 harpacticoid species) and 224 species at offshore stations (139 nematode species and 85 harpacticoid species). Nematodes comprised between 80 and 100% of total abundance. Therefore, nematodes strongly dominated the faunal patterns.

In order to compare nematode and harpacticoid copepod assemblages from different inshore and offshore locations, total abundance, diversity (H') and evenness (J') indices were calculated (Figures 3 & 4). This allows a visual interpretation of any trends (e.g. increasing or decreasing diversity at different sampling locations) and their statistical significance, whereas this judgement is more difficult for results obtained by multivariate data analyses.

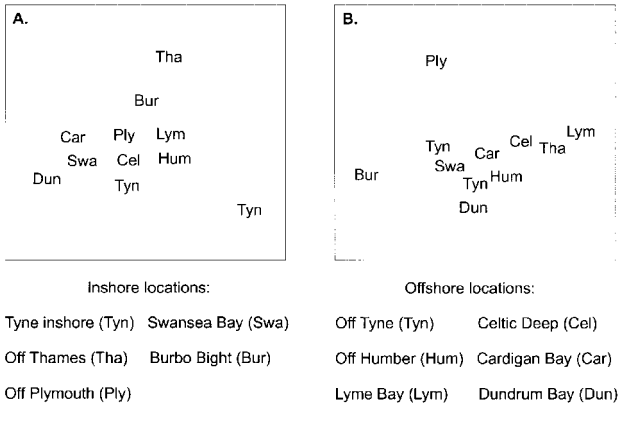

Figure 2. PCA ordination of sediment data from inshore and offshore locations: (A) particle size distribution (total variance explained by the first two principal components =80%); (B) concentration of trace metals (total variance explained by the first two principal components =82%). For variables involved in the ordinations see Tables 3 & 4.

Compared to other inshore locations, nematode abundance was significantly higher off the Thames. Values were significantly higher ($P<0.05$) at the Tees inshore location than at other stations except off the Thames and in the Burbo Bight. Diversity and evenness indices for nematode assemblages were highest at the Tees inshore location and lowest in Burbo Bight compared to other inshore stations (Figure 3A).

Differences in nematode assemblages collected at offshore locations expressed in terms of abundance and evenness were not statistically significant at $P<0.05$. The Shannon–Wiener index was significantly higher in the Celtic Deep than off the Tyne and in Lyme Bay (Figure 3B).

Abundance of harpacticoid copepods was significantly higher at the Tees inshore location and off Plymouth than at other inshore locations. Highest diversity was observed off Plymouth and lowest evenness occurred at the Tees inshore location (Figure 4A).

Offshore, the abundance of harpacticoid copepods was significantly lower in the Celtic Deep than off the Tyne, off the Humber and in Dundrum Bay. Abundance was also significantly higher in Dundrum Bay than off the Humber. Diversity of harpacticoid copepod assemblages was higher in the Celtic Deep compared with most other stations. The evenness of assemblages at this station was higher than that of assemblages collected off the Tyne (Figure 4B).

The MDS ordinations for nematode and harpacticoid copepod assemblages collected at inshore and offshore locations are presented in Figures 5 & 6. Analysis of both the nematode and harpacticoid copepod components generally results in good discrimination between different locations. However, in contrast to the nematode assemblages (Figure 5A), harpacticoid copepod assemblages at the Tyne and Tees inshore locations and in the Burbo Bight do not form distinct clusters (Figure 6A). Despite these differences in multivariate patterns, results from the RELATE analyses indicate a statistically significant similarity in the biotic structure of nematode and harpacticoid copepod assemblages at inshore and offshore locations (inshore: $\rho=0.20, P<0.02$; offshore: $\rho=0.35, P<0.01$).

