ANNEX 5

THE BENTHIC COMMUNITIES OF THE NORTH SEA: A SUMMARY OF THE RESULTS OF THE NORTH SEA BENTHOS SURVEY

1 GENERAL ASPECTS OF THE SURVEY

The biota living near, on, or in the sea floor are collectively called the benthos. Distinction is made between plants (phytobenthos) and animals (zoobenthos), living within the sediment (infauna) or moving about on its surface (epifauna). The infauna is split into categories according to size: macrobenthos (animals larger than 1 mm), meiobenthos (animals between 50 μm and 1 mm), and microbenthos (protozoans, fungi, bacteria, smaller than 50 μm). Most frequently the three fractions are defined methodologically based on the mesh sizes of the sieves used to separate the specimens from the sediments (1 mm and 50 μm).

The zoobenthos of the southern and central North Sea was sampled during the North Sea Benthos Survey executed in April-May 1986. Macro- and meiozoobenthos were sampled at 197 stations covering the ICES grid from 51°N to 58°N and from 2°30'W to 8°15'E (see Figure 1). At each of these stations preferably three box cores and one van Veen grab, but sometimes only Van Veen grabs, were taken. The complete list of replicates, dates, samples and stations has been reported to ICES (Anonymous, 1986) and is available from Dr C. Heip on request. Additional samples for epifauna were taken with a beamtrawl or dredge.

Before sampling, two intercalibration exercises had been performed. The first exercise aimed at intercomparison of the sampling gear and processing methods (sieving, washing, fixation, etc.). The results clearly showed that comparisons of macrofauna data are very difficult and that standardization of gear and processing, as well as taxonomic intercalibration, will be essential for future comparative studies. The second intercalibration exercise showed the necessity of a standardized method of estimating the ash-free dry weight of macrobenthic organisms. The results of both exercises have been presented to ICES (Heip *et al.*, 1985; Duineveld and Witte, 1987).

Most of the stations were analysed for macrofauna biomass, density and species composition, for meiofauna density and copepod species composition, for epifauna composition, density and biomass, for sediment grain sizes, protein content, plant pigment content, organic matter and a series of heavy metals: Zn, Pb, Cd, Ni, Cr, Co, Cu, Mn and Fe.

Data on macrofauna and epifauna distribution, density and biomass have also been gathered by the Aberdeen laboratory of the Scottish Office, Agriculture and Fisheries Department (formerly the Department of Agriculture and Fisheries for Scotland) from the northern North Sea during eight cruises from 1980 to 1985, always in spring or early summer. The area covered extends between 56°15'N and 60°45'N and 3°30'W and 7°30'E. A total of 119 stations were sampled for macrobenthos, and 152 stations for epibenthos (Basford *et al.*, 1990).

The analyses presented for the macrofauna are based on samples from 177 stations of the ICES North Sea Benthos Survey (NSBS) (of which 63 were sampled by two different laboratories), and on samples from 61 stations in the northern North Sea lying on the ICES grid, 7 of which overlap with NSBS stations. Thus, species composition, density and diversity have been determined at 231 stations, and total biomass at 214 stations. For the analysis of the infaunal assemblages, stations sampled twice were treated as different stations. For the spatial trend analysis of total density, total biomass and diversity, the average of the values of the two laboratories was used on stations sampled twice.

The meiofauna at 171 stations from the NSBS was analysed, of which 134 were sampled by two or more laboratories.

The results presented in this paper for the epifauna are a summary of the separate analyses in the Dutch, German and Danish sectors of the North Sea (Duineveld *et al.*, 1991; Künitzer, 1989, 1990a) and in the northern North Sea (Basford *et al.*, 1989, 1990).

The macrofauna and meiofauna data have been collected in a file which was distributed to the participants and which will be made available to interested scientists as part of a special volume in the ICES Cooperative Research Report series on the distribution of species in the North Sea.

2 THE MACROFAUNA

2.1 Abundance of species

Taxonomic problems were solved during workshops held on Helgoland in 1988 (Heip and Niermann, 1988) and Texel in 1989. Ultimately, a total of 709 macrofauna species (including some non-determined but distinct species or species-groups) were determined.

The distribution of individual species varies, some species being more cosmopolitan than others. Species with more restricted distributions can be used to describe the assemblages that inhabit specific areas. In the North Sea some species, e.g. *Spiophanes bombyx, Pholoe* sp., *Goniada maculata* and *Amphiura filiformis* (see Figure 2) occur widely at nearly all depths and in a wide variety of sediments.

Most species are either distributed south of a parallel to the northern edge of the Dogger Bank (50 m depth contour) or north of it. Species with a southern distribution may also occur in the central North Sea but never north of the 100 m contour at 57-58°N: examples are *Ophiura albida, Echinocardium cordatum, Chamelea gallina* and *Tellimya ferruginosa* (see Figure 3). Some of these species occur mainly in the central North Sea, such as *Chaetoderma nitidulum* and *Ampelisca tenuicornis* (not shown here). Species with a northern distribution were rarely found south of the 50 m depth contour, e.g., *Ophiura affinis, Montacuta substriata, Antalis entalis* and *Minuspio cirrifera* (see Figure 4).

The distribution of species also seems to be determined by the sediment type. On coarse sediments *Echinocyamus pusillus, Pisione remota, Glycera lapidum* and *Spisula elliptica* occur all over the North Sea (see Figure 5), while *Sphaerosyllis bulbosa* and *Glycera celtica* are restricted to coarse sediments along the Scottish coast, and *Polycirrus medusa* and *Phoxocephalus holbolli* are restricted to coarse sediments in the south and east of the North Sea (see Figure 6). On fine sands *Aricidea minuta, Bathyporeia elegans* and *Ophelia borealis* occur all over the North Sea (see Figure 7), but *Bathyporeia guilliamsoniana, Fabulina fabula, Urothoe poseidonis* and *Sigalion mathildae* were only found in the southern North Sea on fine sand at depths less than 30 m (see Figure 8). Sediments of muddy fine sand occur mainly in the southern North Sea at 30-50 m depth and in the west of the northern North Sea (see Figure 9). Species with a wide distribution on this type of sediment are *Eudorella truncatula, Glycinde nordmanni* and *Harpinia antennaria* (see Figure 10). *Callianassa subterranea, Nucula nitidosa, Chaetopterus variopedatus* and *Synelmis klatti* are restricted to the southern North Sea (see Figure 11) and *Leucon nasica, Thyasira ferruginea, Laonice sarsi* and *Molgula* sp. are restricted to the northern North Sea (see Figure 12).

Stations were grouped according to their similarity in species composition using TWINSPAN analysis (Hill, 1979). The analysis was run twice, firstly, solely with binary (presence or absence of a species) data and, secondly, taking the actual abundances of the species into account. Both classifications gave about the same results. Coherent assemblages of species were recognized covering large areas of the North Sea. The eight groupings obtained after three successive steps of division of the stations (first, second and third dichotomy, Figure 13) can be summarized into seven faunal assemblages (Figure 14).

At the first dichotomy, stations were separated along the 70 m depth contour into stations to the north (indicator species: *Spiophanes kroyeri, Minuspio cirrifera, Myriochele* sp.) and stations to the south of it (indicator species: *Echinocardium cordatum, Magelona* sp., *Bathyporeia elegans*), showing that the fauna north of the 70 m depth contour is different from the fauna south of it.

At the second dichotomy among the stations south of the 70 m depth contour, those on coarser sediment (group I, no indicators) were separated from those on fine sand (group II, indicators: *Amphiura filiformis, Pholoe* sp., *Phoronis* sp., *Mysella bidentata, Harpinia antennaria, Cylichna cylindracea, Nephtys hombergi*). Among the northern stations those along the Scottish coast on coarse sediment (group IV, indicators: *Sphaerosyllis bulbosa, Hesionura elongata*) were separated from the other stations in the central and northern North Sea (group III, indicators: *Levinsenia gracilis, Thyasira* sp.).

At the third dichotomy the eight final groupings were obtained. The stations northwest of Denmark (group Ib, indicators: *Aonides paucibranchiata, Phoxocephalus holbolli, Pisione remota*) were separated from the other stations on coarser sediment (group Ia, indicators: *Nephtys cirrosa, Echinocardium cordatum, Urothoe poseidonis*). The stations on fine sand were divided into those on muddy fine sand south of the Dogger Bank (group IIa, indicators: *Nucula nitidosa, Callianassa subterranea, Eudorella truncatula*) and those on fine sand in the central North Sea at 50-70 m depth (group IIb, indicators: *Ophelia borealis, Nephtys longosetosa*). Stations deeper than 70 m were divided along the 100 m depth contour into those of the northern North Sea (group IIIb, indicators: *Minuspio cirrifera, Thyasira* sp., *Aricidea catherinae, Exogone verugera*) and those of the central North Sea at about 70-100 m depth (group IIIa, no indicators).

Total abundance shows a weak gradient with latitude. There is a tendency for density to increase towards the north (Figure 15), but the trend is less clear and less linear than for biomass and diversity. In a model where, in addition to latitude, chlorophyll-*a* content and median grain size were used as predictors, sediment characteristics accounted for the larger part of the variance.

The variation in total density within the assemblages (Figure 13) is too high to show clear differences between assemblages. Densities seem to be lower in the assemblages on shallow coarse sediment (groups Ia and Ib). They seem to be highest in group IIIb but at stations in this group a finer mesh of 0.5 mm mesh size was used, and therefore densities are higher than they would have been by using a 1 mm mesh and are not directly comparable to the densities in groups I and II.

2.2 Biomass

The biomass was determined as ash-free dry weight (AFDW) (organic matter) for the four main taxonomic categories of the macrofauna: Mollusca, Polychaeta, Crustacea and Echinodermata. The distribution maps of biomass are shown in Figures 16-17.

The average total biomass over all stations is 7 g AFDW/m^2. Rachor (1982) summarized available biomass values, and estimated the biomass as 3.2 g AFDW/m^2. This value corresponded to the stock as used in the North Sea model of Andersen and Ursin (1977), but was about twice as high as biomass values used by Steele (1967, 1974)

Total biomass (after log transformation) shows a clear and significant trend with latitude. This is shown in Figure 18 where for each degree latitude the mean $\pm$ standard error of the biomass is expressed. Towards the north, biomass decreases considerably. The major shift is not caused by one major taxonomical group overtaking another as one goes north (Figure 19). Rather, the same trends seem to be operating in the different groups.

