The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities*

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During a synoptic survey carried out in April–May 1986, 171 localities were sampled in the North Sea as delimited by the Straits of Dover in the south and approximately by the 100 m isobath in the north. Meiobenthos included Nematoda, Copepoda, Turbellaria, Gastrotricha, Polychaeta, Oligochaeta, Priapulida, Kinorhyncha, Ostracoda, Halacarida, Isopoda, Tanaidacea, Bryozoa, Cnidaria, Sipunculida, Echiurida, Nemertini and Tardigrada. Nematodes were the dominant group in virtually all stations, their densities ranging from 61 to 4167 individuals. $10 \, cm^{-2}$. Only in the Southern Bight, where nematode numbers were low, did harpacticoids sometimes represent the dominant meiobenthic taxon. There was a tendency for nematode (and total meiobenthos) density to increase towards the north. A total of 278 copepod species belonging to 105 genera and 22 families were identified. Over 40% of the species were new to science; new taxa were found particularly among the interstitial families which were most important in terms of species diversity. Copepod density decreased rapidly to the north and this trend was followed by diversity. Individual ash-free dry weight (AFDW) was determined for 98 species of copepod. Total biomass reached a peak in the south (low mean individual AFDW, high density) and in the north (high mean individual AFDW, low density), but was low in the Central North Sea where the copepod communities were impoverished both qualitatively and quantitatively. Using the classification technique TWINSPAN (two-way indicator species analysis), it was impossible to define meaningful clusters (TWIN groups) on the basis of the 18 major meiobenthic taxa. However, seven distinct communities could be recognized on the basis of the copepod composition: (1) TWIN A largely coincided with the Southern Bight and showed high densities of predominantly interstitial species (Cylindropsyllidae, Paramesochridae, Cyclopinidae) and a few characteristic taxa from coarse sediments; (2) TWIN B was found in the coastal zone of the Netherlands, Germany and Denmark, and in the Dogger Bank, and was dominated by large Ectinosomatidae and Ameiridae, and by interstitial Leptastacidae; (3) TWIN C represented an impoverished community north of the Dogger Bank and consisted of large mud-dwelling species belonging to the Diosaccidae, Laophontidae and Ameiridae; (4) between the Scottish coast and Norwegian Deeps and in the Silver Pits Zosimidae, Cletodidae and Idyanthidae were the most important families (TWIN D); (5) TWIN E grouped the Norwegian Deeps, Devil's Hole and Farne Deep and showed a typical deepwater fauna represented by Ancorabolidae, Cerviniidae, Stenocopiinae and bathyal cletodid genera. Two minor clusters (α, β) coincided with the Dutch Wadden Sea (1 station) and the river outlets (Thames, Wash, Meuse/Scheldt) whose meiobenthos is subject to pollutants. Canonical Correspondence Analysis (CCA) clearly separated the five major twin groups. TWIN A–C were significantly correlated with sediment and could be arranged along a gradient of decreasing median grain size and increasing silt/clay content. TWIN D was clearly related to latitude whilst TWIN E showed a clear preference for depth.

Key words: North Sea; meiobenthos; copepod communities; biomass; diversity; latitudinal trends; synoptic survey.

Received 22 May 1991; accepted 11 November 1991.

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Introduction

Since Smidt's (1951) early work on the Danish Wadden Sea and McIntyre's (1964) study of the Fladen Ground meiobenthos, much information has been gained on the species composition, density and biomass of meiobenthic assemblages. Heip *et al.* (1990) summarized this knowledge, resulting from 40 years of meiobenthos research in the North Sea, and concluded that only the coastal areas of Belgium, the Netherlands and Germany were relatively well known (Fig. 1). Large areas of the North Sea have not been investigated and in particular the lack of basic data from deeper localities makes it impossible to present a comprehensive picture of North Sea meiobenthos. Even for the easily accessible, shallow areas of the Central North Sea such as the Dogger Bank and the eastern sandbanks (Jutland, Little Fisher, Turbot), information on meiobenthos remains fragmentary. There were several attempts to define biological regions within the North Sea but these were all based on planktonic communities or more recently on macrobenthic infauna and epifauna (Basford *et al.*, 1989, 1990; Eleftheriou & Basford, 1989). The question remains whether meiobenthos or its component major taxa can also be applied to define communities on a large geographical scale.

A synoptic survey of the North Sea benthos was organized during April–May 1986 in the area delimited by the Straits of Dover in the south and approximately by the 100 m isobath in the north. This sampling programme involved the cooperation of 10 laboratories from France, Belgium, The Netherlands, Germany and the UK. During this survey we sampled a grid of 171 localities for meiobenthos and for various physicochemical sediment parameters. This paper presents an analysis of the distribution of the major meiobenthic taxa, and assesses the major environmental factors affecting the various copepod communities.

Materials and methods

The sampling area

The present investigation was conducted as part of the North Sea Benthos Survey (NSBS) executed in April–May 1986. This synoptic survey covered a total of 197 localities arranged in the ICES grid from the Straits of
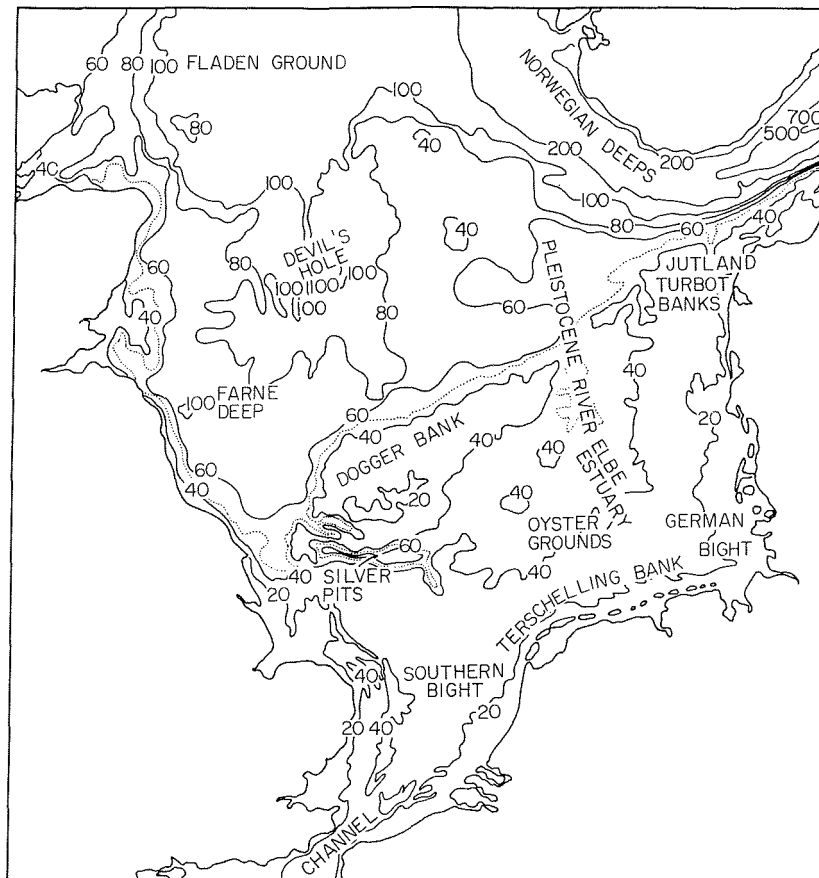

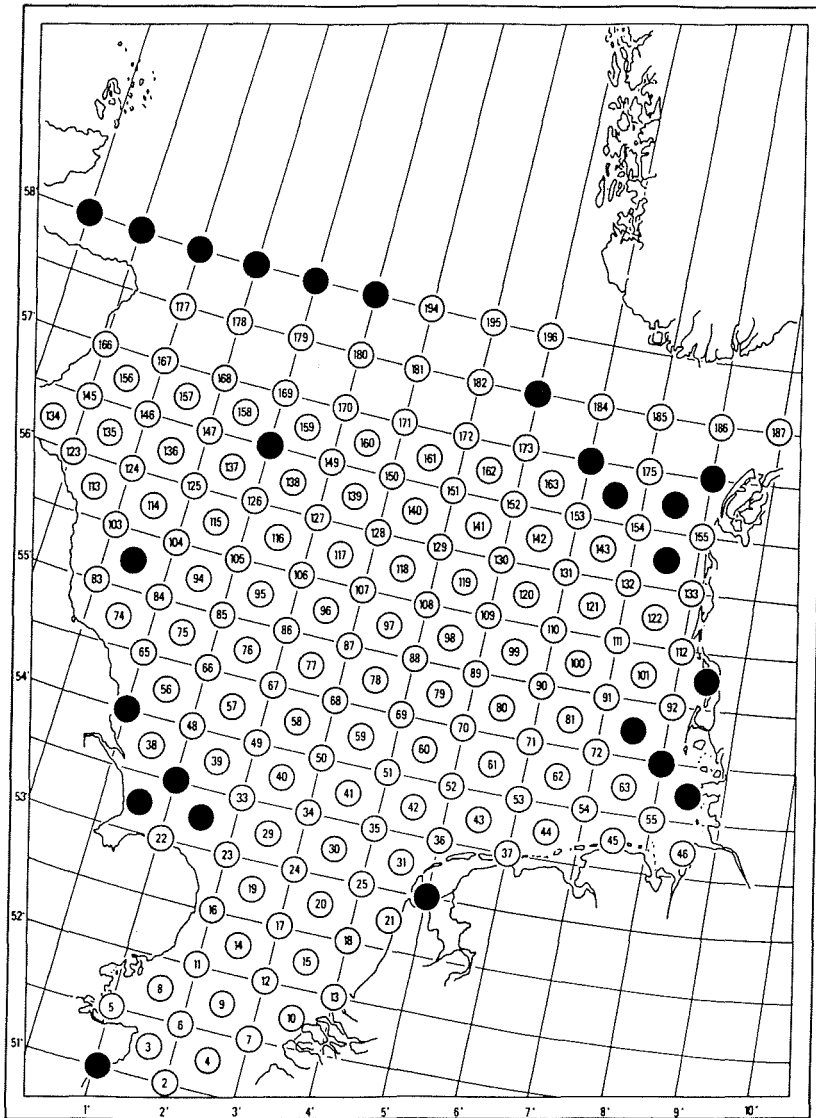Figure 1. Map showing bathymetry of southern and central North Sea.

Figure 2. North Sea map showing sampling localities of North Sea Benthos Survey. Filled circles indicate localities that were not sampled.

Dover in the south to approximately the 100 m isobath in the north and from 2°30′ W to 8°15′ E. Only 171 stations were sampled for meiobenthos (Fig. 2), and a complete list of the sampling data was reported elsewhere (Anonymous, 1986) and is available from the ICES database on request. Stations not being sampled included localities along the Danish coast (102, 144, 164, 165, 174, 176, 183) and in the German Bight (64, 73, 82), in the Dutch Wadden Sea (26), in the mouth of the Humber and The Wash (27, 28, 32, 47), and in the Fladen Ground off the northeastern coast of Scotland (188–193). Some are shallow localities and were for that reason not accessible by the research vessels used. Others were not sampled because of the unfavourable weather conditions at the time of sampling.

Bottom samples were taken with a Van Veen grab (0.184 m^2) or preferably with a box corer (0.068 m^2) or with both sampling gears. Usually four subsamples (10 cm^2) were taken with perspex cores, but only one subsample was provided for the localities sampled by the Nederlands Instituut voor Onderzoek der Zee (NIOZ, Texel) and by the Forschungsinstitut Senckenberg (Wilhelmshaven). Some of the latter stations were either sampled by both or by other laboratories as well so that for 134 out of 171 localities two or more subsamples (10 cm^2) were provided. Use of the Van Veen grab in sandy bottoms might cause a considerable loss of interstitial water when lifting on board, resulting in an overestimation of the relative abundance of the surface-

dwelling species such as copepods and an underestimation of the relative abundance of the interstitial small-sized types which often represent the bulk of the copepod community in coarse sediments. Conversely, in fine sediments where surface-dwelling species are dominant the bow-wave of the Van Veen grab may push epibenthic species away before sampling. Hence, box corer samples were preferred whenever they were available.