ANOSIM and SIMPER results in Table 5 show that the species composition of nematode assemblages at all inshore locations were significantly different from each other at $P<0.05$. The average dissimilarity between

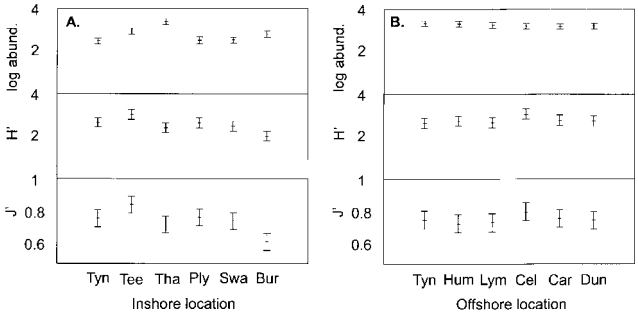

Figure 3. Means (±95% pooled confidence intervals) of abundance (log), diversity (H') and evenness (J') of nematode assemblages from inshore and offshore locations based on absolute abundance: (A) inshore locations; (B) offshore locations. Abbreviations as in Figure 2.

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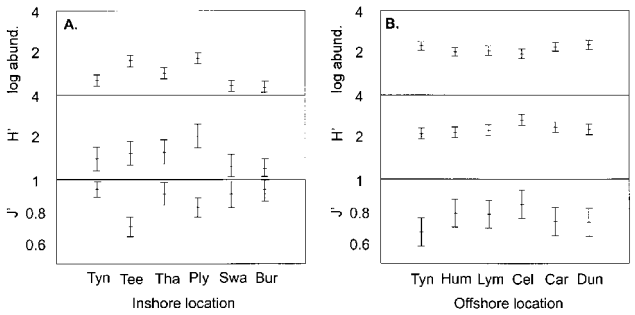

Figure 4. Means (±95% pooled confidence intervals) of abundance (log), diversity (H') and evenness (J') of harpacticoid copepod assemblages based on absolute abundance: (A) inshore locations; (B) offshore locations. Abbreviations as in Figure 2.

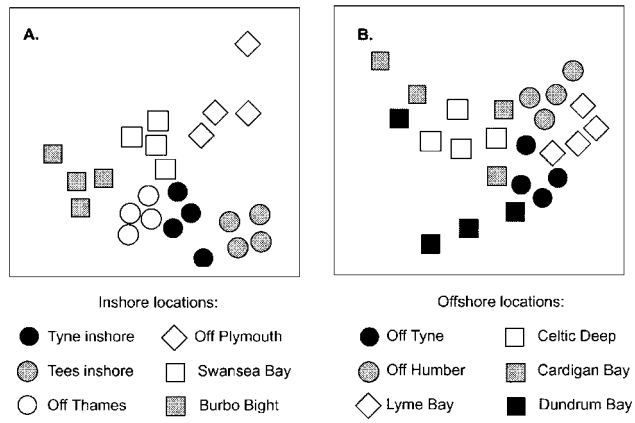

Figure 5. Non-metric multidimensional scaling (MDS) ordination based on relative abundance of nematode species: (A) inshore locations (stress=0.13); (B) offshore locations (stress=0.15).

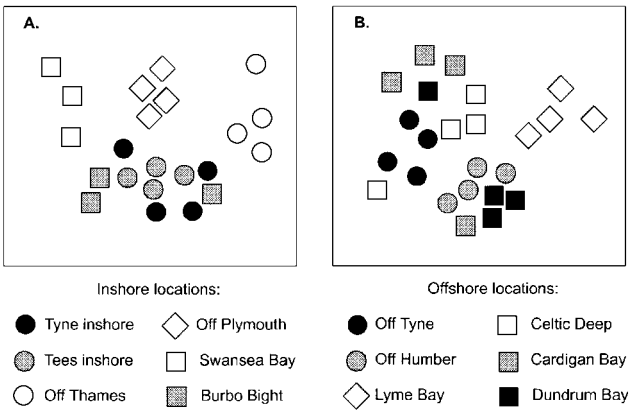

Figure 6. Non-metric multidimensional scaling (MDS) ordination based on relative abundance of harpacticoid copepod species: (A) inshore locations (stress=0.12); (B) offshore locations (stress=0.18).

nematode assemblages was 67%. Nematode assemblages at all offshore locations, apart from the two northernmost locations in the Irish Sea (Cardigan Bay and Dundrum Bay), were significantly different from each other in terms of species composition with an average dissimilarity of 57%.