Apart from latitude, sediment composition (logarithm of fraction smaller than 62 μm) and chlorophyll-*a* content of the sediment also influence the total biomass, and the biomass of most separate groups, significantly (Table 1). But in the separate regressions, latitude accounts for a larger part of the variance than sediment. Also depth shows an effect on the biomass values in the separate regressions, but in all analyses with both depth and latitude but one, only the regression coefficient of latitude remains significantly different from zero.

For biomass of molluscs, the model with latitude and chlorophyll-*a* accounts for a smaller proportion of variance (squared multiple r = 0.100) than the model with silt content and chlorophyll-*a* as predictors (squared multiple r = 0.147). However, especially with silt content of the sediment, the relation may be non-linear.

The relation between biomass and silt content, as clarified by distance-weighted least squares smoothing (McLain, 1974; Wilkinson, 1988), is shown in Figure 20. The locally weighted smooth line clearly suggests that biomass increases with silt contents between 0.1 and 1%, remains relatively uncorrelated for silt contents between 1 and 10%, and decreases with silt content for very fine sediments (silt content >10%). The relationship of (log transformed) total biomass with (log transformed) chlorophyll-*a* content of the sediment is relatively linear (Figure 21).

The mean weight of the individuals, obtained by dividing total biomass by total density in each sample, also shows a very clear gradient with latitude (Figure 22). Towards the northern part of the North Sea, individual size becomes considerably smaller: the difference in mean weight is much more than one order of magnitude. Adding sediment as a predictor variable does not increase the squared multiple r (0.371 for the model with latitude and chlorophyll-*a*, 0.364 using only latitude). The results are biased because the samples obtained by the Aberdeen laboratory were sieved with a smaller mesh size (0.5 mm instead of 1 mm), but the trends also exist for the other data.

The variation in mean biomass per assemblage (Figure 13) is very high. The mean biomass is lowest in the northern North Sea (groups IIIb and IV). The biomass increases towards the shallower southern North Sea and reaches the highest values south of the Dogger Bank (groups Ia and IIa).

2.3 Diversity

The average number of species per assemblage (Figure 13) gradually increases from the assemblages shallower than 30 m (groups Ia and Ib) to the assemblages in 30-70 m depth (groups IIa and IIb) and is highest in the assemblages in areas deeper than 70 m (groups IIIa and IIIb). Towards the Scottish coast (group IV), species number decreases again.

Diversity, as measured by Hill's diversity index N_1 (=exp(H')), shows a significant trend with latitude (Figure 23). Towards the north of the North Sea, diversity increases considerably. In addition to latitude, both depth and longitude show an effect. Other environmental variables have no clear influence. The 'best' model has both latitude and longitude as predictors. Other diversity measures (N_0, N_2, N_∞) show the same trend (they are strongly correlated) but are subject to more variability then N_1.

The effect of different sample sizes on the estimation of diversity indices was not very important for N_1. After standardization to 50 individuals, its relation with latitude is not too different from the relationship shown in Figure 23. In accordance with the conclusions of Soetaert and Heip (1990), the effect is more pronounced on N_0, the number of species. Here much variability is taken away by standardization, and a very clear relationship with latitude ensues (Figure 24). Latitude, longitude and depth show an effect on the standardized number of species, and all regression coefficients remain significantly different from zero in a multiple regression.

3 THE MEIOFAUNA

3.1 Abundance of Species

At nearly all stations, nematodes are the dominant meiofauna group (Figure 25). Their densities range from 61 to 4167 ind./10 cm^2. The average density over all stations was 759 ind./10 cm^2. They become especially dominant from 54°N, although there is no trend in nematode density with latitude (Figure 26). Nematode species have not been determined until now.

Only in the Southern Bight are copepods sometimes as numerous or more numerous than nematodes (Figure 27). A total number of 278 species of copepods was found, belonging to 105 genera and 22 families. 121 species are new to science! The total number of species known from the North Sea has doubled due to the NSBS. It can be estimated that at least 1500 species of benthic copepods exist in the North Sea.

Since Raffaelli and Mason (1981) made the attractive suggestion to use the ratio of free-living nematodes to benthic copepods as a practical pollution indicator, the literature on using meiofauna in pollution monitoring has been fueled with controversy (see Lambshead, 1984, for review). Most authors have now abandoned the nematode/copepod ratio because it oversimplifies the complex responses of meiofauna populations to the environment. The North Sea Benthos Survey provided the opportunity to assess the potential of the nematode/copepod ratio as a pollution indicator on a large geographical scale (Figure 28).

It is conceivable that meiofaunal populations are most highly subjected to pollution in the Southern Bight. Yet, the nematode/copepod ratio is remarkably low in this area, 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 (Figure 28) makes it unnecessary to invoke pollution as an explanation. On the other hand, the nematode/copepod 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.

The distribution of Kinorhynchs is clearly related to the median grain size of the sediment (Figure 29). The genera Echinoderes and Semnoderes only occur in sandy sediments and were only found in the Southern Bight and in the entrance of the Firth of Forth. The genera Pycnophyes and Kinorhynchus were recorded from the central North Sea and are largely confined to the eastern part. The same area is also characterized by the presence of larval Priapulids.

Copepod density and diversity decrease with latitude (see Figures 30 and 31). The highest value is 181 ind./10 cm^2 in the Southern Bight against a minimum of 18 ind./10 cm^2 in the Norwegian Deeps. Biomass decreases until 57°N, but then increases again (Figure 32). Average individual weight increases with latitude (Figure 33).

The larger size of copepods in the north is due to the gradual replacement of interstitial, small species by epibenthic, larger species. The mean weight of the northern species is nearly three times higher than that of the southern species. The combination of a large number of small individuals in the south and a small number of large animals in the north results in the two-peaked biomass curve.

While a TWINSPAN analysis on the basis of the major taxa of the meiofauna did not permit a delimitation of any meaningful groupings, a TWINSPAN analysis of the copepod data demonstrates the existence of five large groupings (see Figures 34 and 35). In the first dichotomy, the deep-water species are separated from the shallow-water species. The separation between the two groups coincides with a southeast-northwest boundary. Characteristic deep-water species are *Anoplosoma sordidum* and *Cerviniopsis clavicornis*; characteristic shallow-water species are *Leptastacus laticaudatus* and *Paraleptastacus espinulatus*.

The second dichotomy of the deep-water cluster results in two groups. TWIN D is a heterogeneous cluster of 48 stations situated between the Norwegian Deeps and the Scottish coast. Important families are Cletodidae, Zosimidae and Idyanthidae, which co-occur at nearly all stations.

TWIN E corresponds to the northeastern part of the area (Norwegian Deeps) and consists of stations with depths between 84 and 100 m with fine to medium sand. Dominating families are the Cletodidae (with different genera than in TWIN D) and Ancorabolidae. A similar fauna was found in isolated stations from the Devil's Hole (91 m) and Farne Deep (107 m).

Within the shallow stations, three groups are distinguished. TWIN A is the most characteristic assemblage in the North Sea, with 22 extremely diverse stations in the Southern Bight up to 53.5°N. The area consists of fine to coarse sands with a low silt content. Copepod densities range from 24 to 651 individuals per 10 cm^2. Indicator species are *Kliopsyllus holsaticus*, *Leptopontia curvicauda* and others. These species live in the interstitial areas to which they have become adapted through miniaturization of the body or by becoming wormlike. Nearly half of the species found here are new to science. This community appears to be unique for the North Sea, although similar sediment types, i.e., sands with a median grain size of 250-300 μm, exist elsewhere.

TWIN B coincides with the eastern coastline of the central North Sea, extending from the Terschelling Bank to the entrance of the Skagerrak in the east, stations on the Dogger Bank and stations north of the Wash between 53°N and 54°N in the west. The stations contain fine to very fine sand with a low amount of silt and clay. The fauna is characterized by a mixture of minute interstitial forms (Leptastacidae and some Ectinosomatidae and Ameiridae) and large burrowing species (fusiform Ectinosomatidae and Ameiridae).

TWIN C reflects a transition assemblage between the coastal Ectinosomatidae-Leptastacidae assemblage and the deep-water community TWIN D. This group consists of 51 stations and is impoverished in terms of both densities and species number. Interstitial copepods are completely absent. The fauna consists of large silt-living species belonging to the Diosaccidae, Laophontidae and Ameiridae.

An ordination using canonical correspondence analysis (CCA) with the environmental variables depth, silt and clay content, and median grain size and with longitude and latitude shows that all sediment characteristics are significantly correlated (Figure 36). There is almost no correlation between these variables and depth. Latitude is more closely related to depth than to sediment characteristics.

The identity of the five major twin groups is clearly retained in the ordination diagram. The three southern groups, A, B and C, show a close correlation with the sediment and can be arranged along a gradient of decreasing grain size, with the coarsest in A and the finest in C. TWIN groups D and E cluster with depth and latitude.

4 THE EPIFAUNA

Basford *et al.* (1989, 1990) distinguished four assemblages in the northern North Sea. On the stations on better sorted, coarser sediments, Group 1 (characterized by Porifera) occupies shallower stations with a slightly lower carbon content than those in Group 2 (represented by tunicates and the crustacean *Spirontocaris lilljeborgi*). Stations on finer sediments can be divided into Groups 3 and 4 according to depth. Group 3 is characterized by *Pagurus bernhardus*, *Crangon allmani*, *Spatangus purpureus* and *Colus gracilis*, Group 4 by the sea-pen *Pennatula phosphorea*.

The Dutch, German and Danish sectors of the North Sea can also be divided into four regions (Figure 37): north of the Dogger Bank, the Dogger Bank, the Oyster Ground, and the Southern Bight (Duineveld *et al.*, 1991). The distribution of the epifauna is determined by depth and sediment characteristics. South of 56°30'N latitude, the biomass of the epifauna has comparatively high values around the Dogger Bank, on the southern border of the Oyster Ground, and along the Dutch coast. In the southern North Sea echinoderms make up most of the biomass, whereas on the Dogger Bank bryozoans and in the central North Sea anthozoans rank highest.

5 DISCUSSION

The main patterns of macrobenthic species distributions show that the bottom fauna of the North Sea is composed of northern elements, that do not extend further south than the north of the Dogger Bank, and southern elements going not further north than the 100 m contour. Northern and southern species therefore mix in the central North Sea and northern and southern assemblages overlap along the 70 m contour. The occurrence of cold water species north of the Dogger Bank and of warm water species in the southern North Sea was already recognized by Ursin (1960), Kirkegaard (1969) and Petersen (1977). None of these authors however showed that the southern species occurred as far north as the 70-100 m depth contour.