Processing

Meiobenthos samples were fixed and preserved in a hot (about 70°C), 4% formaldehyde solution. Animals were subsequently extracted by centrifugation-flotation in LUDOX TM® colloidal silica (Heip *et al.*, 1985) or by decantation using a 38 µm sieve when the sediment proved too coarse. Copepods were first picked out of the samples, since their identification often required dissection. The remaining meiobenthos was counted and identified at high taxonomic level (phylum or class) under a stereoscopic microscope, after staining with Rose Bengal. All copepods were identified down to species level.

Individual dry weights of copepods were determined on a Mettler M3 electronic microbalance (± 0.1 µg). Batches of 20–150 (according to size) specimens belonging to the same species were rinsed three times in double-distilled water, dried for 2 h at 110°C, cooled in a desiccator, and weighed. Only adults were selected for weighing and no attempt was made to separate the sexes because of the paucity of some of the species. Females and males were evenly represented in every batch. However, females carrying eggs were not selected since it was found that the presence of an ovisac could increase ash-free dry weight (AFDW) by over 40%.

Mathematical techniques – Statistical analysis

Distribution maps
Maps were produced using the program DIHOMAP (Herman & Braat, 1991). This program addresses a database and maps the densities of species and higher taxonomical groups. The radius of the symbols is proportional to the log-transformed density. Details of this are given by the associated box and whisker plots.

The box is drawn between the first and third quartile of the (log-transformed) data. The position of the median on the log-transformed scale is indicated by the vertical bar. The back-transformed value of the median is indicated above this line. The whiskers are the lines extending from both sides of the box to the left and right. They extend to the most extreme observation lying within the boundary quartile value ± 1.5 times the interquartile distance. Their back-transformed value is indicated below the box and whisker plot. Observations falling beyond the whiskers are called outliers. Their number (not their value!) is given by the numbers to the right and left of the whiskers.

The radius of outliers is equal to the smallest or largest radius indicated below the box and whisker plot. For intermediate values the radius is interpolated between these extremes. This interpolation is linear on a log (density) scale.

Concentric circles indicate data derived from two replicates taken by different laboratories.

Measures of species diversity
The following Hill's diversity numbers (Hill, 1973) were used as measures of diversity of the copepod community and calculated on the raw data:

N_0 = the number of species in the sample (species richness); equals in this study the "species density" (number of species per unit area = $10 \, cm^2$) as all copepods in the sample were identified.

N_1 = exp (H'), with H' the Shannon–Wiener diversity index calculated with natural logarithms.

Classification
Two-way indicator species analysis (TWINSPAN) (Hill, 1979) was used to classify the stations for which copepods were examined. TWINSPAN is a polythetic divisive technique that first performs a primary ordination on the samples by reciprocal averaging, and then uses this ordination to obtain a classification of the species according to their ecological preferences. The synecological relations of the various species can be expressed in an ordered two-way table constructed from the sites-by-species matrix. TWINSPAN also identifies one to several differential species (= indicator species) which are particularly diagnostic of each division (twin group) in the dendrogram (indicator ordination). In addition, preferential species which appear to prevail in one side of a dichotomy may be selected as well. In order to handle quantitative data as well, each species abundance is replaced by the presence of one or more pseudo-species. Each pseudo-species is defined by the minimum abundance of the corresponding species (cut level); thus the more abundant a species, the more pseudo-species will be defined.

Ordination
In many cases it is useful to parallel TWINSPAN classification with an ordination. The ordination technique used is canonical correspondence analysis (ter Braak, 1986). The resulting ordination diagram not only expresses the pattern of variation in species composition, but also reflects the major relations between the species/stations and each of the given environmental variables. The stations of each twin group are positioned as points (symbols) in the CCA diagram. The environmental variables are represented by arrows and can be interpreted in conjunction with the station points. Each arrow determines an axis in the biplot and the station points must be projected onto this axis. The order of the projection points corresponds approximately to the ranking of the weighted

(a)

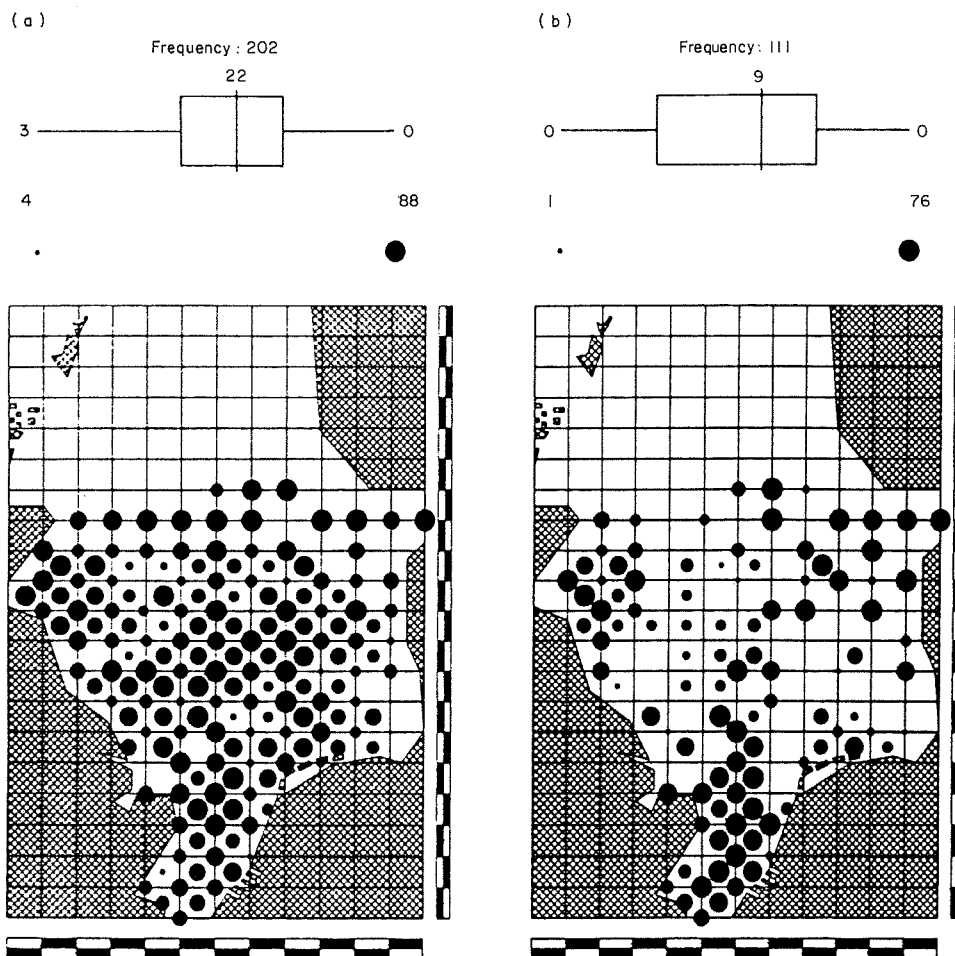Frequency : 202

(b)

Frequency: 111

Figure 3. Log of total density of the major soft-bodied taxonomic groups of the meiobenthos in the North Sea. (a) Turbellaria. (b) Gastrotricha. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed density (see text for details).

averages of the species with respect to a particular environmental variable. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and therefore more closely related to the pattern of variation of species composition shown in the ordination diagram. Arrows that point in the same direction indicate positively correlated variables, perpendicular arrows indicate lack of correlation and arrows pointing in the opposite direction indicate negatively correlated variables.

Results

Total meiobenthos

Meiobenthos included Nematoda, Copepoda, Platyhelminthes (Turbellaria), Gastrotricha, Polychaeta, Oligochaeta, Priapulida, Kinorhyncha, Ostracoda,

Halacarida, Isopoda, Tanaidacea, Bryozoa, Cnidaria (Hydrozoa), Sipunculida, Echiurida, Nemertini and Tardigrada. Nematodes were nearly always the dominant group in the meiobenthos, their densities ranging from 61 to 4167 ind. $10 \, cm^{-2}$ ($\bar{x} = 759$ ind. $10 \, cm^{-2}$). Only in the Southern Bight were harpacticoids sometimes as abundant as nematodes or were even the dominant taxon of the meiobenthos. In the remaining localities nematodes accounted for at least 85% of the meiobenthos; Harpacticoida or Turbellaria (and in a few cases Gastrotricha) ranked second in abundance. The other groups were present especially in medium coarse or coarse sands but they were far less common than the main taxa. Figure 3a and 3b illustrate the distribution and density of the two dominant soft-bodied meiobenthic taxa, the Turbellaria and the Gastrotricha.

The central part of the Southern Bight (south of 53°30′ N) contained stations with high numbers of

interstitial copepods and relatively low nematode densities. This community extended to the coastal zone of Belgium and The Netherlands but was apparently absent in the shallow offshore area of Britain although the sediment type was virtually the same (median grain size averaged 250–300 μm). The Southern Bight community seems to be unique for the entire North Sea; values of the nematode:copepod ratio were low and ranged between 16 and 25. Only a few localities along the western coast of Denmark and around the Isle of Sylt gave indication of a similar nematode:copepod ratio (Fig. 4a). There was no monotonic trend discernible for the N/C ratio with latitude (Fig. 4b).

Although coarse sediments generally favour the development of a characteristic interstitial fauna it is striking that the mesopsammic harpacticoids were not typical for the German Bight and the west coast of Denmark. Particularly in the entrance to the Skagerrak where very coarse sediments were found, these tiny copepods seemed to be outnumbered by other ecotypes, i.e. epi/endobenthic copepods. Here, high densities of gastrotrichs were recorded.

The distribution of the kinorhynch genera was clearly related to the median grain size. Four genera were recorded, and these can be assigned to two ecological groups. *Echinoderes* and *Semnoderes* are typical representatives of sandy sediments and particularly the latter genus is known to inhabit coarse substrata. These genera were found only in the Southern Bight and in the entrance to the Firth of Forth (Fig. 5). The latter record is not surprising as the sediments in this isolated area were fine or medium sands in contrast to the very fine sediments (below 200 μm) of the surrounding waters. A similar case was found in the German Wadden Sea (station 46). Conversely, species of the genera *Pycnophyes* and *Kinorhynchus* were recorded in the central part of the North Sea and never in the Southern Bight. Their distribution was largely confined to the eastern part of the central area (Fig. 5). It is known from the literature that these genera are associated with very fine sediments. The same area was also characterized by the occurrence of Priapulida (larvae of *Priapulus caudatus*), a taxon that was entirely absent in the Southern Bight and occurred only sporadically in the western part of the North Sea.

Nematodes, generally the most abundant meiobenthic taxon in marine sediments, became even more abundant with latitude (and thus depth) up to 53°30′ N. From this latitude was a tendency for nematode density to decrease towards the north, but the trend was not linear (Fig. 6a). The relation between total meiobenthos density and latitude fitted the picture obtained for the nematodes (Fig. 6b).