Despite a higher average dissimilarity of 87% inshore and 77% offshore, differences in harpacticoid copepod assemblage structure between samples collected in the Burbo Bight, the Tyne and Tees inshore locations and in Swansea Bay were not statistically significant at $P<0.05$ (Table 6). This reflects the relatively higher variability of the harpacticoid copepod data. Additionally, differences between harpacticoid copepod assemblages collected off the Tyne and in the Irish Sea (Cardigan Bay and Dundrum Bay) were not statistically significant at $P<0.05$.

Table 5. *Dissimilarities (%) between nematode assemblages from inshore and offshore locations based on relative abundance.*

	Tyne inshore	Tees inshore	Off Thames	Off Plymouth	Swansea Bay
Inshore locations					
Tees inshore	57*				
Off Thames	56*	65*			
Off Plymouth	72*	72*	72*		
Swansea Bay	59*	74*	60*	64*	
Burbo Bight	66*	80*	62*	78*	64*

	Off Tyne	Off Humber	Lyme Bay	Celtic Deep	Cardigan Bay
Offshore locations					
Off Humber	56*				
Lyme Bay	53*	49*			
Celtic Deep	54*	55*	60*		
Cardigan Bay	55*	60*	62*	54*	
Dundrum Bay	59*	66*	64*	59*	56

*, denotes significant difference at $P<0.05$.

Table 6. *Dissimilarities (%) between harpacticoid copepod assemblages from inshore and offshore locations based on relative abundance.*

	Tyne inshore	Tees inshore	Off Thames	Off Plymouth	Swansea Bay
Inshore locations					
Tees inshore	60				
Off Thames	91*	89*			
Off Plymouth	84*	82*	93*		
Swansea Bay	94*	99*	100*	86*	
Burbo Bight	81	56	98*	95*	100

	Off Tyne	Off Humber	Lyme Bay	Celtic Deep	Cardigan Bay
Offshore locations					
Off Humber	75*				
Lyme Bay	86*	80*			
Celtic Deep	71*	79*	82*		
Cardigan Bay	76	77*	87*	79*	
Dundrum Bay	78	58*	81*	79*	67

*, denotes significant difference at $P<0.05$.

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Significant differences between inshore locations were largely the result of changes in the relative abundance of the nematode species *Sabatieria breviseta* Stekhoven, 1935, *Richtersia inaequalis* Riemann, 1966, *Microlaimus turgofrons* Lorenzen, 1971 and *M. zosterae* Allgen, 1930. Only approximately 4% of all nematodes collected at the Tees inshore location belonged to *S. breviseta*, whereas proportions at other inshore locations were significantly higher, ranging from 12% off Plymouth to 36% in the Burbo Bight. Nematode assemblages collected at stations on the east coast of the UK were characterized by higher proportions of *R. inaequalis* and *M. zosterae* than those from locations off the west coast. The relative abundance of *M. turgofrons* was significantly higher at the Tees inshore location, off Plymouth and in Swansea Bay than at any other inshore location.

Sabatieria breviseta dominated the nematode assemblages at all offshore stations. Results from the SIMPER analyses reveal that significant differences between nematode assemblages at different stations were not only due to changes in abundance of this numerically dominant species. Despite relatively low abundance at most stations, *Leptolaimus elegans* (Stekhoven & De Coninck, 1933), *Paramonohystera* sp. and *Terschellingia longicaudata* De Man, 1907 discriminated well between stations. More than two thirds of all nematodes collected off the Humber and in Lyme Bay belonged to *S. breviseta*. This was a significantly higher proportion than at any other offshore location. Relative abundance of *L. elegans* was highest at the two northern-most stations off the Tyne and in Dundrum Bay. Although generally low, the proportion of *Paramonohystera* sp. was significantly higher at the eastern stations (off the Tyne and off the Humber) and in the Irish Sea (Celtic Deep and Cardigan Bay) than at other offshore locations. Relative abundance of *T. longicaudata* was significantly higher off the Tyne and in Lyme Bay.

Inshore, harpacticoid copepod assemblages were dominated by members of the family Ectinosomatidae, except in Burbo Bight where they were completely absent. Apart from this family, two other harpacticoid species were common in Plymouth: *Rhizothrix curvata* (Brady & Robertson in Brady (1880), 1880) and *Heteropsyllus curticaudatus* T. Scott, 1894. *Asellopsis intermedia* (T. Scott, 1895) was a significant element of the community only at the location off the Thames and *Pseudameira crassicornis* Sars, 1911 was common off the Tees.