The classification of the benthic fauna into assemblages is a matter of scale. The analysis shown here has been carried out on a broad scale and shows the differences in species composition within the large area of the North Sea. If the benthic infauna of certain parts of the North Sea is analysed, as has been done for the area off the coast of Northumberland (Buchanan, 1963), the Fladen Ground (McIntyre, 1961), the German Bight (Salzwedel *et al.*, 1985), the northern North Sea (Eleftheriou and Basford, 1989), the vicinity of the Ekofisk and Eldfisk oilfields (Gray *et al.*, 1990) or even for a limited area within the area covered by the NSBS (Künitzer, 1990a; Duineveld *et al.*, 1991), the seven assemblages described are divided further. The question is in how much detail we would like to look at small-scale distribution.

The classification of assemblages showed that macrobenthic assemblages were separated by the 30 m, 50 m, 70 m and 100 m contours. Jones (1950) already showed that there is a correlation between the distribution of the animal communities and certain physical factors. Biological factors, such as relationships with other organisms, the presence of suitable food animals for predators, parasitism, commensalism, etc., seem to be of secondary importance.

The separation of the macrobenthic infauna into northern and southern components along the 70 m contour might be a result of the current pattern in the North Sea. Most of the Fair Isle-Orkney inflow of Atlantic water moves eastwards at about 57°30'N and only part of it travels southwards down the coast of England (Lee, 1980). The shallow southern North Sea is, in contrast to the deeper northern areas, influenced by the English Channel which influence extends up to the Dogger Bank. The northern North Sea and part of the central North Sea is, therefore, influenced by a different type of water than the rest of the North Sea.

Another factor determining the distribution of assemblages is the annual variation of temperature in bottom waters. Large areas of the southern North Sea are not stratified during most of the year (Tomczak and Goedecke, 1962), while in the stratified areas north of the Dogger Bank summer temperatures are less than 7°C. In winter the southern North Sea is colder (4°C) than the rest of the North Sea (5-7°C). These differences in temperature north and south of the Dogger Bank might explain why cold water species do not go farther south than the Dogger Bank. The explanation for why warm-water species are not found below 70-100 m depth, although they survive the cold summer temperatures in the central North Sea, might lie in the general current pattern.

A third factor which may cause the differences among the macrofaunal assemblages is the availability of food. Large stocks of pelagic copepods only develop in the northern North Sea. They consume the summer production of phytoplankton (Fransz and Gieskes, 1984). The faecal pellets do not reach the deep water, being recycled higher in the water column (Krause, 1981), thus limiting this source of food to the benthos during the summer months. This could explain the low biomass of infauna in the northern North Sea. Farther south, main parts of the phytoplankton production reach the bottom, resulting in better food supply to the benthos, especially in summer months. Already Buchanan (1963) stated that a relevant ecological factor for benthic assemblages can be found in the quality of the suspended matter, together with the speed and nature of its flow over the bottom.

The separation of macrofaunal assemblages along the 30 m depth contour can be caused by several environmental factors. No thermal stratification of the water column develops in summer months in the shallow coastal areas, whereas below 30 m depth a stratification may develop (Tomczak and Goedecke, 1964). Strong tidal currents exist in the shallow coastal zones and the wave action reaches the bottom, stirring up fine particles of sediment and organic matter. These areas therefore consist of sand and gravel, while in areas of 30 to 50 m depth the deposit usually consists of muddy fine sand. As a consequence of these environmental differences, the food availability must be different resulting in different feeding types.

In addition to depth, the sediment structures the distribution of assemblages. Depth and sediment are interrelated since coarser sediments usually occur in shallower areas. As shown in this study, several macrobenthic species occur on all types of sediment, while other species are restricted to sediments of a certain grain size. This holds for all groups: polychaetes, molluscs, echinoderms and crustaceans.

In areas where the macrobenthos assemblages seem to be determined by different water masses, the sediment might be of less importance in structuring the assemblages. In areas where the water masses are more uniform, the sediment becomes the structuring factor.

For copepods it appears that sediment characteristics are the main determinants to explain their distribution in the relatively shallower parts of the southern North Sea. In the northern parts and in stations deeper than 80 m, depth is the main factor explaining copepod distribution. In general, copepods show a clear response to the known environmental variables.

Sediment grain size has often been regarded as the most significant parameter influencing the distribution of meiofauna. 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 (Figure 38) in general confirms the importance of sediment grain size. However, 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 investigated in their feeding biology. Huys (in press) described the presence of large glands which produce long mucus strands investigated at the rear end of the body in which high numbers of rod-shaped bacteria, small diatoms and unidentifiable debris are trapped.

Thus, although depth and sediment type are important in structuring the harpacticoid assemblages, they are not the only factors that structure harpacticoid communities. 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.

Because of the greater influence of depth on epifaunal assemblages, the epifaunal communities seem to more closely reflect hydrographic subdivisions of the North Sea, as proposed by Glémarec (1973). The influence of the different water masses has also been shown by Frauenheim *et al.* (1989). In summer the North Sea could be divided in two main clusters situated to the north and to the south of the Dogger Bank. In winter the two main clusters divide the North Sea into a western and an eastern part. They concluded that these differences of epibenthos characteristics are correlated with seasonal changes in water body distributions.

The epifauna on the Dogger Bank and the central North Sea is dominated by filter-feeding species, in contrast to the scavenging or predating epibenthic species in the southern North Sea. This could point to different ways in which energy is transferred through the benthic system.

The benthic assemblages seem to reflect general environmental differences within the North Sea which should be taken into account when assessing the effects of anthropogenic changes in the North Sea. These changes might be different among the various assemblages.

Also for the interpretation of the trends in total biomass, diversity and total density of the macrofauna with latitude, it is useful to consider the general trend of both water depth and longitude with latitude. Towards the north, the North Sea becomes deeper. And, while north of 58°N latitude almost all stations sampled are situated to the west of 2°E longitude, the southern North Sea (i.e., south of 54°N latitude) is situated east of 2°E longitude. For biomass, density and individual weight, latitude invariably explained more variation than depth.

Thus, latitude shows the effects of both depth and another, unfortunately unknown, variable. The correlation between benthic biomass and chlorophyll-*a* content of the sediments certainly indicates a link with surface productivity. But the differences in primary production cycles in the northern and southern North Sea possibly have larger effects than a different chlorophyll-*a* content of the sediments. It is also conceivable to think of effects of fisheries, but these are difficult to quantify.

The effect of longitude on diversity possibly shows the importance of current patterns on species distributions. Several species (e.g., *Leucon nasica* and *Thyasira ferruginea*) are restricted to the western part of the northern North Sea.

In addition to latitude, depth and longitude, sediment characteristics (silt content, median grain size) account for a major part of the variance.

The distribution of species and trends in biomass, diversity and density may in general be explained by the following factors: current patterns and water masses, depth and stratification, surface productivity, sediment distribution and bottom shear stress, fisheries and other human impact, and the history of the North Sea. A comprehensive interpretation of the observed trends in terms of these factors has not been attempted further than the observations mentioned above.

This analysis of the North Sea Benthos Survey results is still preliminary. Lack of funding has prevented a thorough final analysis, including the spatial correlation with environmental variables, the distribution patterns of individual species, the analysis of the nematodes, a comparison between the meio- and the macrofauna, and a joint analysis of all epibenthic data obtained during the North Sea Benthos Survey.

As an example of the kind of information that will be published in a volume of the ICES Cooperative Research Report series, a series of figures representing species distributions is given in Figures 2-12.

More detailed discussions of the results can be found in Künitzer (1989, 1990a,b); Künitzer *et al.* (1992); Heip *et al.* (1990, 1992); Huys *et al.* (1990, 1992); Basford *et al.* (1989, 1990); Eleftheriou and Basford (1989); and Duineveld *et al.* (1991).

The results can be used to identify specific areas for more detailed studies (e.g., processes such as bentho-pelagic coupling, or regions with specific features such as the Dogger Bank). The results should also be compared with data on (demersal) fish production. Finally, the results can be used to identify specific areas for a more specified monitoring programme (such as the Monitoring Master Plan of the North Sea Task Force).

The Benthos Ecology Working Group recommends that this type of synoptic mapping be repeated at a certain interval (e.g., every 20 years).

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Table 1 Multiple linear regression of (log transformed) biomass and environmental variables.

	latitude	chl-*a*	log(silt)	depth
Total	*	*	*	
Mollusca		*		*
Polychaeta	*	*	*	
Echinodermata	*	*		
Crustacea	*		*	
Remainder		*		

* indicates that the environmental variable has a significant (5%) independent contribution to the explanation of the dependent variable in the 'best' model (i.e., in the model with all partial regression coefficients significantly different from zero and the highest squared multiple r).

chl-*a* = chlorophyll-*a*.