TWINSPAN was applied to classify the stations on the basis of absence or presence of the 18 major meiobenthic taxa but did not produce any meaningful groupings. One of the shortcomings of TWINSPAN is that taxa that are
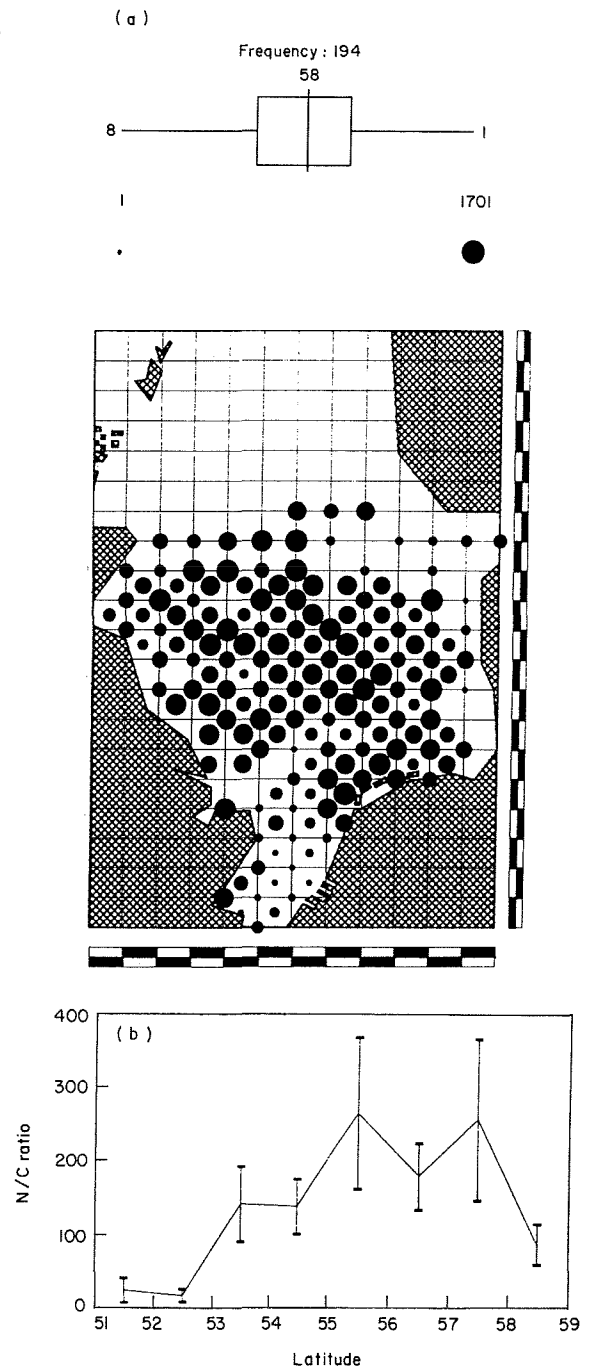

Figure 4. (a) Log of nematode:copepod ratio. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed N/C ratio (see text for details). (b) Trend of nematode:copepod ratio with latitude. Per degree latitude nematode:copepod ratio of all stations falling in that zone is averaged. Error bars indicate standard errors of the mean.

rare and moreover occur in stations with low diversity determine the arrangement of the stations. For example,
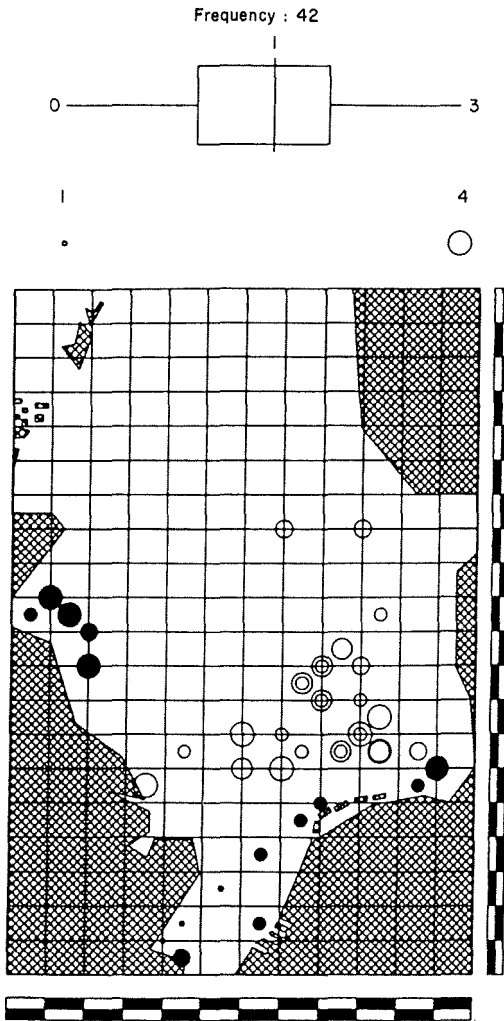
Figure 5. Log of total density of the Kinorhyncha in the North Sea. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed density (see text for details). Empty circles denote mud-dwelling genera (*Pycnophyes*, *Kinorhynchus*), filled circles denote sand-inhibiting genera (*Semnoderes*, *Echinoderes*).
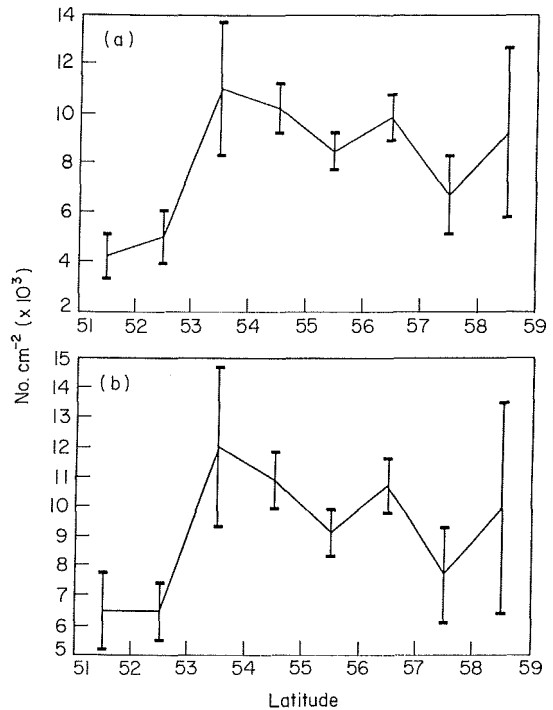

Figure 6. Trend of total density with latitude. Per degree latitude the density of all stations falling in that zone is averaged. Error bars indicate standard errors of the mean. (a) Nematoda. (b) Total meiobenthos.

the first TWINSPAN dichotomy was primarily determined by the Cnidaria and the Tardigrada, the second division basically by the minor taxa Isopoda and Halacarida, etc. Of the major groups only the various pseudo-species of the Gastrotricha seemed to contribute in shaping the early subdivisions of the dendrogram.

Copepoda

The fauna

The harpacticoid community predominantly included adults and post-metamorphosed stages (copepodites). Examination of the copepod fauna from one sample

(10 cm^{-2}) of each of the 171 selected stations resulted in a total number of 7710 individuals. All copepods were identified to species level. The complete faunal data are available from the authors on request. A total number of 278 species belonging to 105 genera and 22 families were identified. Surprisingly, 121 species (43.5%) turned out to be new to science. A high number of novel species was recorded for the Paramesochridae (27), Cylindropsyllidae (24), Ectinosomatidae (17) and Ameiridae (14). For both the Paramesochridae and the Cylindropsyllidae, the North Sea Benthos Survey resulted in a doubling of the species number for the North Sea area as delimited by the ICES boundaries. The examination of the interstitial copepod fauna revealed also nine new genera.

The vast majority of the fauna belonged to the Harpacticoida. The Cyclopoida were represented by the primarily mesopsammic family Cyclopinidae (six species). An additional number of calanoids and planktonic cyclopoids (Oithonidae) was omitted in the analysis.

Qualitatively important families were Paramesochridae (44 species), Cylindropsyllidae (38), Ameiridae (35), Ectinosomatidae (34), Cletodidae (26), Laophontidae and Diosaccidae (21). A total number of 105 genuinely interstitial species were recorded, including the Paramesochridae, Cylindropsyllidae, Cyclopinidae and small-sized representatives of the Ameiridae, Canthocamptidae, Diosaccidae and Ectinosomatidae. The remainder consisted

Table 1. Total number of specimens found and the number of occurrences in the total data set for the top 50 species of the survey.

Family	Species	Total number of specimens	Frequency
Leptastacidae	*Leptastacus laticaudatus*	356	41
Leptastacidae	*Paraleptastacus espinulatus*	294	42
Cylindropsyllidae	*Evansula pygmaea*	235	22
Leptastacidae	*Arenocaris bifida*	199	32
Cylindropsyllidae	*Leptopontia curvicauda*	195	20
Ectinosomatidae	*Arenosetella germanica*	132	19
Paramesochridae	*Kliopsyllus holsaticus*	130	15
Paramesochridae	*Intermedopsyllus intermedius*	116	17
Diosaccidae	*Psammotopa phyllosetosa*	107	23
Diosaccidae	*Protopsammotopa norvegica*	98	16
Diosaccidae	*Typhlamphiascus confusus*	96	17
Paramesochridae	*Kliopsyllus constrictus*	95	11
Cylindropsyllidae	*Boreopontia heipi*	94	12
Cylindropsyllidae	*Stenocaris kliei*	82	13
Ectinosomatidae	*Halectinosoma herdmani*	80	25
Paramesochridae	*Paramesochra mielkei*	80	13
Ectinosomatidae	*Pseudobradya beduina*	79	16
Ameiridae	*Interleptomesochra eulittoralis*	78	20
Cletodidae	*Stylicletodes longicaudatus*	78	19
Cyclopinidae	*Metacyclopina brevisetosa*	74	15
Leptastacidae	*Paraleptastacus holsaticus*	73	17
Ectinosomatidae	*Ectinosoma melaniceps*	71	11
Ectinosomatidae	*Bradya scotti*	68	16
Idyanthidae	*Idyanthe pusilla*	65	11
Leptastacidae	*Leptastacus* sp. 2	65	14
Diosaccidae	*Bulbamphiascus imus*	60	15
Ameiridae	*Pseudameira crassicornis*	56	17
Diosaccidae	*Paramphiascopsis longirostris*	55	22
Ameiridae	*Proameira hiddensoensis*	55	13
Paramesochridae	*Kliopsyllus paraholsaticus*	54	13
Paramesochridae	*Apodopsyllus listensis*	51	8
Cylindropsyllidae	*Syrticola flandricus*	50	12
Paramesochridae	*Wellsopsyllus gigas*	50	17
Leptastacidae	*Leptastacus* sp. 1	49	12
Ectinosomatidae	*Halectinosoma propinquum*	48	17
Paramesochridae	*Paramesochra helgolandica*	47	7
Thalestridae	*Pseudotachidius coronatus*	47	6
Paramesochridae	*Scottopsyllus minor*	46	11
Ectinosomatidae	*Pseudobradya minor*	43	12
Cylindropsyllidae	*Cylindropsyllus laevis*	42	10
Cletodidae	*Enhydrosoma* sp. 1	42	11
Longipediidae	*Longipedia helgolandica*	42	8
Ectinosomatidae	*Pseudobradya* sp. 1	42	9
Cylindropsyllidae	*Stenocaris minor*	42	13
Ameiridae	*Ameiropsis brevicornis*	41	14
Cylindropsyllidae	*Cylindropsyllus remanei*	41	9
Ectinosomatidae	*Halectinosoma sarsi*	41	19
Cylindropsyllidae	*Arenopontia* sp. 3	40	9
Cletodidae	*Cletodes tenuipes*	39	8
Paramesochridae	*Kliopsyllus* sp. 4	39	7

mainly of large epibenthic or burrowing harpacticoids. *Euterpina acutifrons* and *Microsetella norvegica* are likely to be contaminants derived from the plankton since these species are generally believed to be holoplanktonic.

Total number of specimens found and the number of occurrences in the total data set are given for the 50 most abundant species in Table 1.

Biomass

Determination of biomass is invaluable in quantitative ecological investigations. However, most published data give only rough estimates on total meiobenthic biomass. Direct weighing is often circumvented through calculation of the total volume, either (a) by approximating it to a particular geometric shape, or (b) by a crude division

of the organisms into a number of shapes whose volumes are summed up, or (c) by using length and width measurements and a conversion factor derived from plasticine models made from scale drawings (Gee & Warwick, 1984). Obviously, application of biomass conversion factors, based on average individual weights, to material from which they were not originally calculated can result in significant errors. Reliable biomass values can be obtained if the average individual dry weight of each species is measured. In practice, this approach is far too time-consuming for most ecological work and direct dry weight measurements of the rarer species can easily be over- or underestimated when the number of specimens in the batch is insufficiently high.