In general, the harpacticoid copepod species *Longipedia coronata* Claus, 1863, *Danielssenia typica* Boeck, 1873 and *Cletodes longicaudatus* Boeck, 1873 were largely responsible for differences between sampled offshore locations around the UK. Apart from a few juveniles of *Longipedia*, these species were not present in Lyme Bay where the distinctive species were *Haloshizopera conspicua* Por, 1964, *Rhizothrix curvata* (Brady & Robertson in Brady (1880), 1880) and the cyclopoid copepod *Cyclopina kieferi sensu* Herbst, 1962.

Relationships between environmental variables and meiofauna assemblage structure

Results from the RELATE analyses in Table 7 reveal statistically significant relationships between meiofaunal distribution patterns and measured environmental variables at $P<0.05$. Nematode and harpacticoid copepod species distribution patterns at inshore and offshore locations were significantly correlated with variables based on particle size distribution and concentrations of trace metals.

Table 7. *Spearman rank correlations (ρ) between meiofauna assemblage structure and environmental variables at inshore and offshore locations. For variables involved in the calculations see Tables 3 & 4.*

	Particle size distribution		Concentration of trace metals	
	ρ	P	ρ	P
Inshore locations				
Nematodes	0.19	0.04	0.30	<0.01
Harpacticoid Copepods	0.35	<0.01	0.43	<0.01
Offshore locations				
Nematodes	0.45	<0.01	0.25	<0.01
Harpacticoid Copepods	0.21	0.01	0.40	<0.01

Inshore, a combination of the concentrations of chromium, arsenic and mercury best explained nematode assemblage structure (ρw=0.65) and a combination of particle size and concentrations of chromium, zinc and cadmium produced the highest rank correlation coefficient for harpacticoid copepods (ρw=0.63).

A combination of particle size and arsenic concentration best explained nematode assemblage structure at offshore locations (ρw=0.41). Observed patterns of harpacticoid copepod assemblages were mainly related to the sorting coefficient and the concentrations of chromium and copper in the sediment (ρw=0.46).

There was no statistically significant co-variation of the concentrations of trace metals and the sand and silt/clay content of the sediments (P between 0.06 and 0.52) except for nickel (P=0.02).

DISCUSSION

Results from this study indicate that differences in species composition of the meiofauna assemblages between different inshore and offshore locations provide a sensitive and clear measure of environmental status. Determining changes in species distribution patterns offers a potentially more sensitive means of assessing environmental characteristics than is possible by reference to abundance, diversity and evenness since marked changes in species composition may occur without corresponding changes in the other measured variables (Moore & Bett, 1989). Warwick & Clarke (1991) applied a range of univariate and multivariate techniques to a number of benthic data sets in order to assess their relative sensitivity. They found that species-dependent multivariate methods were more sensitive than species-independent univariate methods in discriminating between sites or times, a finding which has been confirmed by McRae et al. (1998).

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Meiofauna species distribution patterns were explained well by variables derived from particle size distributions and concentrations of trace metals. The concentrations of correlated trace metals were relatively low at most stations and an unlikely cause of biological effects. However, elevated concentrations of most trace metals at inshore locations compared to offshore might indicate anthropogenic impacts in the inshore environment and a correlation between the structure of meiofauna assemblages and unmeasured contaminants is possible.

A combination of particle size and concentrations of chromium, zinc, arsenic, mercury and cadmium best explained nematode and harpacticoid assemblage structure at inshore locations. Relatively high concentrations of these trace metals in the Burbo Bight were clearly correlated with low diversity of meiofauna. This might indicate anthropogenic impact at this site. The disposal of sewage sludge into Liverpool Bay has been the subject of a long-term multidisciplinary scientific investigation since the early 1970s. This has shown that the addition of sludge is one of many factors including the outflow from the polluted Mersey Estuary—influencing the quality of the water and sediments in this area (Head, 1981; Norton et al., 1984; Rees et al., 1992).