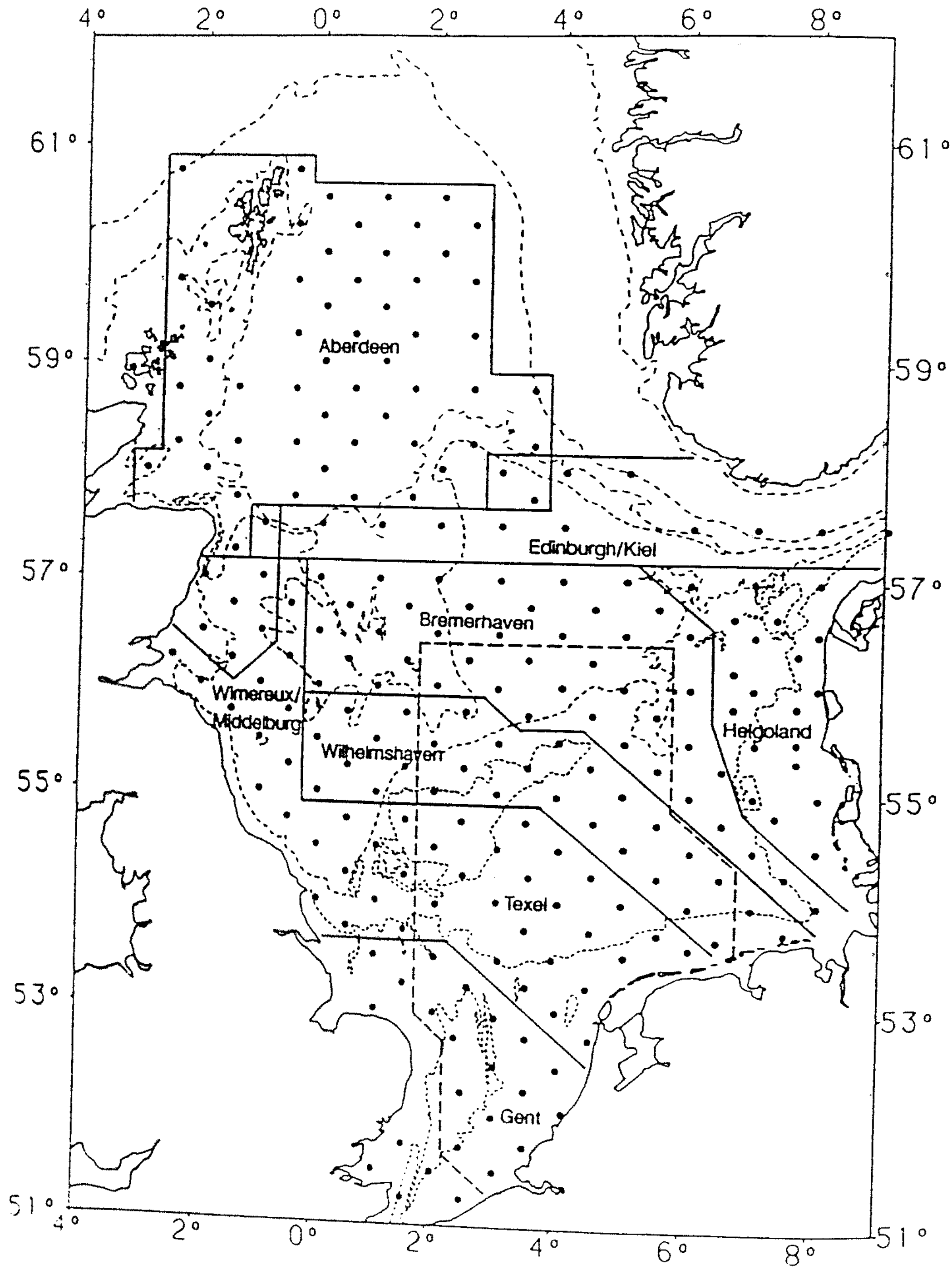


Figure 1 Stations sampled by participants in the North Sea Benthos Survey (NSBS) in 1986. Stations in the northern North Sea were sampled by the Marine Laboratory, Aberdeen, between 1980 and 1985.

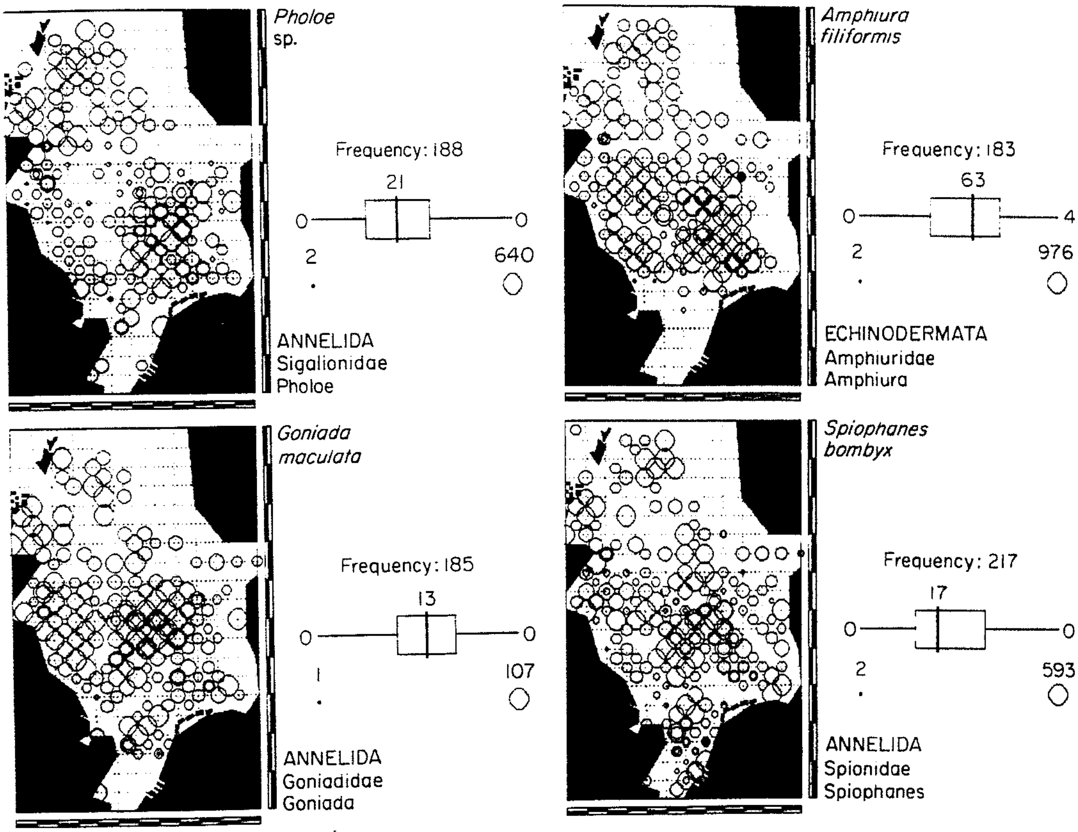


Figure 2 Distribution and density of species with a wide occurrence in the North Sea.

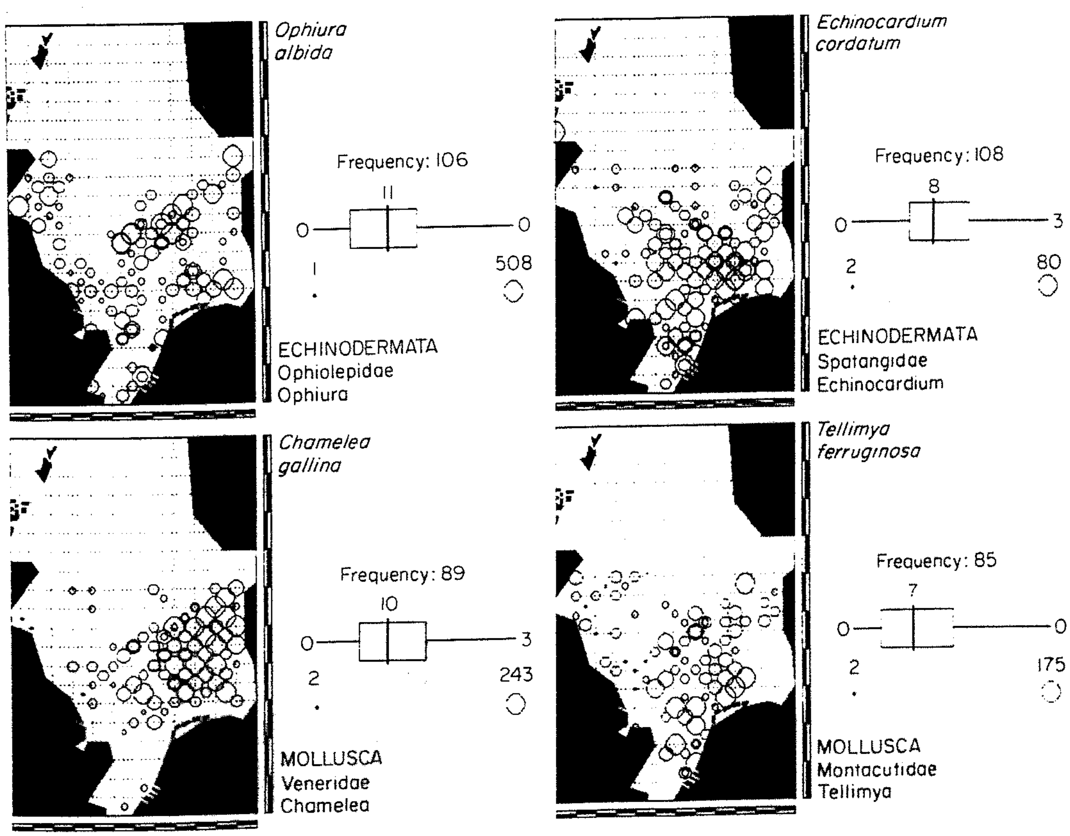


Figure 3 Distribution and density of species with a southern occurrence in the North Sea.

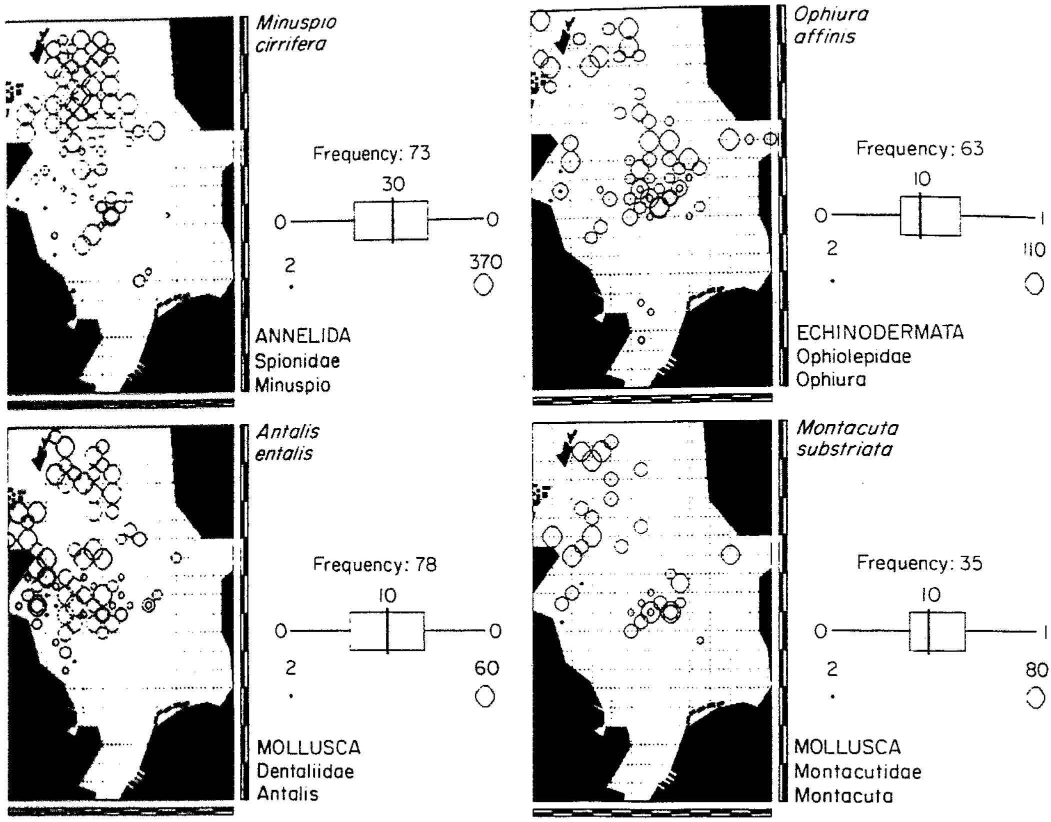


Figure 4 Distribution and density of species with a northern occurrence in the North Sea.