Literature values on individual ash-free dry weights of copepods are scarce (Goodman, 1980; van Damme *et al.*, 1984; Herman *et al.*, 1984; Herman & Heip, 1985) and are determined for species taken from small geographical areas where a particular aspect was under investigation. A survey of the copepod fauna on such a large scale as the North Sea offered the opportunity of compiling a checklist of specific biomass values for copepods since numerous specimens were available for many species. This list can be extended at any time when new data become available and could refine considerably the calculation of the overall copepod biomass in future investigations.

The dominance of small-sized harpacticoids in the Southern North Sea made it hard to determine accurately the biomass of the copepod fraction of the meiobenthos. Hence, special emphasis was placed on the determination of individual dry weights of interstitial copepods such as the Cylindropsyllidae, Leptastacidae and Paramesochridae. A total of 98 different species belonging to 21 families and 73 genera were weighed (Table 2). The other copepods were assigned to one of these 98 values according to their size, shape and exoskeletal properties. It has to be remarked that overall total biomass figures will usually be slight overestimates since they were based on adults only, and no attempt has been made to divide the species into different size- and biomass-classes according to their copepodid stages. These overestimates will be negligible in the Southern North Sea where mesopsammic copepods dominate.

Latitudinal trends

There is a distinct and significant trend for copepod density to decrease towards the north (Fig. 7a). Highest values (181 ind. 10 cm^{-2}) were recorded in the Southern Bight between 51.5° and 52°N where tiny interstitial copepods showed an overwhelming dominance in the community. Density decreased rapidly towards the Dogger Bank and reached its minimum average value (18 ind. 10 cm^{-2}) in the Norwegian Deeps.

Diversity N_1 (expressed in equivalent number of species) calculated on the total sample showed a similar trend with latitude (Fig. 7b). This trend is most distinctive in the Southern Bight with an average of 38 species found in the southern stations off the Belgian coast and only 13 species south of the Dogger Bank. In the Northern North Sea diversity showed a tendency opposite to the density trend. The low number of species recorded between 57° and 58°N approximately coincides with the 100 m isobath.

The mean individual weight (AFDW), obtained by dividing total biomass by total density showed a completely opposite trend (Fig. 8b). Towards the north individual size increased considerably, due to the gradual replacement of interstitial by large epibenthic species. The mean ash-free dry weight of the nordic species was nearly three times the value for the Southern Bight species. This difference in AFDW combined with the latitudinal trend displayed by density explains why total biomass reaches a peak in both the south and the north (Fig. 8a). In the Southern Bight low individual size and weight is compensated by maximum values for density; in the northern North Sea large, epipelic (=mud-dwelling) species with strongly chitinized exoskeletons (e.g. Cletodidae) occurred in low to very low numbers.

Classification

A TWINSPAN run with standard options resulted in a dendrogram with 34 clusters of which four were one-sample clusters (Fig. 9). A total of 877 species and pseudospecies were recognized. The first dichotomy separated the deepwater samples from the shallow stations. Since depth is only partially correlated with latitude, the separation between the two station-groups coincided with a southwest–northeast boundary rather than with an east–west isobath. The first cluster groups 110 stations located in the entrance to the Firth of Forth (Scotland) and in the Southern North Sea, i.e. south and east of the Dogger Bank, including the Dogger Bank stations. Indicator species for this cluster were two small-sized Leptastacidae *Leptastacus laticaudatus* and *Paraleptastacus espinulatus*. Fifty-five stations were grouped in the second cluster. The most highly preferential species for this deepwater cluster were the stenocopiid *Anoplosoma sordidum* and the continental shelf cerviniid *Cerviniopsis clavicornis*. Seven main twin groups, based on ordination, can be derived from Figure 9. The second dichotomy of the shallow water cluster divided the stations in two secondary clusters of equal size (55 stations) corresponding to twin groups α, TWIN A and TWIN B, and to TWIN C and β, respectively. The secondary division of the deepwater cluster results in two more twin groups TWIN D and TWIN E. No genuine indicator species could be identified for the cluster combining TWIN A, TWIN B and the one-station cluster α. Cluster α constituted the first offshoot in the latter cluster and represented station 37 only (Fig. 9). This locality is situated in the Dutch Wadden Sea (Fig. 10) and apparently is

Table 2. Individual ash-free dry weight (μg) and number of specimens weighed (n) for 98 copepod species.

|	AFDW ind.$^{-1}$ (μg)	n		AFDW ind.$^{-1}$ (μg)	n
Ameiridae			**Laophontidae**		
Ameirinae			*Asellopsis hispida*	1.65	35
Ameira longipes	1.14	25	*Asellopsis intermedia*	1.61	28
Ameira parvula	0.91	35	*Heterolaophonte stroemi*	3.60	35
Ameira tenella	0.79	40	*Laophonte cornuta*	3.75	45
Ameiropsis brevicornis	1.20	50	*Laophonte elongata*	2.65	34
Ameiropsis mixta	0.73	50	*Laophonte inopinata*	3.06	37
Interleptomesochra eulittoralis	0.38	45	*Laophonte thoracica*	2.45	26
Proameira hiddensoensis	0.79	30	*Paralaophonte congenera*	2.45	31
Pseudameira crassicornis	0.71	36	*Pseudolaophonte spinosa*	5.87	20
Pseudameira mixta	0.65	42	*Pseudonychocamptus proximus*	3.81	26
Sarsameira exilis	3.05	35			
Sarsameira parva	0.65	30	**Leptastacidae**		
Sicameira leptoderma	0.52	28	*Arenocaris bifida*	0.26	75
Stenocopiinae			*Leptastacus laticaudatus*	0.27	65
Anoplosoma sordidum	1.96	33	*Leptastacus* sp. 6	0.78	35
Malacopsyllus fragilis	2.25	29	*Paraleptastacus espinulatus*	0.22	100
Stenocopia longicaudata	3.16	45	*Paraleptastacus holsaticus*	0.41	100
Ancorabolidae			**Longipediidae**		
Ancorabolus mirabilis	0.91	23	*Longipedia coronata*	6.87	25
			Longipedia helgolandica	5.89	25
Canuellidae			*Longipedia minor*	5.71	25
Canuella perplexa	4.82	50			
			Normanellidae		
Cerviniidae			*Normanella mucronata*	1.51	38
Cervinia bradyi	7.33	20			
Cervinia synarthra	6.05	20	**Paramesochridae**		
Cerviniopsis clavicornis	7.70	20	*Apodopsyllus listensis*	0.23	85
Eucanuella spinifera	6.21	20	*Apodopsyllus spinipes*	0.18	50
			Apodopsyllus sp. 1	0.25	65
Cletodidae			*Diarthrodella secunda*	0.18	70
Argestes mollis	6.40	25	Gen. 1 sp. 1	0.39	46
Cletodes limicola	1.21	35	Gen. 2 sp. 1	0.17	85
Enhydrosoma garienis	0.91	45	*Intermedopsyllus intermedius*	0.56	74
Rhizothrix curvata	0.79	38	*Kliopsyllus constrictus*	0.19	125
			Kliopsyllus holsaticus	0.14	150
Cyclopinidae			*Kliopsyllus paraholsaticus*	0.18	100
Metacyclopina brevisetosa	0.28	50	*Leptopsyllus elongatus*	0.20	72
			Paramesochra helgolandica	0.24	114
Cylindropsyllidae			*Paramesochra mielkei*	0.28	133
Boreopontia heipi	0.41	55	*Paramesochra similis*	0.31	78
Cylindropsyllus laevis	1.29	31	*Scottopsyllus minor*	0.22	108
Cylindropsyllus remanei	0.58	25	*Wellsopsyllus gigas*	0.58	65
Evansula pygmaea	0.51	65			
Leptopontia curvicauda	0.39	52	**Paranannopidae**		
Stenocaris minor	0.61	40	*Danielssenia typica*	2.28	35
			Psammis longisetosa	1.96	26
Diosaccidae					
Amphiascus minutus	1.06	35	**Tachidiidae**		
Bulbamphiascus imus	4.48	22	*Euterpina acutifrons*	1.83	20
Haloschizopera pygmaea	0.93	36	*Microarthridion littorale*	1.46	65
Paramphiascoides vararensis	2.25	25			
Paramphiascopsis longirostris	3.06	30	**Tetragonicipitidae**		
Psammotopa phyllosetosa	0.47	55	*Pteropsyllus consimilis*	3.10	15
Pseudamphiascopsis herdmani	7.02	18			
Pseudomesochra longifurcata	0.94	28	**Thalestridae**		
Stenhelia gibba	0.87	25	*Dactylopusia vulgaris*	2.00	65
Typhlamphiascus confusus	4.25	35	*Pseudotachidius coronatus*	4.33	25
Ectinosomatidae			**Thompsonulidae**		
Arenosetella germanica	0.35	65	*Thompsonula hyaenae*	1.96	34
Bradya typica	4.27	27			
Ectinosoma melaniceps	1.48	35	**Tisbidae**		
Halectinosoma gothiceps	1.11	45	*Tisbe furcata*	1.20	25
Halectinosoma herdmani	1.53	40			
Halectinosoma propinquum	2.98	26	**Zosimidae**		
Halectinosoma sarsi	3.15	35	*Tachidiella minuta*	1.11	29
Pseudobradya beduina	1.45	48	*Zosime major*	1.39	48
Pseudobradya minor	1.45	50	*Zosime typica*	1.21	55
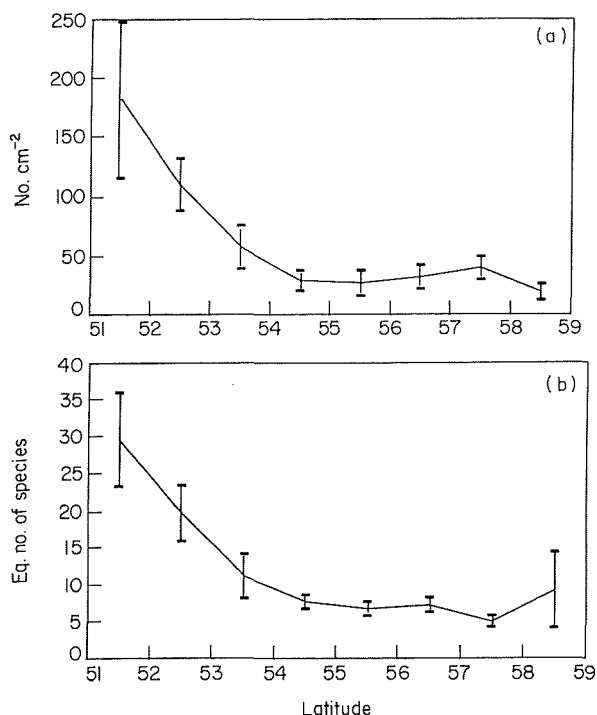
Figure 7. Copepoda. Trend of density (a) and diversity N_1 (b), calculated on the total sample, with latitude. Per degree latitude density and diversity of all stations falling in that zone is averaged. Error bars indicate standard errors of the mean.
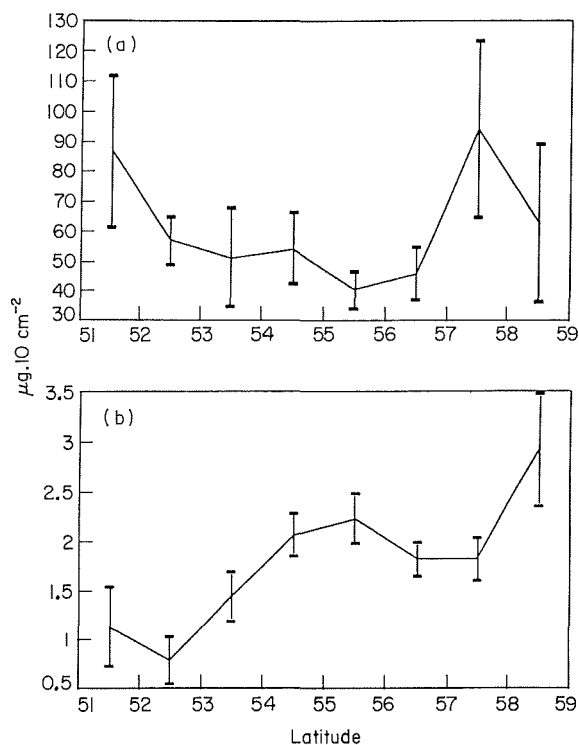

Figure 8. Copepoda. Trend of total biomass (a) and mean individual ash free dry weight (b), with latitude. Per degree latitude the biomass and individual AFDW of all stations falling in that zone is averaged. Error bars indicate standard errors of the mean.

influenced by the low salinity in this area. The only (indicator) species found is *Tachidius discipes*, a typical representative of estuarine and near-coastal localities where lower salinities prevail.