Somerfield et al. (1995) compared patterns in community structure of nematodes, harpacticoid copepods and macrofauna along a transect through a dredgings disposal site in Liverpool Bay. Assemblages within the disposal site differed significantly from those outside. Nematode assemblages were sensitive to sediment structure and the on-going disposal of dredgings at the site, whereas the assemblage structure of harpacticoid copepods and macrofauna were related to concentrations of metals. This result is in agreement with Gee et al. (1992) who analysed meiofauna communities along a drilling site off the Dutch coast and across the German Bight. In general, significant differences in assemblage structure appeared to be correlated with corresponding changes in sediment granulometry and water depth. Sediment granulometry seemed to be the single most important factor in determining nematode assemblage structure along the German Bight transect. However, despite the overwhelming dominance of physical variables in the study by Gee et al. (1992), the inclusion of trace metals such as zinc and mercury in the analyses increased the correlation with harpacticoid copepods.

Rank correlation coefficients between nematode and harpacticoid copepod assemblage structure and measured environmental variables were higher at inshore locations than offshore, indicating that other unmeasured but correlated factors, such as inter- and intraspecific competition could be more important in determining meiofauna assemblage structure in the offshore environment.

The abundance and diversity of meiofauna assemblages were generally higher offshore than inshore. This difference is likely to be a result of both natural processes and the concentration of trace metals or other correlated factors. Compared with the more stable environment offshore, the inshore environment shows large fluctuations of abiotic factors including wave and tidal current action, salinity and temperature over different time-scales which generally results in a lower species diversity. As benthic organisms are intimately associated with the sediment, they have to adapt to a range of environmental conditions (Soetaert et al., 1995).

Copepod assemblages at inshore locations were dominated by ectinosomids which are predominantly found at the sediment–water interface and depend more on the quality of the overlying water than of the sediment itself. The almost complete absence of copepods in the Burbo Bight may be indicative of deterioration of both sediment and water quality resulting from heavy dumping of river sludge and industrial waste.

At offshore locations, *Longipedia coronata* is also epibenthic in habit, dependent on good water quality and on distinctly muddy substrates. *Danielssenia typica* inhabits the surface layer of the sediment while *Cletodes longicaudatus* is a slightly deeper-burrowing species, but both prefer sediment with a high silt/clay content, hence their absence in Lyme Bay. The former species is probably more depth sensitive than the latter, being replaced at deeper stations, such as the Celtic Deep, by other genera of Paranannopidae.

Monitoring of the effects of natural and man-made changes by examining meiofauna assemblage structure has proved useful. The clear separation of meiofauna assemblages collected at offshore and inshore locations suggests a high taxonomic resolution and a wide range of adaptations of nematodes and harpacticoid copepods to varying environmental conditions. Meiofaunal monitoring should be considered where there is difficulty in adequate sampling of the macrofauna, e.g. due to impoverishment, and meiofauna might also be a useful monitoring tool to identify subtle changes in the ecosystem in response to contaminant inputs (Moore & Bett 1989).

Significance

Management decisions aimed at protecting the marine environment against adverse effects of human activities and conserving biological diversity require a more holistic approach than hitherto. The use of both macrofauna and meiofauna techniques in routine monitoring therefore not only provides complementary information on environmental conditions and greater flexibility to meet site-specific study requirements but also widens the scope for evaluation of the status of the benthic ecosystem as a whole.

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Appendix 1. *Relative and absolute abundance of dominant nematode species at inshore locations.*