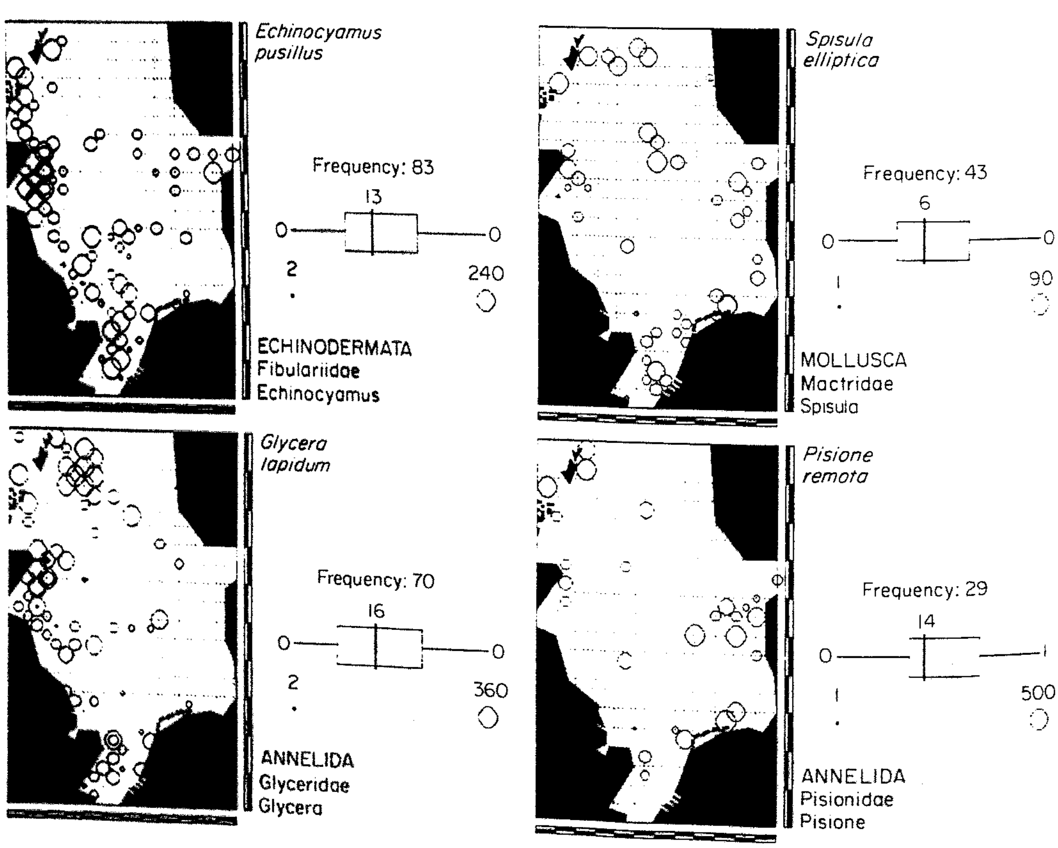


Figure 5 Distribution and density of species with a wide occurrence on coarse sediments in the North Sea.

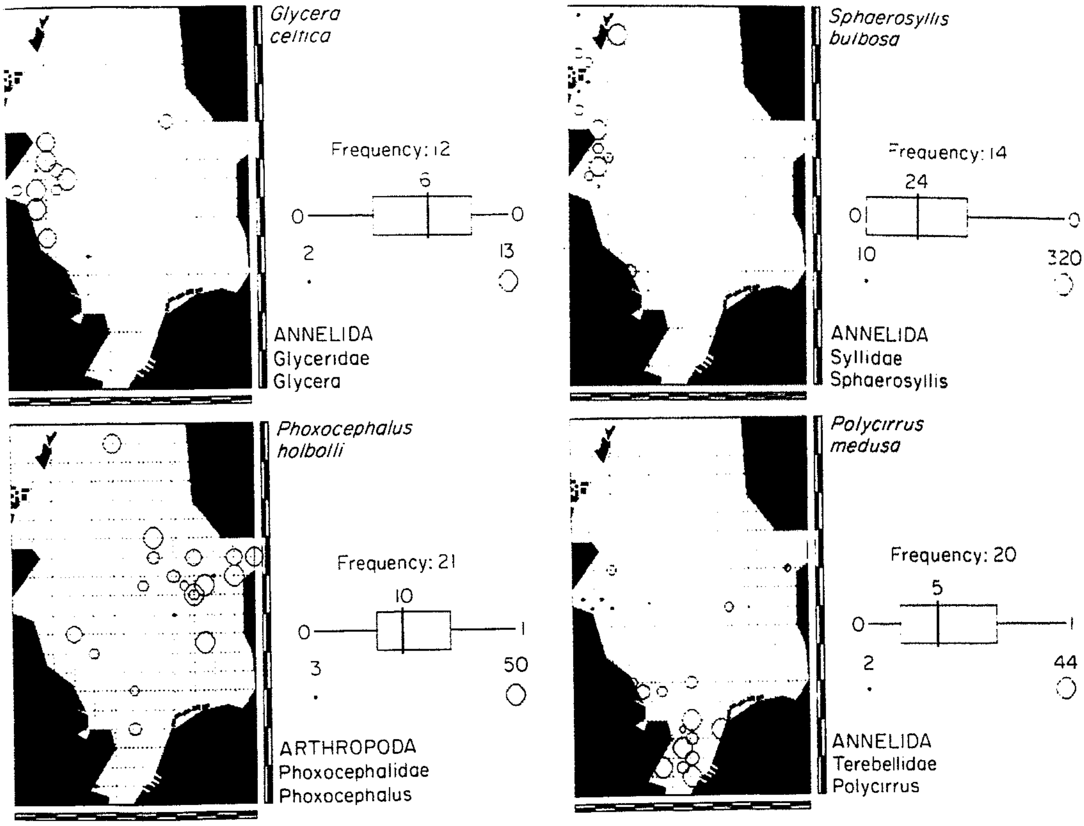


Figure 6 Distribution and density of species with a restricted occurrence on coarse sediments in the North Sea.

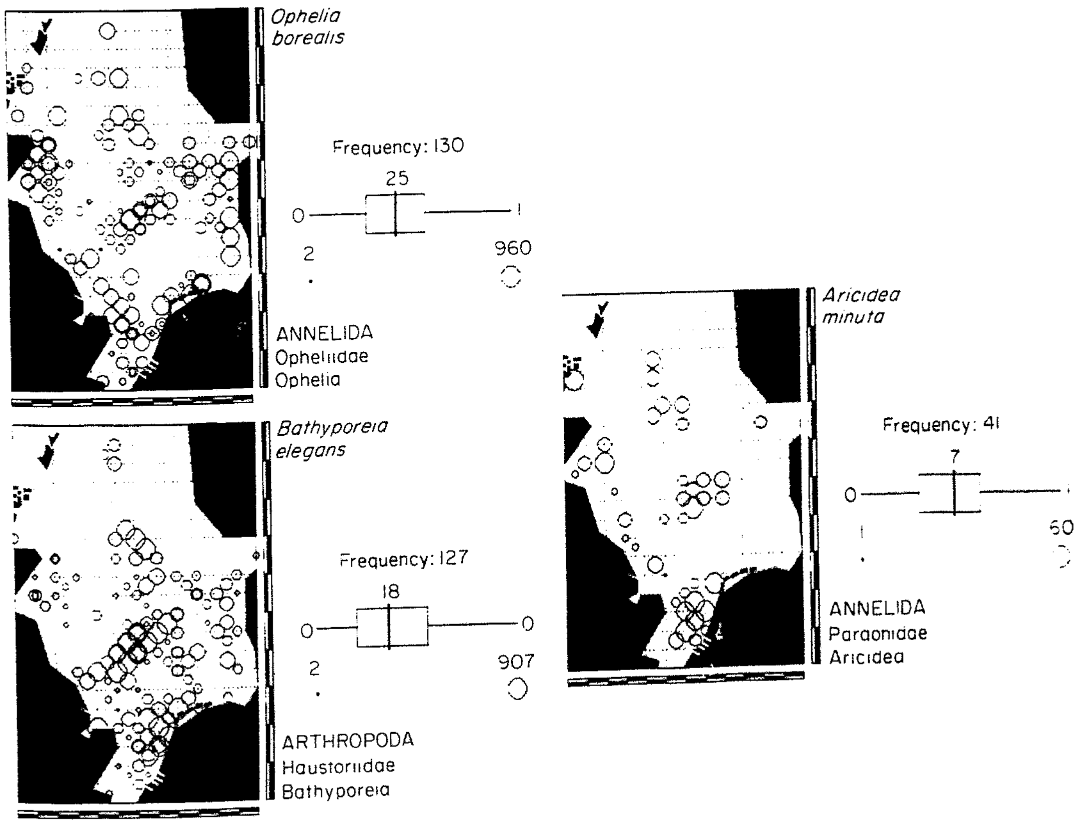


Figure 7 Distribution and density of species with a wide occurrence on fine sand in the North Sea.