Due to their distribution pattern (Fig. 11d) certain Leptastacidae such as *Arenocaris bifida* and *Leptastacus laticaudatus* can be considered as preferential (together with the fusiform burrower *Halectinosoma herdmani*) for the joint cluster [TWIN A–TWIN B]. Another leptastacid *Paraleptastacus espinulatus* is an indicator species for the group.

TWIN A. TWIN A represents perhaps the most distinctive community found in the North Sea. It consists of 22 highly diverse stations located in the area traditionally referred to as the Southern Bight (except stations 92, 155 and 166) and roughly demarcated in the north at 53.5°N (Fig. 10). This area is bounded by the Belgian coast and Dutch Delta area in the east and the coast of Norfolk in the west, but excludes The Wash and the coastal area off the rivers Thames and Rhine/Meuse. Overall, the Southern Bight consists of fine ($< 250\,\mu m$) to medium coarse (250–$500\,\mu m$) sandy sediments with a low silt clay content reaching a maximum of 2.6% in station 19. Copepod densities ranged from 24 to 651 ($\bar{x} = 178$) ind. $10\,cm^{-2}$, which are the highest observed in this study. On the

average copepods accounted for 25% of the meiobenthos, occasionally contributing as much as 50% of the total density at some stations. The Southern Bight (19 stations) contains approximately 50% of the total number of species found during the North Sea Benthos Survey. Indicator species for this twin group are *Kliopsyllus holsaticus*, *Leptopontia curvicauda*, *Intermedopsyllus intermedius*, *Evansula pygmaea* and *Metacyclopina brevisetosa*. Nearly all other representatives of the families Paramesochridae, Cylindropsyllidae and Cyclopinidae were selected as preferential species.

The great majority of the fauna was made up by mesopsammic (= interstitial) species inhabiting the space between the sand particles. These animals crawl or swim within the lacunae with no, or only negligible, disturbance to the structure of the sediment. The harpacticoid species from this area can be said to have adapted to the interstitial habitat primarily by miniaturization of the body (Paramesochridae, Cyclopinidae) or adoption of extreme vermiformicity (cylindrical shape) and reduction of the appendages (Cylindropsyllidae). The Southern Bight assemblage posed great difficulties as to accurate identification because nearly half of the species (61) were new to science. It contained all North Sea Cylindropsyllidae (Fig. 11c) and Leptastacidae (Fig. 11d), and all but one
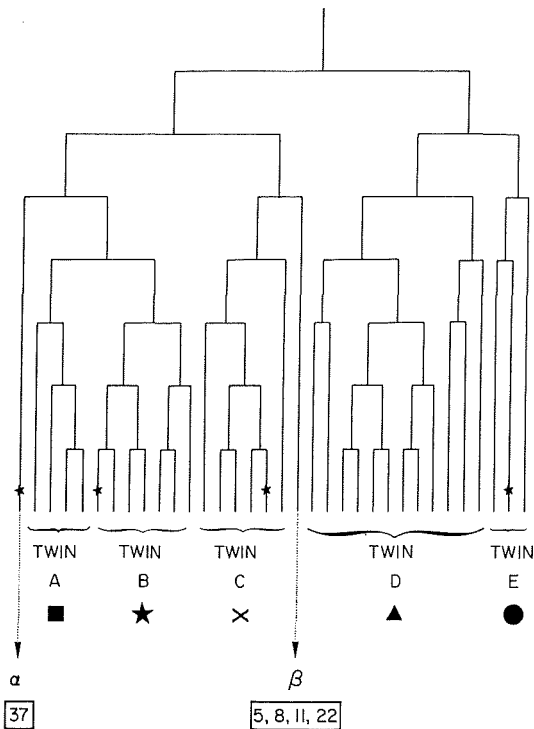
A similar community dominated by interstitial species was found in two localities along the Danish coast (Fig. 10). Station 92 (427 ind. 10 cm^{-2}) is situated near the Isle of Sylt. Mielke (1975) already reported on a diverse mesopsammic assemblage from the coarse sandy sediments in this area whilst Herbst (1974) described several interstitial cyclopinids from the same deposits. The second station (155) is associated with the Jutland Bank in the north; the coarse sandy sediment is inhabited by a high number (390 ind. 10 cm^{-2}) of interstitial species. However, Paramesochridae were less abundant and were primarily replaced by vermiform Ectinosomatidae and Diosaccidae.

Finally, TWIN A also included a third station (166) that is geographically isolated from the Southern Bight. This Firth of Forth station was separated first from the rest of TWIN A because of the mixed species composition made up of Leptastacidae and epibenthic faunal elements (Laophontidae); the absence of other interstitial species was remarkable.

TWIN B. TWIN B could not be identified by any indicator species nor did the analysis point to any preferential species. This twin group essentially coincided with: (i) the zone along the eastern coastline of the Central North Sea, extending from the Terschelling Bank in the south, over the German Bight and the Danish westcoast, to the entrance to the Skagerak in the north, (ii) the localities (38, 39, 40, 50) north of The Wash between 53° and 54°N, and (iii) the shallow stations located at the Dogger Bank (Fig. 10). The latter two regions are separated by a complex of deep trenches ("Silver Pits") which harbour a different copepod fauna (see TWIN D). In general, shallow stations with fine to very fine sandy sediments with a low amount of silt and clay were grouped in this cluster. The fauna was characterized by a mixture of minute interstitial species and large burrowing forms. The mesopsammic component is dominated by Leptastacidae (*Leptastacus, Paraleptastacus, Arenocaris*) which is the only exclusively interstitial family that extends into this zone (Figs 11d, 12). Conversely, Cylindropsyllidae, Cyclopinidae and Paramesochridae were completely absent north of TWIN A (Fig. 12); they were replaced by a few interstitial representatives of the families Ectinosomatidae and Ameiridae whose relative abundances were low. The majority of the community, however, consisted of fusiform Ectinosomatidae (*Ectinosoma, Halectinosoma, Pseudobradya*) and, to a lesser extent, Ameiridae (*Ameira, Proameira, Pseudameira*). Densities were low, ranging from 3–81 ind. 10 cm^{-2}.

TWIN C. TWIN C reflects a transition community between the coastal Ectinosomatidae–Leptastacidae association (TWIN B) and the deepwater community (TWIN D) north of the Dogger Bank. A few stations are located east of the Firth of Forth where they are inter-

Figure 9. TWINSPAN dendrogram based on the species composition of the Copepoda (★ indicates 1-sample clusters).

(*Wellsopsyllus gigas*) of the 44 recorded Paramesochridae species (Fig. 11a). Representatives of these three families were associated with small Ameiridae (*Interleptomesochra, Leptomesochra, Parevansula, Sicameira*) and vermiform Diosaccidae (*Psammotopa, Protopsammotopa*) and Ectinosomatidae (*Hastigerella, Arenosetella*). A typical element of the Southern Bight community was the cyclopoid family Cyclopinidae (Fig. 11b). Due to their adaptations to the mesopsammic lifestyle, these tiny cyclopoids (*Metacyclopina, Cyclopina*, three new genera) show a remarkable convergence with the paramesochrid harpacticoids. In many stations the interstitial community was accompanied by characteristic coarse sediment-inhabiting species such as *Rhizothrix* spp. (Cletodidae) and various Tetragonicipitidae (*Pteropsyllus, Tetragoniceps*).

The species composition strongly resembled the mesopsammic assemblage of the coarse sands of the Kwinte Bank as described by Willems *et al.* (1982). The similarity between the harpacticoid associations from the Southern Bight and that of the coarse sands of the French Catalonian coast (Soyer, 1970) and the coarse sand association of the Irish Sea (Moore, 1979) suggests that the copepod faunas of medium and coarse (> 300 μm) offshore deposits are similar, provided that the sands are well-sorted and clean. Comparison with earlier studies in the Southern Bight also reveals that the community is stable in time (e.g. Huys *et al.*, 1986).
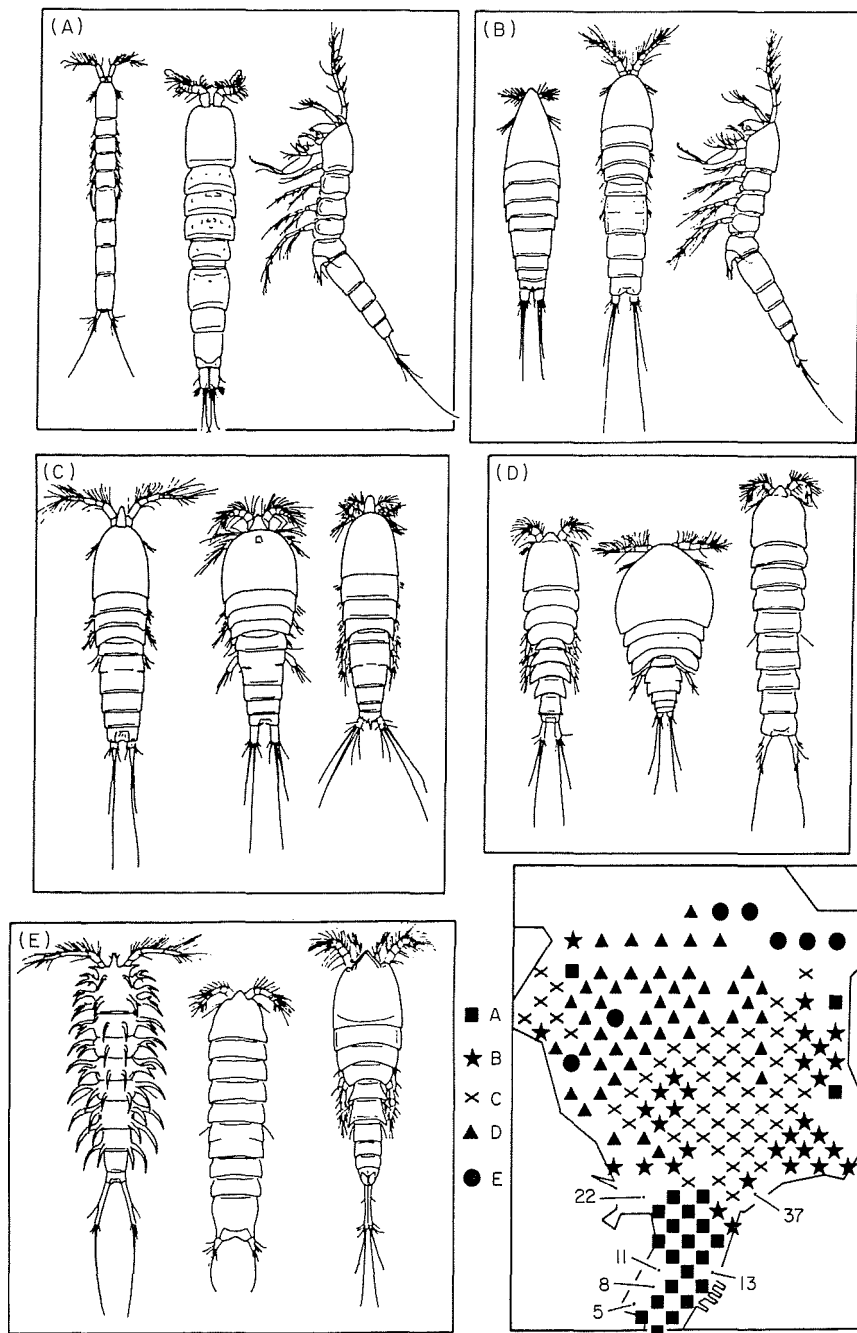
Figure 10. Distribution of the five main TWINSPAN station-groups in the North Sea. For each twin group the most important ecotypes are illustrated.