	Relative abundance (%)	Absolute abundance
Tyne inshore		
Sabatieria breviseta Stekhoven, 1935	23 ±6	75 ±32
Richtersia inaequalis Riemann, 1966	9 ±5	29 ±11
Microlaimus zosterae Allgen, 1930	14 ±5	48 ±33
Microlaimus turgofrons Lorenzen, 1971	6 ±3	20 ±14
Daptonema normandicum (De Man, 1890)	13 ±4	41 ±17
Tees inshore		
Prochromadorella septempapillata Platt, 1973	5 ±2	52 ±43
Richtersia inaequalis Riemann, 1966	9 ±1	96 ±53
Microlaimus zosterae Allgen, 1930	8 ±4	102 ±97
Microlaimus turgofrons Lorenzen, 1971	16 ±8	190 ±153
Off Thames		
Prochromadorella septempapillata Platt, 1973	5 ±2	161 ±75
Sabatieria breviseta Stekhoven, 1935	32 ±9	936 ±140
Richtersia inaequalis Riemann, 1966	8 ±3	241 ±57
Paramonohystera sp.	18 ±6	557 ±202
Off Plymouth		
Sabatieria breviseta Stekhoven, 1935	12 ±6	42 ±24
Marylynnia complexa (Warwick, 1971)	6 ±1	20 ±5
Molgolaimus demani Jensen, 1978	12 ±8	42 ±32
Aponema torosa (Lorenzen, 1973c)	7 ±12	28 ±52
Microlaimus turgofrons Lorenzen, 1971	10 ±7	38 ±30
Paramonohystera sp.	5 ±2	15 ±4
Terschellingia longicaudata De Man, 1907	17 ±9	59 ±33
Swansea Bay		
Sabatieria breviseta Stekhoven, 1935	27 ±4	103 ±46
Comesa vitia (Warwick, 1971)	14 ±3	53 ±21
Molgolaimus demani Jensen, 1978	5 ±4	17 ±16
Microlaimus turgofrons Lorenzen, 1971	10 ±8	33 ±24
Thalassomonhystera venusta (Lorenzen, 1979)	9 ±3	36 ±25
Metalinhomoeus sp.	5 ±3	22 ±22
Burbo Bight		
Sabatieria breviseta Stekhoven, 1935	36 ±17	230 ±70
Spirinia parasitifera (Bastian, 1865)	28 ±20	202 ±148
Leptolaimus limicolus Lorenzen, 1972c	5 ±2	31 ±14

Appendix 2. *Relative and absolute abundance of dominant harpacticoid copepod species at inshore locations.*

	Relative abundance (%)	Absolute abundance
Tyne inshore		
Pseudobradya minor (T. & A. Scott, 1896)	51 ±33	2 ±1
Stenhelia (S) aemula (T. Scott, 1893)	11 ±16	1 ±1
Tees inshore		
Halectinosoma herdmani (T. & A. Scott, 1896)	12 ±10	6 ±5
Pseudobradya minor (T. & A. Scott, 1896)	34 ±17	13 ±8
Pseudameira crassicornis Sars, 1911	43 ±24	19 ±16
Off Thames		
Halectinosoma angulifrons (Sars, 1919)	15 ±12	2 ±1
Enhydrosoma propinquum (Brady & Robertson in Brady, 1880)	14 ±21	3 ±5
Asellopsis intermedia (T. Scott, 1895)	8 ±6	1 ±1
Off Plymouth		
Halectinosoma cooperatum Bodin, Bodiou & Soyer, 1971	17 ±10	8 ±2
Haloschizopera pygmaea (Norman & T. Scott, 1905)	5 ±4	3 ±3
Heteropsyllus curticaudatus T. Scott, 1894	31 ±5	18 ±11
Rhizothrix curvata (Brady & Robertson in Brady (1880), 1880)	8 ±4	4 ±3
Swansea Bay		
Halectinosoma cooperatum Bodin, Bodiou & Soyer, 1971	47 ±50	1 ±1
Tachidiella minuta Sars, 1909	40 ±53	1 ±1
Burbo Bight		
Pseudameira crassicornis Sars, 1911	67 ±58	1 ±1

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Appendix 3. *Relative and absolute abundance of dominant nematode species at offshore locations.*