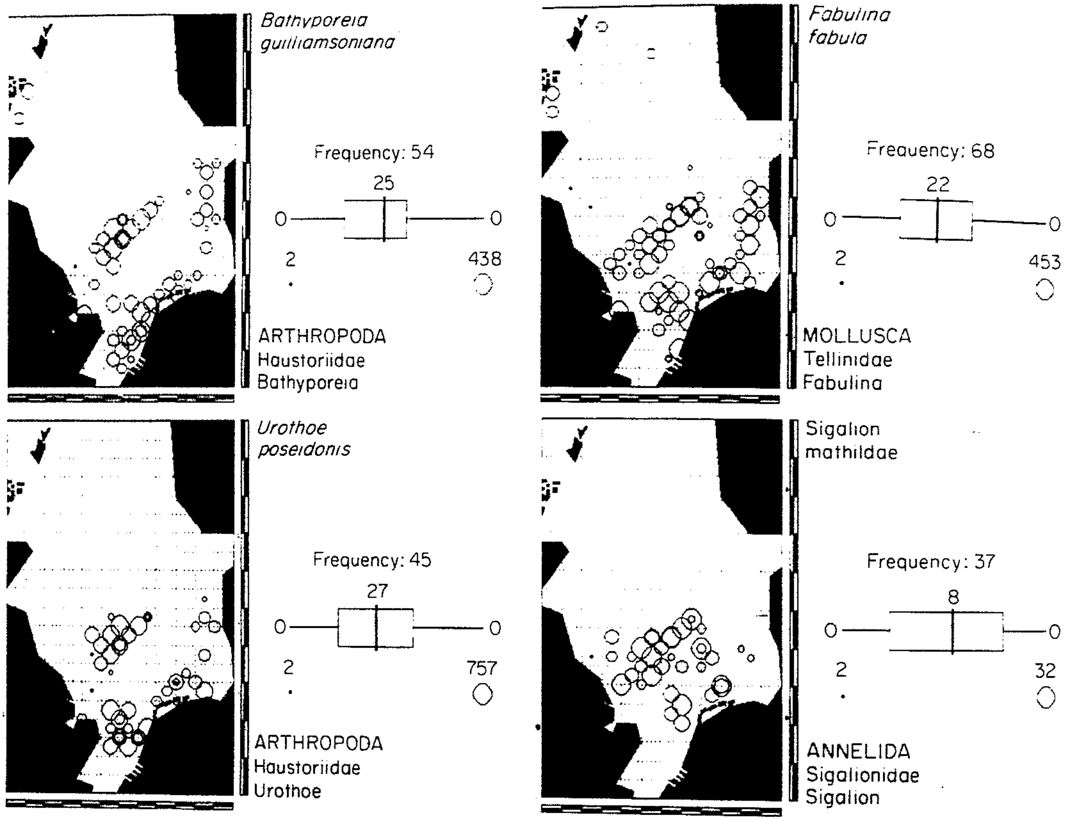


Figure 8 Distribution and density of species with a restricted occurrence on fine sand in the southern North Sea.

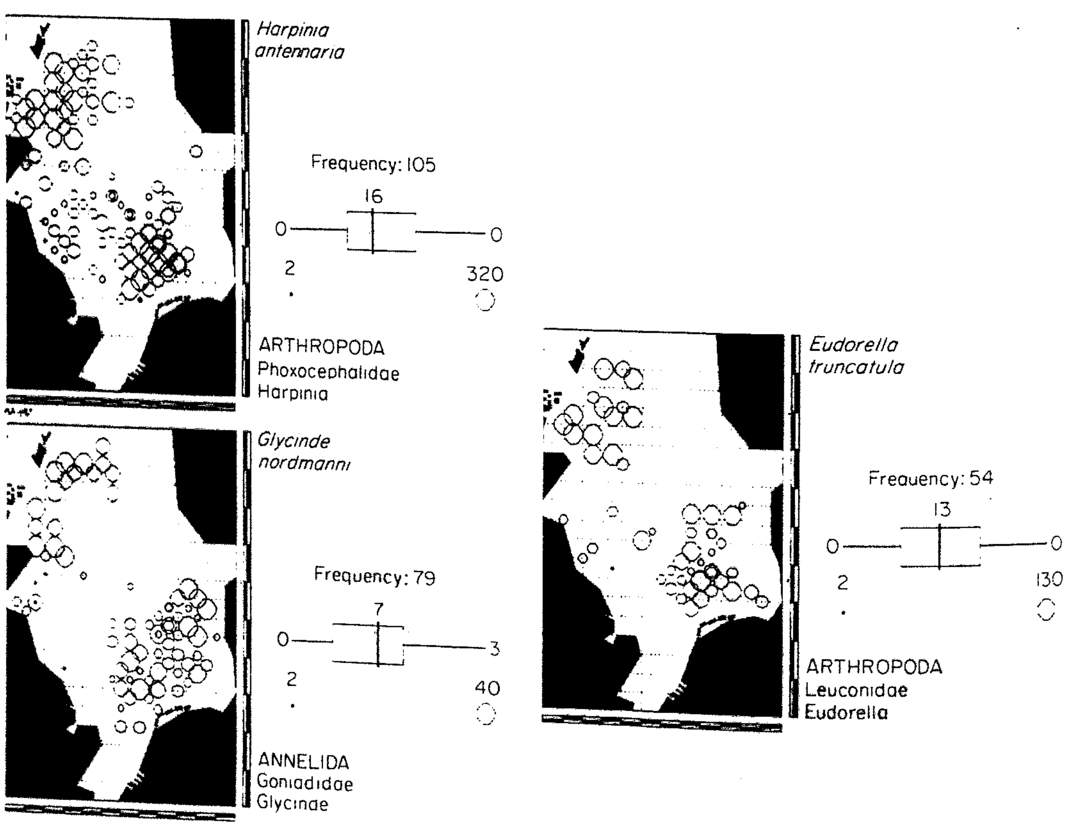


Figure 10 Distribution and density of species with a wide occurrence on muddy fine sand in the North Sea.

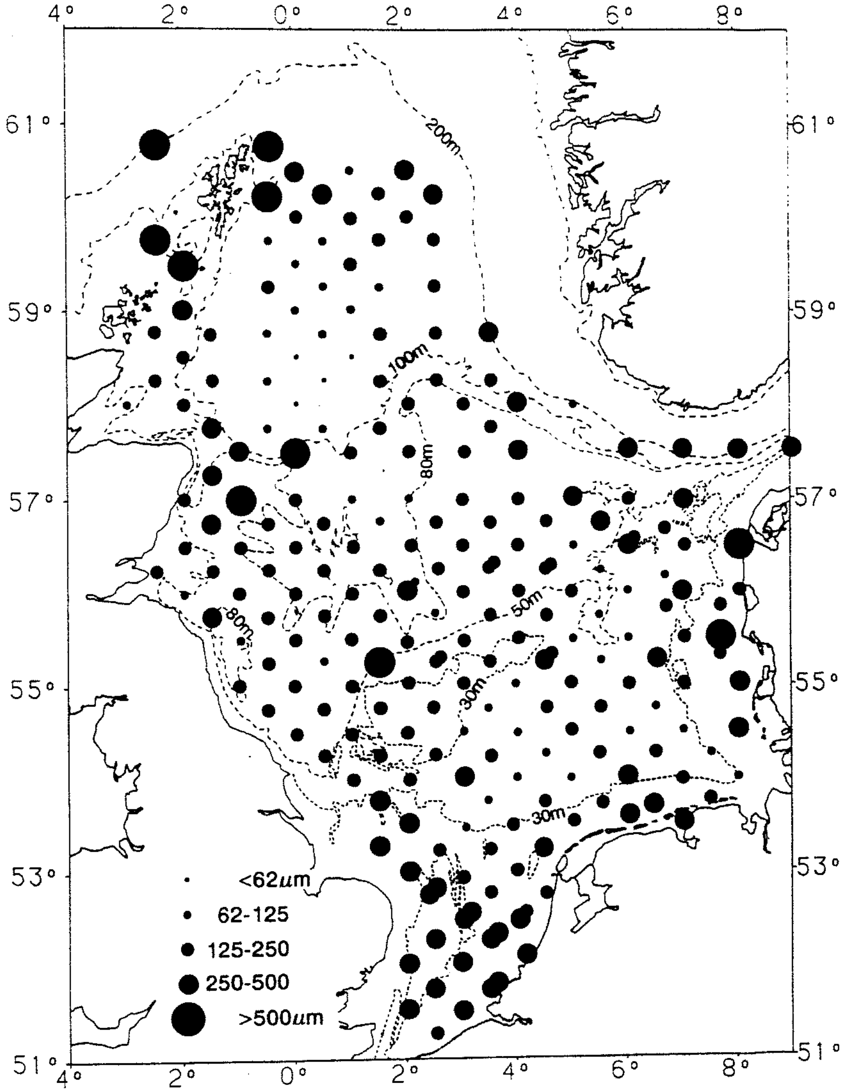


Figure 9 Median grain size of the sediment at each station (analysed by Irion, Wilhelmshaven, and Basford, Aberdeen) and depth distribution in the North Sea.

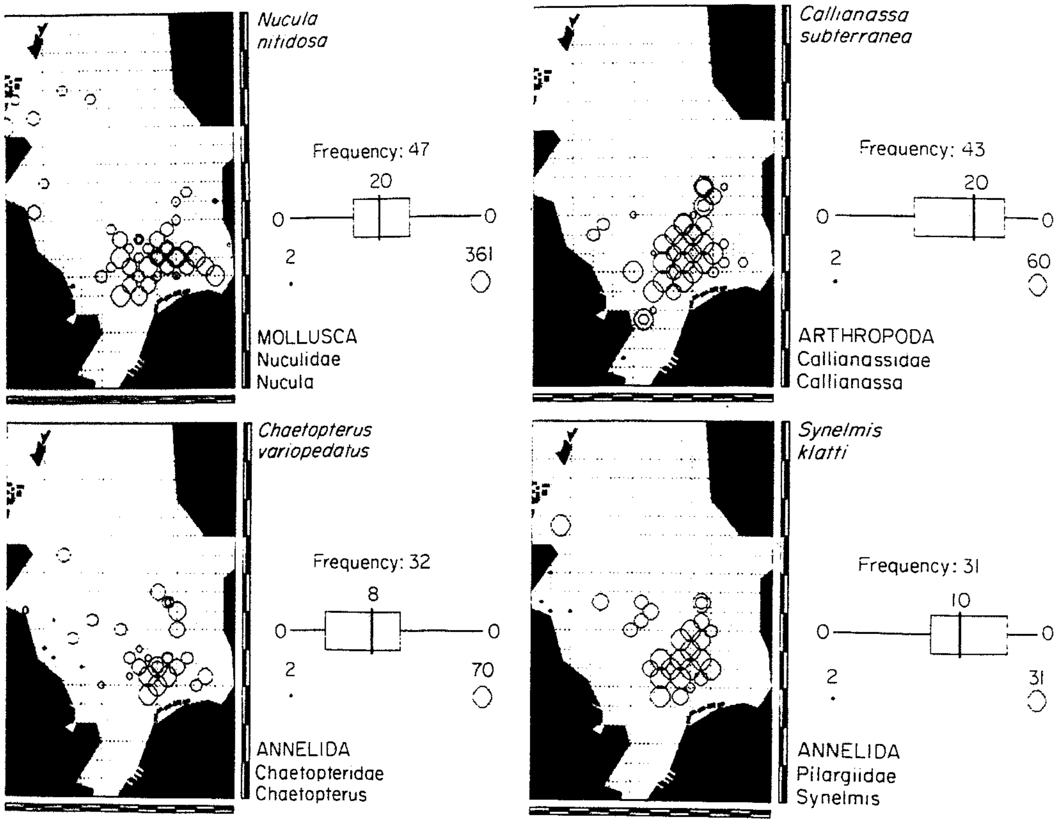


Figure 11 Distribution and density of species with a restricted occurrence on muddy fine sand in the southern North Sea.