spersed with stations belonging to the second twin group (Fig. 10). This station-group consisted of 51 stations and was impoverished both qualitatively and quantitatively. A clearly preferential species for this twin group was *Paramphiascopsis longirostris*, whilst interstitial copepods were completely absent. Total densities ranged between 5 and 45 ind. 10 cm^{-2}. The fauna consisted of large pelophilic (= mud-dwelling) species belonging to the Diosaccidae (*Paramphiascopsis, Stenhelia, Bulbamphiascus, . . .*), Laophontidae (various genera) and Ameiridae (*Ameiropsis, Pseudameira, Sarsameira*). Within the Ectinosomatidae, the larger species were still important with the smaller
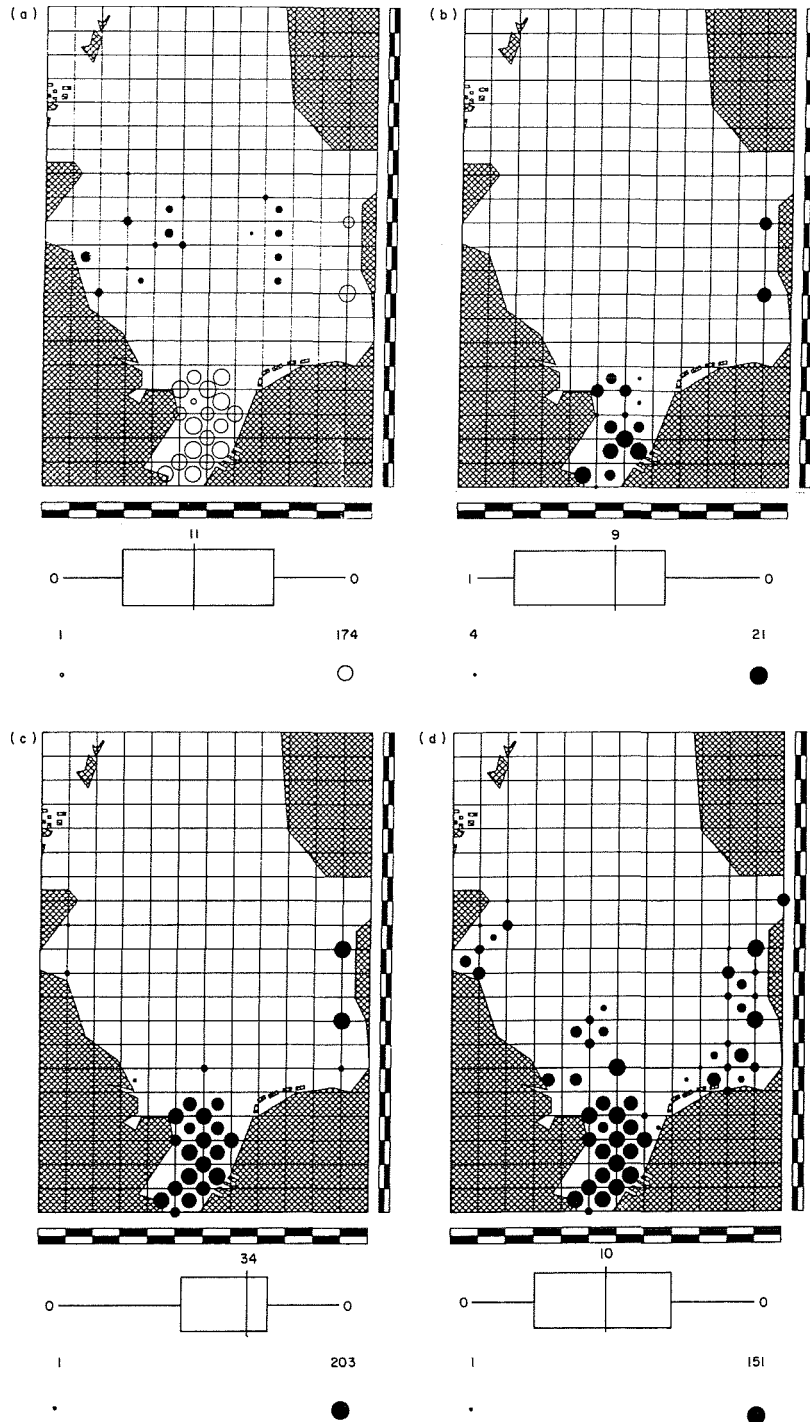
Figure 11. Log of total density of the major interstitial families of the Copepoda in the North Sea. (a) Paramesochridae (filled circles denote records of *Wellsopsyllus gigas*). (b) Cyclopinidae. (c) Cylindropsyllidae. (d) Leptastacidae. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed density (see text for details).

burrowing forms being replaced by bigger representatives of the same genera (*Halectinosoma, Pseudobradya*) or of *Bradya*. The polyarthran genus *Longipedia* was abundant throughout the transition zone (Fig. 13c) with *L. minor* and *L. helgolandica* widely distributed in the south and *L. coronata* and *L. scotti* in the north.
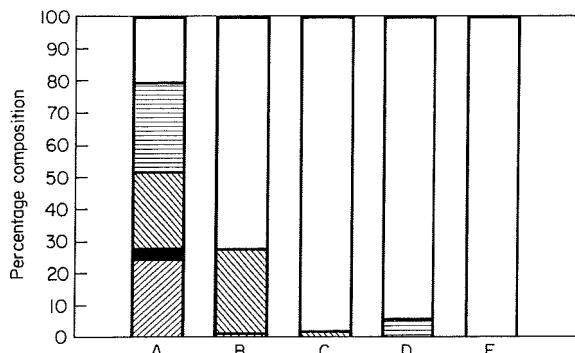
Figure 12. Composition of the North Sea Copepoda per twin group showing importance of exclusively interstitial families in southern twin groups. ▨ Cylindropsyllidae, ■ Cyclopinidae, ▧ Leptastacidae, ▤ Paramesochridae, □ others.

The faunistic picture of the interstitial Southern Bight community is disturbed by the river plumes of the Wash, the Humber and the Thames (Fig. 10). Stations (5, 8, 11, 22) located in the respective river outlets were devoid of interstitial species and cluster together in group β (Fig. 9). Instead, low densities and few species were recorded. Station 13, influenced by the Rhine–Meuse estuary, apparently belonged to the same cluster, however, it was omitted in the TWINSPAN analysis because no copepods were encountered. *Microarthridion littorale* and/or *Canuella perplexa* were (strict) preferential species in all the stations. Earlier studies revealed a similar situation for the Westerschelde estuary (e.g. Huys *et al.*, 1986).

TWIN D. TWIN D is a heterogeneous cluster of 48 stations and coincides with the northern part of the North Sea, situated between the Norwegian Deeps and the Scottish coastline (Fig. 10). No proper indicator species could be identified for the group, but the most important families, both in terms of diversity and density, were the Cletodidae, Zosimidae and Idyanthidae. These three families nearly always occurred together in every station of the area. The Cletodidae were represented by various species of the genera *Cletodes*, *Enhydrosoma* and *Stylicletodes* which are typical faunal elements of deep (40–80 m), muddy bottoms. The Zosimidae (*Zosime*, *Tachidiella*) occupy the same depth range (Fig. 13a) and like the Cletodidae are adapted for an endopelic existence, i.e. shallow burrowing in muddy substrates. The Idyanthidae (Fig. 13b), on the other hand, is characteristic of the flocculent upper layer and encompasses epibenthic genera (*Idyella*, *Idyanthe*, *Tachidiopsis*). This assemblage was also found in stations 99 and 120 which were located in a deep trench penetrating the transition zone (TWIN C) and coinciding with the incision of the Pleistocene River Elbe estuary. Finally, two characteristic species for this area were the giant mud-dwelling

paramesochrid *Wellsopsyllus gigas* (Fig. 11a), originally described from the Fladen Ground (Wells, 1965), and the diosaccid *Typhlamphiascus confusus*.

The deep Silver Pits (stations 49, 56, 57) formed an isolated subcommunity with low densities and an impoverished fauna consisting exclusively of Zosimidae and Idyanthidae.

TWIN E. TWIN E corresponds to the northeastern part of the study area (Norwegian Deeps). The deepwater stations 184, 185, 186, 195 and 196 can be allocated to this region where the depth varies between 84 and 100 m. To a large extent the sediments consisted of fine to medium sand. The silt clay content of the sediment over most of this area ranged between 1.3 and 3.3%, reaching a maximum of 12.4% in the deepest station 196. Copepods occurred in densities ranging from 23–128 ind. 10 cm^{-2}. The community was dominated by the families Cletodidae and Ancorabolidae, and by the deepwater species *Pseudotachidius coronatus* (Pseudotachidiinae). The genera *Eurycletodes*, *Mesocletodes*, *Argestes* and *Heteropsyllus* accounted for more than 90% of the Cletodidae and seemed to have replaced the genera *Cletodes*, *Stylicletodes* and *Enhydrosoma* of the adjacent area (TWIN D). The Ancorabolidae, consisting exclusively of Ancorabolinae, is a typical component of the deepwater fauna of fjords and was represented here by three species (*Ancorabolus mirabilis*, *Echinopsyllus normani* and *Ceratonotus pectinatus*); they represented > 35% of the copepod fauna in most of the stations (Fig. 14b). Other characteristic faunal elements of this assemblage, not found in any of the others, were the deepwater Stenocopiinae (Ameiridae) (Fig. 14a) represented by three genera (*Stenocopia*, *Malacopsyllus*, *Anoplosoma*), and the Cerviniidae (Fig. 14c) represented by the continental shelf genera *Cervinia*, *Eucanuella* and *Cerviniopsis*. In contrast to the previous community, the relative abundance of Zosimidae and Idyanthidae was negligible. *Typhlamphiascus gracilis* seemed to have replaced *T. confusus* in this deeper area; this phenomenon was also recorded by Por (1964a).