	Relative abundance (%)	Absolute abundance
Off Tyne		
Sabatieria breviseta Stekhoven, 1935	23 ±6	631 ±336
Richtersia inaequalis Riemann, 1966	5 ±5	166 ±195
Leptolaimus elegans (Stekhoven & De Coninck, 1933)	12 ±2	322 ±113
Paramonohystera sp.	7 ±3	174 ±77
Metalinhomoeus longiseta Kreis, 1929	9 ±9	241 ±264
Terschellingia longicaudata De Man, 1907	9 ±5	200 ±98
Off Humber		
Sabatieria breviseta Stekhoven, 1935	33 ±11	842 ±402
Daptonema furcatum (Juario, 1974)	6 ±3	138 ±53
Paramonohystera sp.	5 ±3	109 ±74
Eleutherolaimus stenosoma (De Man, 1907)	6 ±4	154 ±117
Lyme Bay		
Sabatieria breviseta Stekhoven, 1935	32 ±11	635 ±140
Microlaimus turgofrons Lorenzen, 1971	9 ±2	182 ±26
Leptolaimus elegans (Stekhoven & De Coninck, 1933)	6 ±3	132 ±118
Terschellingia longicaudata De Man, 1907	6 ±6	151 ±201
Axonolaimus paraspinosus Stekhoven & Adam, 1931	5 ±2	112 ±77
Celtic Deep		
Sabatieria breviseta Stekhoven, 1935	18 ±5	336 ±103
Pomponema multipapillatum (Filipjev, 1922)	5 ±3	96 ±63
Aponema torosa (Lorenzen, 1973c)	13 ±6	239 ±62
Paramonohystera sp.	7 ±4	114 ±40
Cardigan Bay		
Sabatieria breviseta Stekhoven, 1935	16 ±8	300 ±162
Marylynnia complexa (Warwick, 1971)	14 ±17	302 ±323
Aponema torosa (Lorenzen, 1973c)	6 ±6	142 ±168
Leptolaimus elegans (Stekhoven & De Coninck, 1933)	5 ±3	89 ±44
Paramonohystera sp.	7 ±4	118 ±67
Dundrum Bay		
Sabatieria breviseta Stekhoven, 1935	11 ±4	200 ±46
Molgolaimus demani Jensen, 1978	20 ±16	410 ±347
Leptolaimus elegans (Stekhoven & De Coninck, 1933)	6 ±6	110 ±98
Metalinhomoeus longiseta Kreis, 1929	5 ±4	95 ±62
Terschellingia longicaudata De Man, 1907	5 ±4	92 ±80

Appendix 4. *Relative and absolute abundance of dominant harpacticoid copepod species at offshore locations.*

	Relative abundance (%)	Absolute abundance
Off Tyne		
Danielssenia typica Boeck, 1837	30 ±26	63 ±51
Amphiascoides dispar (T. & A. Scott, 1894)	10 ±2	23 ±5
Proameira signata Por, 1964	7 ±4	15 ±8
Cletodes longicaudatus (Boeck, 1837)	17 ±17	41 ±41
Off Humber		
Longipedia coronata Claus, 1863	24 ±3	32 ±19
Longipedia scotti Sars, 1903	9 ±6	9 ±2
Halectinosoma angulifrons (Sars, 1919)	22 ±7	30 ±18
Danielssenia typica Boeck, 1837	9 ±6	12 ±9
Enhydrosoma propinquum (Brady & Robertson in Brady, 1880)	6 ±5	7 ±7
Lyme Bay		
Halectinosoma herdmani (T. & A. Scott, 1896)	14 ±5	18 ±7
Tachidiella minuta Sars, 1909	14 ±8	16 ±7
Haloschizopera pygmaea (Norman & T. Scott, 1905)	7 ±6	10 ±8
Haloschizopera conspicua Por, 1964	9 ±5	13 ±9
Pseudameira crassicornis Sars, 1911	7 ±8	11 ±14
Enhydrosoma propinquum (Brady & Robertson in Brady, 1880)	6 ±6	7 ±7
Rhizothrix curvata (Brady & Robertson in Brady (1880), 1880)	18 ±9	23 ±12

(*Continued*)

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Appendix 4. *(Continued)*.

	Relative abundance (%)	Absolute abundance
Celtic Deep		
Bradya (Bradya) sp.	10 ±6	8 ±5
Haloschizopera pygmaea (Norman & T. Scott, 1905)	5 ±3	4 ±1
Proameira signata Por, 1964	5 ±3	4 ±1
Cletodes longicaudatus (Boeck, 1837)	11 ±11	12 ±14
Laophonte longicaudata Boeck, 1865	5 ±4	5 ±3
Cardigan Bay		
Longipedia coronata Claus, 1863	13 ±21	15 ±19
Danielssenia typica Boeck, 1837	15 ±22	44 ±68
Stenhelia (D) mastigochaeta Wells, 1965	7 ±7	18 ±22
Haloschizopera bulbifera (Sars, 1911)	12 ±12	33 ±38
Dundrum Bay		
Longipedia coronata Claus, 1863	31 ±18	103 ±79
Longipedia scotti Sars, 1903	11 ±6	34 ±25
Tachidiella minuta Sars, 1909	5 ±3	18 ±17

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