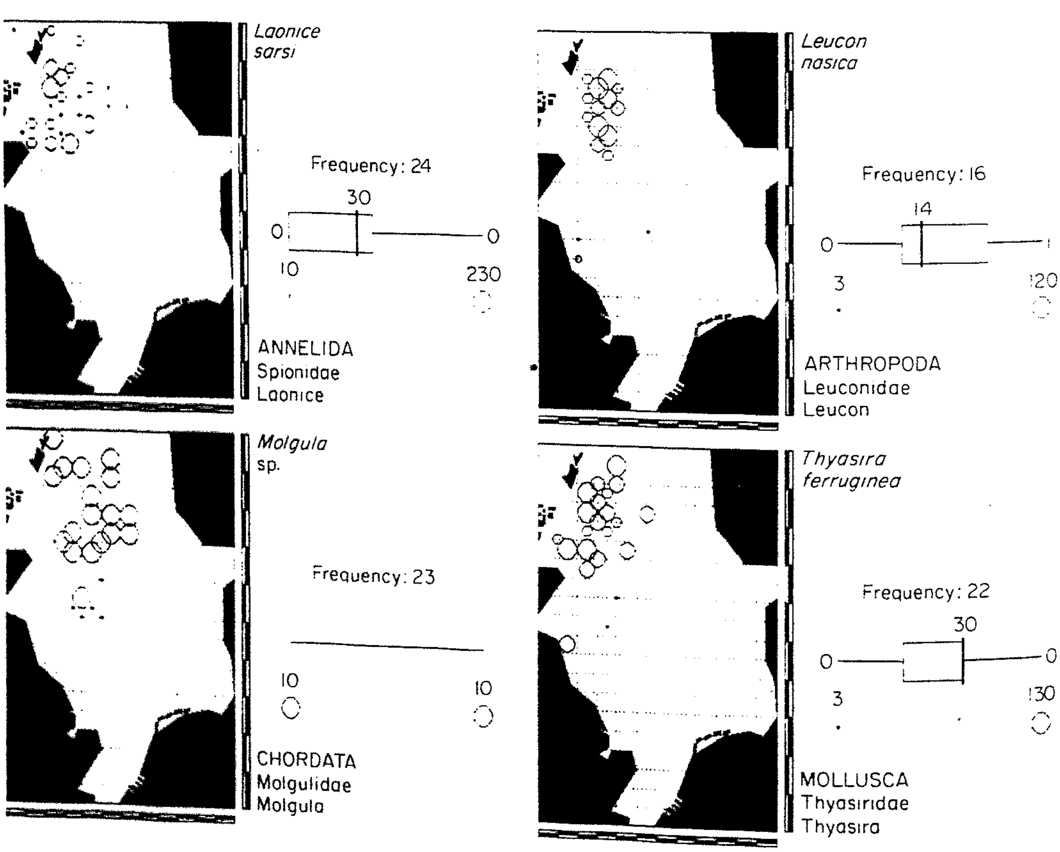


Figure 12 Distribution and density of species with a restricted occurrence on muddy fine sand in the northern North Sea.

1st dichotomy	depth < 70m				depth > 70m			
2nd dichotomy	I		II		III		IV	
depth	mainly <30m		30-70m				<100m	
deposit	coarser sediment		finer sediment		finer sediment		coarser sediment	
3rd dichotomy	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb
depth			30-50m	50-70m	70-100m	> 100m		
deposit			muddy fine sand	fine sand				
indicator species	*Nephtys c.* *Echinocardium c.* *Urothoe p.*	*Aonides p.* *Phoxocephalus h.* *Pisione r.*	*Nucula n.* *Callianassa s.* *Eudorella t.*	*Ophelia b.* *Nephtys l.*	--	*Minuspio c.* *Thyasira sp.* *Aricidea c.* *Exogone v.*	*Ophelia b.* *Exogone h.* *Spiophanes b.* *Polycirrus sp.*	*Protodorvilla k.*
number of stations	52	19	40	61	46	41	12	2
number of species	27 ± 8	29 ± 9	44 ± 9	43 ± 10	54 ± 16	51 ± 13	44 ± 12	
exp (H')	12 ± 4	14 ± 5	14 ± 5	28 ± 5	24 ± 10	25 ± 7	23 ± 5	
$Ind.m^{-2}$	805 ± 728	873 ± 623	1995 ± 1499	1093 ± 686	1224 ± 1233	2863 ± 1844	1775 ± 1114	
biomass (g $AFDW.m^{-2}$)	9.5 ± 9.9	4.3 ± 4.3	12.6 ± 7.5	7.6 ± 6.5	7.4 ± 7.0	3.5 ± 3.7	3.8 ± 2.2	
	-------- southern North Sea --------			--- central North Sea ---		-------- northern North Sea --------		

Figure 13 Scheme of TWINSPAN classification (macro-infauna, species abundance data), showing the environmental and biotic parameters (mean ± SD) of the assemblages and the indicator species.

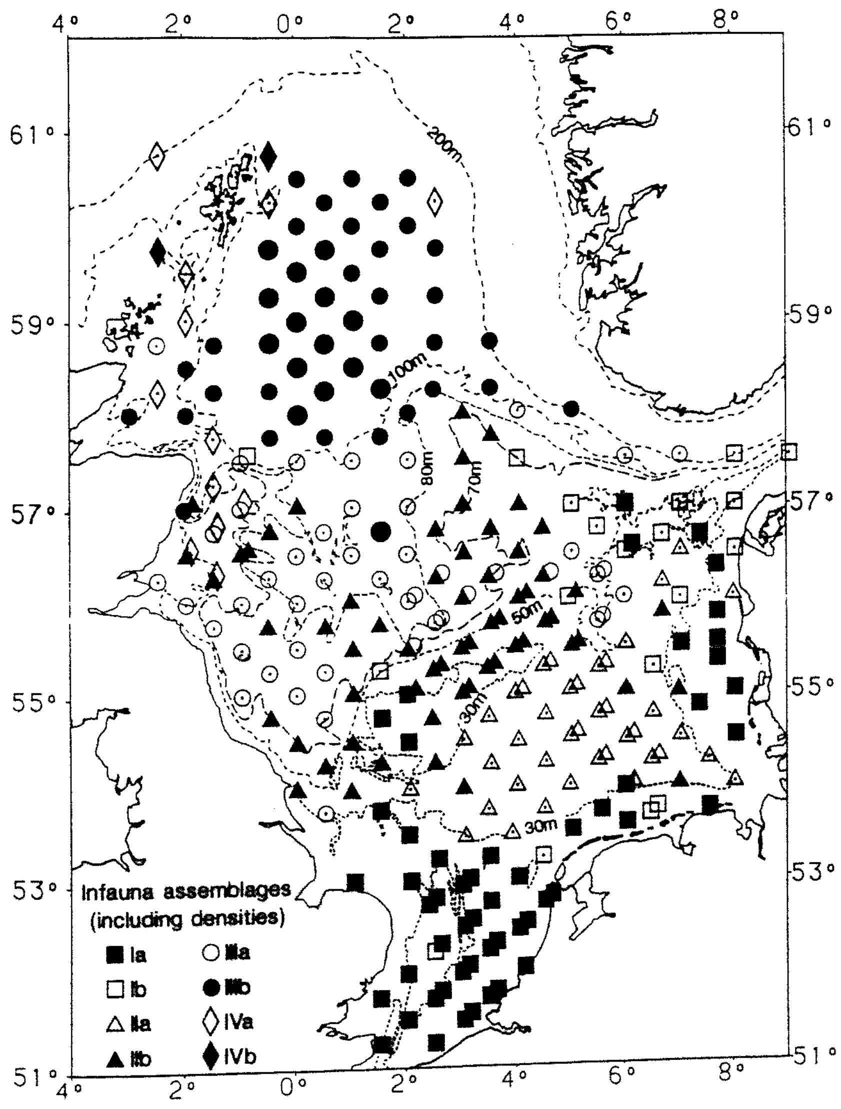


Figure 14 Classification of stations by TWINSPAN, incorporating macrobenthic species abundances.

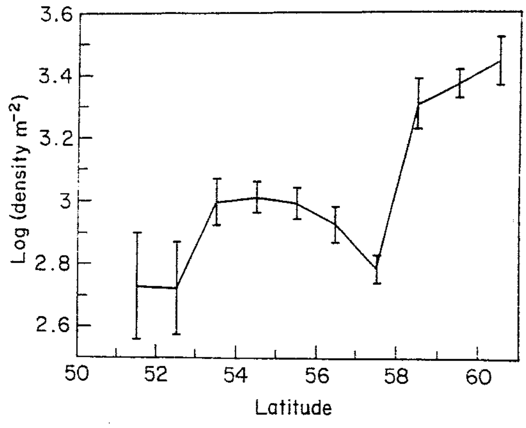


Figure 15 Log density (numbers m^{-2}) as a function of latitude.