It is worthy of note that an analogous community was found in other stations widely separated geographically from the Norwegian Trench (Fig. 10). Both stations had a sediment consisting of very fine sand with a silt clay content being in excess of 9%. Station 137 (91 m) is located in the Devil's Hole, a deep extension of the Fladen Ground, penetrating the Central North Sea. Its copepod fauna was a mixture of "Nordic" cletodid genera, cerviniids and Stenocopiinae. Station 103 was the deepest locality sampled during the North Sea Benthos Survey (107 m) and is situated in the Farne Deep, a depression off the coast of Northumberland. A similar fauna was found here; however, the Stenocopiinae were replaced by Ancorabolinae.
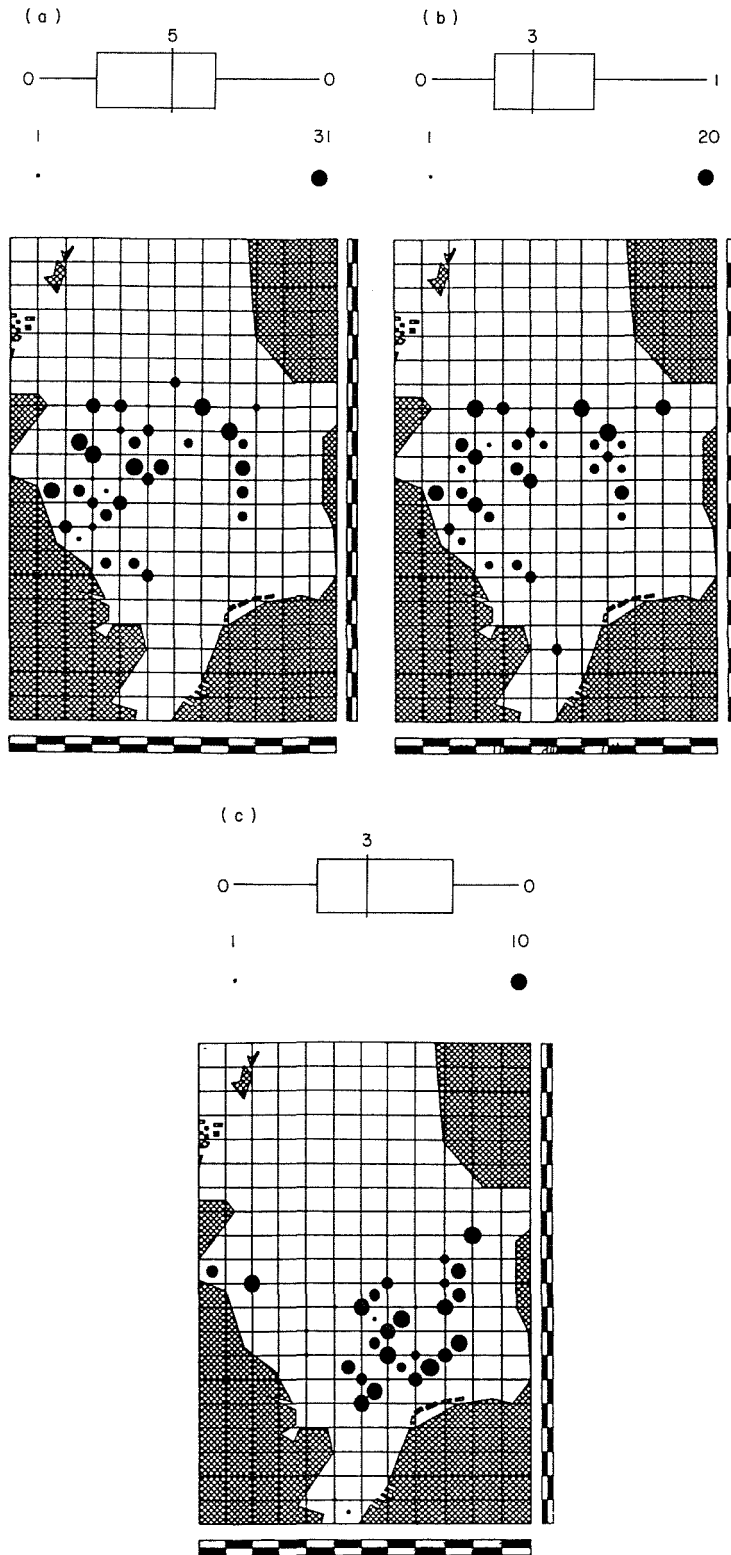
Figure 13. Log of total density of some important copepod families in the Central North Sea. (a) Zosimidae. (b) Idyanthidae. (c) Longipediidae. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed density (see text for details).
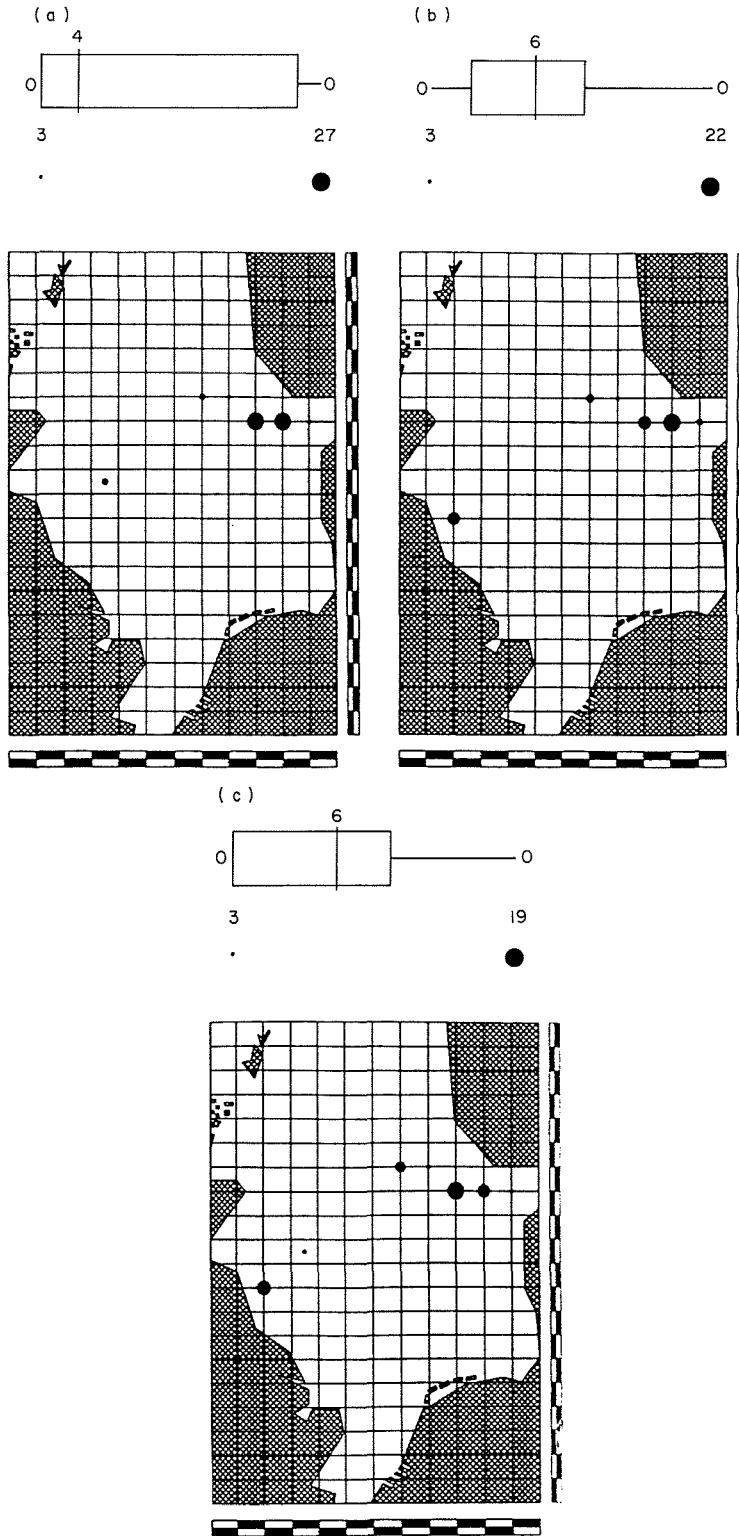
Figure 14. Log of total density of typical deepwater copepod families in the North Sea. (a) Ameiridae (Stenocopiinae). (b) Ancorabolidae. (c) Cerviniidae. Between the minimum and maximum values indicated under the box and whisker plot, the radius of the symbols is proportional to the log-transformed density (see text for details).

The averaged total copepod density per twin group is illustrated in Figure 15a. TWIN A is clearly separated by density which was about 4 to 10 times the mean density of the other groups (Table 3). The central twin groups TWIN B–D are very impoverished.
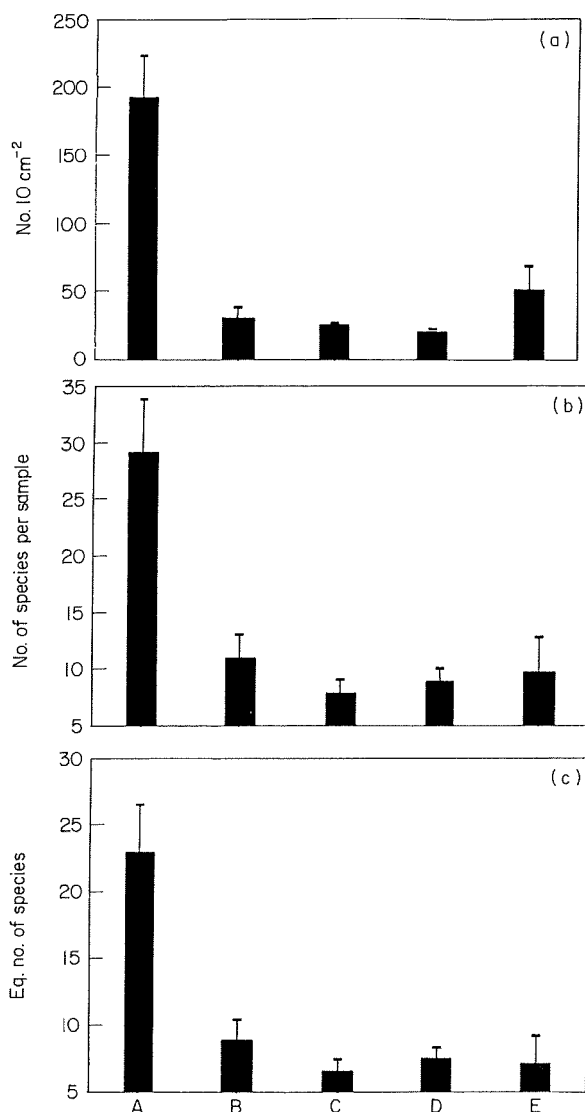
Table 3. Mean density (n. $10\,cm^{-2}$), number of species, diversity N_1, biomass ($\mu g.\ 10\,cm^{-2}$) and individual ash-free dry weight ($\mu g.\ ind.^{-1}$) of Copepoda per twin group.

	Density	No. of species	exp (H')	Biomass	Individual AFDW
Twin A	192	29.1	22.8	85.7	0.52
Twin B	30	10.9	8.9	28.6	0.77
Twin C	25	7.8	6.6	66.1	3.00
Twin D	19	8.9	7.5	32.1	1.57
Twin E	51	9.7	7.1	158.9	3.17

Figure 15. Averaged total density (a), number of species (b) and diversity N_1 (c) of Copepoda per twin group.
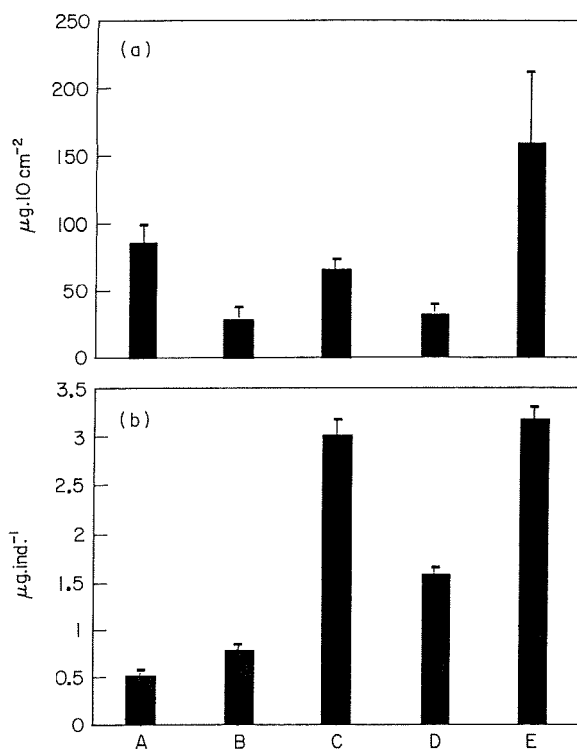
Figure 16. Averaged total biomass (a) and individual ash-free dry weight (b) of Copepoda per twin group.

Species diversity per $10\,cm^{-2}$ followed the trend of density (Figs 15b, c). The number of species in TWIN A was at least three times higher than in the other twin groups. The lowest mean diversity was recorded in transition group TWIN C.

Species abundances per twin group have been converted to biomass values (Fig. 16a) using the data of Table 2. Total biomass was highest in the deepwater twin group E, followed by TWIN A and TWIN C. Individual dry weight was also highest in TWIN E, but the difference with other groups was not as pronounced as for total biomass (Fig. 16b). The copepods of the three northern twin groups had the highest mean individual size, those of TWIN A by far the smallest, TWIN C and D had comparable individual AFDW values.

Ordination

Canonical correspondence analysis was performed on the five major twin groups A–E. Stations belonging to

clusters α and β were omitted in the analysis because granulometric data were not available. Environmental variables used are depth, latitude, longitude, percentage silt, percentage clay and median grain size of the sand fraction.

Silt percentage, clay content and median grain size (in Φ-units) are highly correlated (Fig. 17) and there seemed to be almost no correlation between these variables and depth. Latitude was more closely related to depth than to sediment characteristics; there is a general trend of increasing water depth to the north.
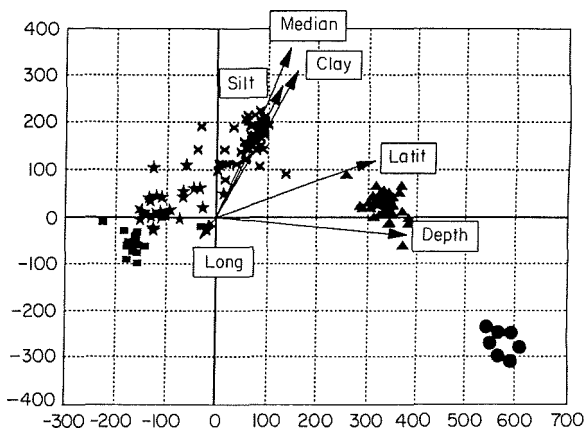

Figure 17. CCA ordination diagram of the five major twin groups based on copepod composition.

The identity of the five major twin groups is clearly expressed in the ordination diagram, with no overlapping between the respective station groups. The three southern twin groups A, B and C show a close correlation with the sediment and can be arranged along a gradient of decreasing grain size. The coarsest sediments are grouped in TWIN A, the finest in TWIN C. The position in the biplot of the northern station groups D and E is obviously related to latitude and to depth. Stations belonging to TWIN E are grouped together mainly because of their great depth and their high latitude; they are clearly separated from the TWIN D station group.

Discussion

The fauna

The percentage of new species recorded during the North Sea Benthos Survey is overwhelming and unexpected. Nearly 44% of the 278 species are new to science. A survey of the ecological literature on Harpacticoida of the Belgian–Dutch continental shelf produced a total number of 276 species. The number of species recorded in the area delimited for the Synopses of the British Fauna (including

the Irish Sea and bounded in the north and the west by the 200 m depth contour, in the south and east by the continental coastline from Brest to Bergen) is estimated at 850. The difference in species number can partly be explained by not having sampled the phytal environment which is known to harbour a species-rich community. It foreshadows an explosive increase in number of species as sampling effort increases. Bearing in mind the unexpected diversity in coarse sediments and the virtual lack of knowledge from the northern North Sea, the total number of benthic copepods harboured by North Sea sediments might safely be estimated at at least 1500 species.

Nematode/copepod ratio

Since Raffaelli & Mason (1981) made the attractive suggestion of using the ratio of freeliving nematodes to benthic copepods as a practical pollution indicator for sandy beaches, the literature on using meiobenthos in pollution monitoring has been fueled with controversy (see Lambshead, 1984 for review). Most authors have now abandoned the N/C ratio because it oversimplifies the complex responses of meiobenthos populations to the environment. The North Sea Benthos Survey provided the opportunity to assess the potential of the N/C ratio as a pollution indicator on a large geographical scale (Fig. 4a).

It is conceivable that meiobenthic populations are most highly subjected to anthropogenic pollution in the Southern Bight. Yet, the N/C ratio is remarkably low in this area, even if only interstitial copepods are included in the estimation of the N/C ratio, and the copepod distribution does not suggest that the southern North Sea is more polluted than the northern North Sea. The fact that there is almost an order of magnitude of disparity between the Southern Bight and the rest of the North Sea (Fig. 4b) makes it unnecessary to invoke pollution as an explanation. On the other hand the N/C ratio varies considerably in the central and northern North Sea, suggesting that nematodes and copepods are influenced independently by a complex suite of environmental parameters. Most likely, the different habitat requirements of nematodes and the two major groups of copepods in relation to the granulometry of the sediment account for this variability. Hence, it is impossible to apply adequately the N/C ratio once the study area is extended to habitats other than sandy beaches (Raffaelli, 1987).

Communities

The topography of the North Sea is an important factor in determining the pattern of water movements and thus the environmental conditions to which the animals and plants in the various areas are subjected. Adams (1987) recognized seven subdivisions of the North Sea by using certain
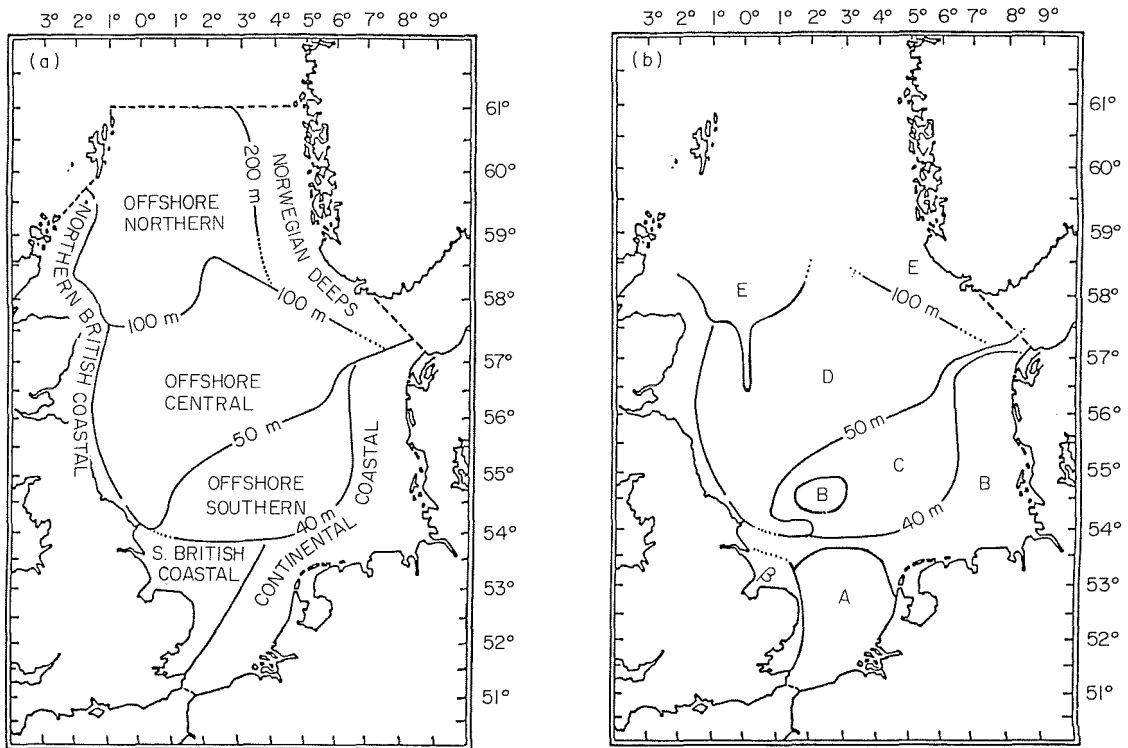
Figure 18. Comparison between Adams' (1987) primary subdivisions of the North Sea (a) and major twin groups (indicated by A to E) based on copepod composition (b).

depth contours and a combination of physical and biological properties of the water masses (Fig. 18a). Adams used the 40 m contour, which appoximately marks the boundary between stratified and well mixed water during the summer, the 50 m contour, which along part of its course coincides with northern flank of the Dogger Bank, the 100 m contour, along which the water masses of the Fair Isle–Orkney current tend to flow, and the 200 m contour, which marks the western boundary of the Norwegian Deeps.

There is a certain resemblance between Adams' (1987) subdivisions and the twin groups obtained in this study (Figs 18a, b). The shallow water cluster made up by TWIN A and B largely coincides with the "Continental Coastal Zone" whose offshore boundary follows the 40 m depth contour except in the southwest where it marks the eastern extent of the "South British Coastal Zone". The latter area was rather arbitrarily defined by Adams (1987) and was not recognized as such in the present study. It might nevertheless be related to cluster β which groups the river plume stations. The "Offshore Southern Zone" coincides with TWIN C except for the Dogger Bank proper and the Silver Pits which belong to TWIN B and TWIN D, respectively. This region lies between the 40 m and 50 m depth contours and its water column becomes stratified during the summer only. The "Offshore Central Zone" whose water mass is mainly North Atlantic in

origin, is delimited by the 100 m and 50 m isobaths in the north and south, respectively, and can almost be identified by TWIN D. In the west the depth varies from 50 to 80 m. Finally, the "Norwegian Deeps" coincide with TWIN E. The "Offshore Northern Zone" was not sampled during the North Sea Benthos Survey.

In contrast to nematodes (e.g. Vincx, 1989; Vincx *et al.*, 1990; Vanreusel, 1990), harpacticoids have been less frequently used to describe North Sea communities, the only comprehensive study being that by van Damme & Heip (1977). Three distinct zones (slightly modified by Govaere *et al.*, 1980) were classified in the Southern Bight according to their harpacticoid copepod composition: the coastal zone with a *Microarthridion littorale–Halectinosoma herdmani* community defined by large epibenthic and endobenthic species, the transition zone characterized by a *Leptastacus laticaudatus–Halectinosoma herdmani* community, and the open sea characterized by the *Leptastacus laticaudatus–Paramesochra helgolandica* community. The interstitial assemblage of the "open sea" as defined by these authors clearly coincides with the community described for TWIN A. The stability in time and space of this Southern Bight community is at least remarkable. Govaere *et al.*'s (1980) conclusions were based on samples collected from 1970 until 1975. Over a time span of two decades the only significant difference found is the dominance ranking of *P. helgolandica*; this

species seems now to be replaced by various other Para-mesochridae (Table 1). The coastal and transition zones were not recognized in the present survey but that might merely be a result from the choice of the sampling grid. The transition zone community can be identified with TWIN B (mixture of Leptastacidae and large burrowers) but did not extend as far south as shown by Govaere *et al.* (1980: Fig. 3).

The description of meiobenthos distribution in terms of communities is a well-established exercise and dates back to the thirties when Remane (1933) used meiobenthic species to define benthic communities in the Kiel Bay. Many of the subsequent studies (e.g. Por, 1964b; Coull & Herman, 1970; Soyer, 1970) attempted to apply the isocommunity concept introduced by Thorson (1957) for macrobenthic communities. This concept was based on the assumption that communities inhabiting the same type of bottom at similar depths are characterized by different species of the same genera, but replacing each other in accordance with the geographical regions. This hypothesis has not stood the test of time and the present survey clearly showed that depth and sediment type are not the only factors that structure harpacticoid communities. For example, the Southern Bight community inhabiting clean sandy bottoms is not found in similar deposits at similar depths in the entrance to the Skagerak. This might indicate that either a major physical variable was not measured, or that the species assemblage was affected by biological interactions that were not investigated. For example, grain size has often been regarded as the most significant parameter influencing the distribution of meiobenthos. This led Wieser (1959) to introduce a minimum critical grain size of approximately 200 µm as a barrier between interstitial sliders and burrowing species. Pennak (1950) on the other hand stated that the size of sand grains has no constant relationship to either distribution or number of organisms. The distribution of the interstitial families of Copepoda in the North Sea (Fig. 11) gives evidence that at least for the Leptastacidae grain size *per se* does not affect their distribution. The genera *Leptastacus* and *Paraleptastacus* which are generally regarded as interstitial sliders (Wells, 1986) do not seem to be affected by the amount of silt which might fill up the interstitial spaces of coarser sands, nor by the actual grain size of the sand fraction. The Leptastacidae are the only vermiform copepods whose distribution extends to the Central North Sea. One of the possible factors explaining this distribution pattern might be sought in their feeding biology. Live observations showed that their feeding strategy is rather different from typical grazing as displayed by many interstitial copepods (e.g. Cylindropsyllidae, Paramesochridae) and does not necessarily depend on sediment type since food particles are passively trapped in the mucus strands produced by the caudal glands. It also explains why Leptastacidae were sometimes found to live in co-existence with genuinely pelophilic harpacticoids.

It is conceivable that similar observations in the future will contribute to our understanding of the distribution patterns of the various copepod families. Sediment characteristics, depth and latitude are obvious variables to account for the structure of meiobenthic communities, however, the underlying biological reasons, which are of paramount importance, are still not well understood.

Acknowledgements

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