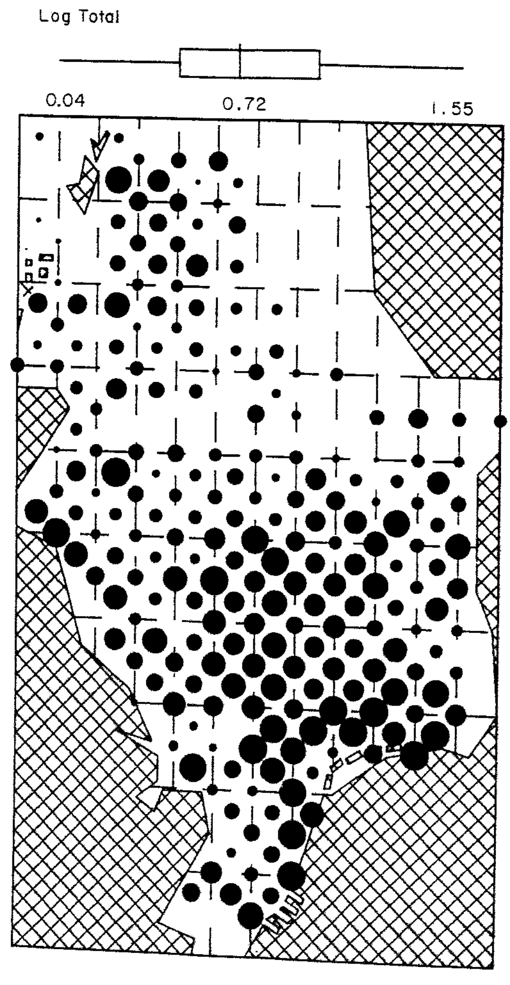


Figure 16 Log of total macrofauna biomass (g ash-free dry weight m^{-2}) of the North Sea.

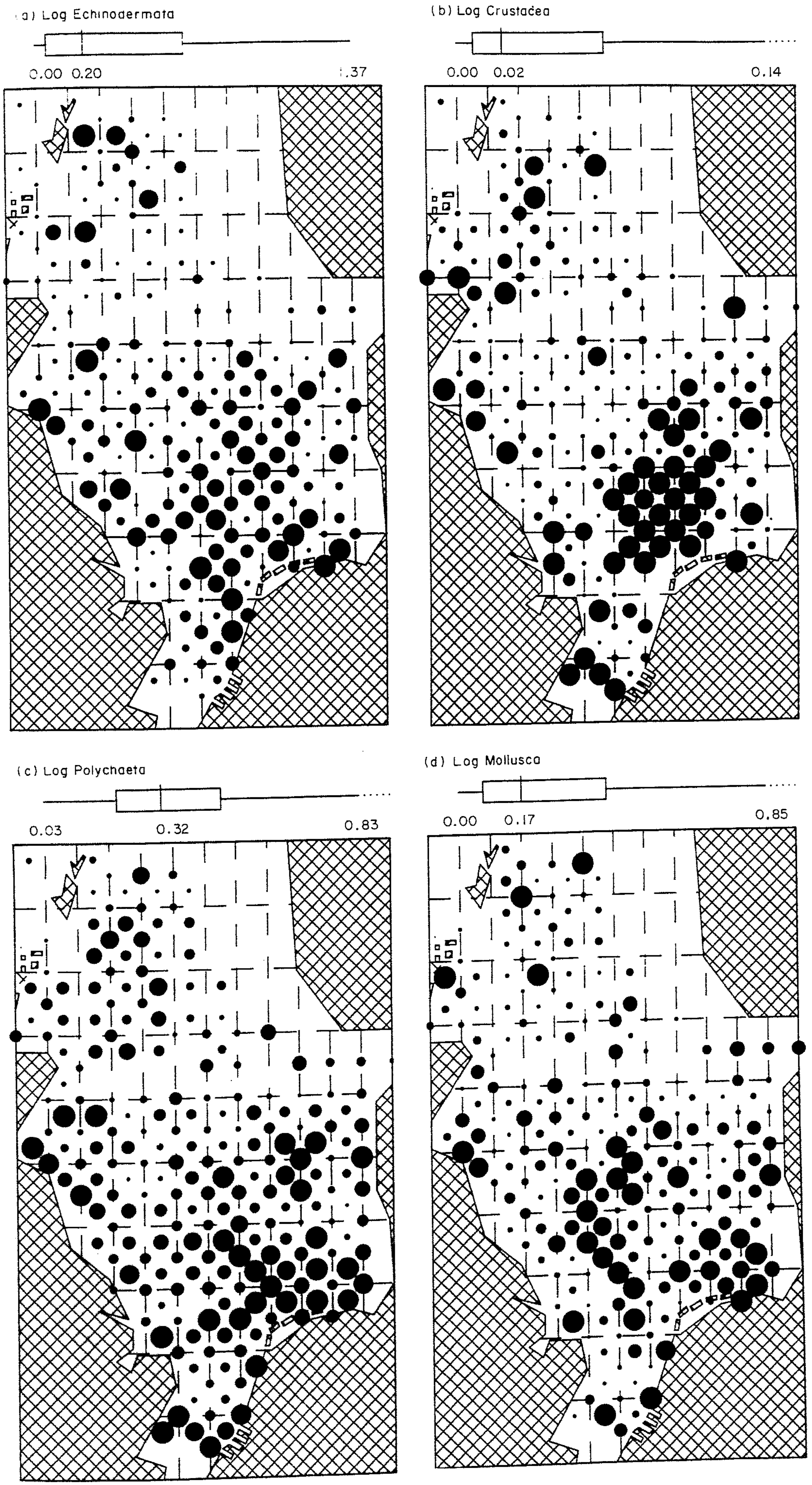


Figure 17 Log of total biomass of the major taxonomic groups of the macrobenthos in the North Sea (g ash-free dry weight m^{-2}). (a) Echonodermata. (b) Crustacea. (c) Polychaeta. (d) Mollusca.

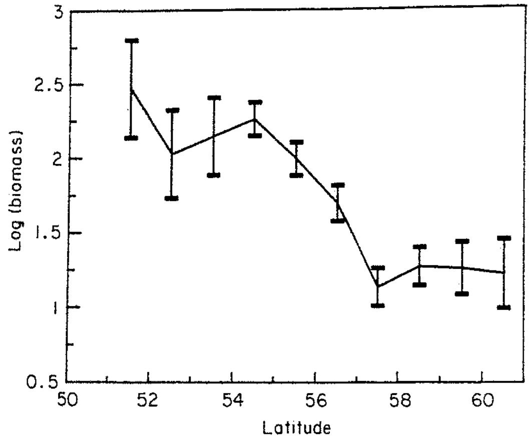


Figure 18 Log of total macrofauna biomass (g AFDW m^{-2}) as a function of latitude.

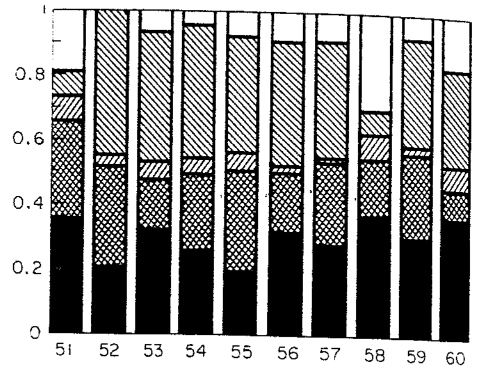


Figure 19

Fraction of total biomass represented by the large taxonomic groups of the macrofauna. ■ Polychaeta, ▩ Mollusca, ▨ Crustacea, ▧ Echinodermata, □ remainder.

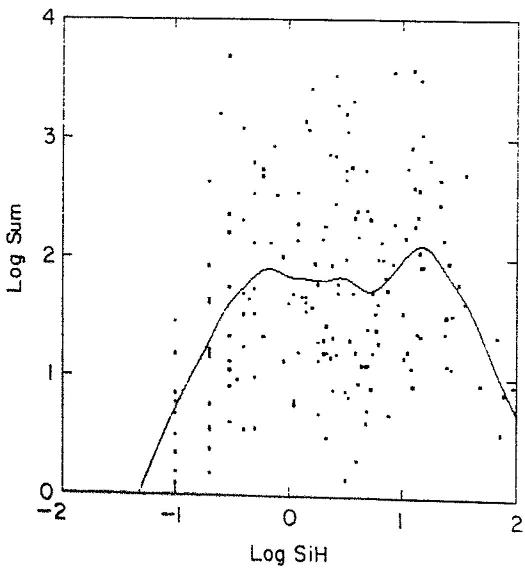


Figure 20 Relationship of (log transformed) total biomass (g AFDW m^{-2}) with (log transformed) % sediment <62 μm.

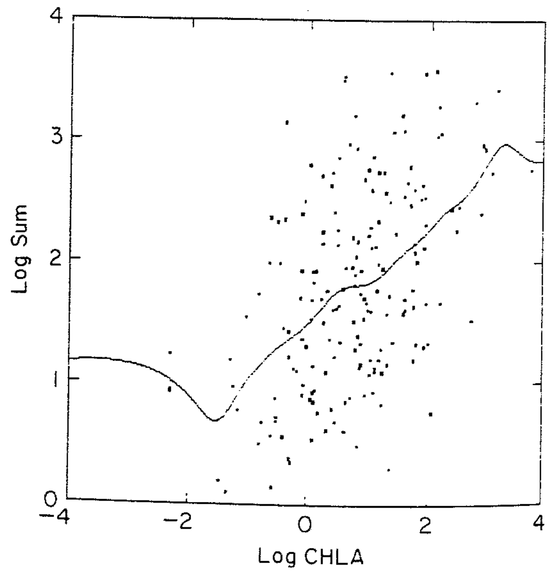


Figure 21 Relationship of (log transformed) total biomass (g AFDW m^{-2}) with (log transformed) chlorophyll-*a* content of the sediment (μg chl-*a* per 5 cm^2 sediment).

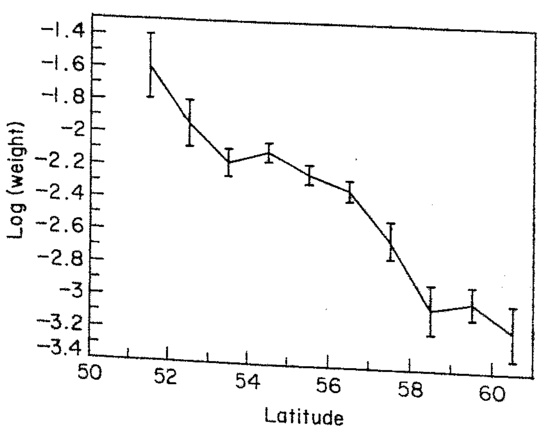


Figure 22 Log individual weight (g AFDW ind^{-1}) as a function of latitude.

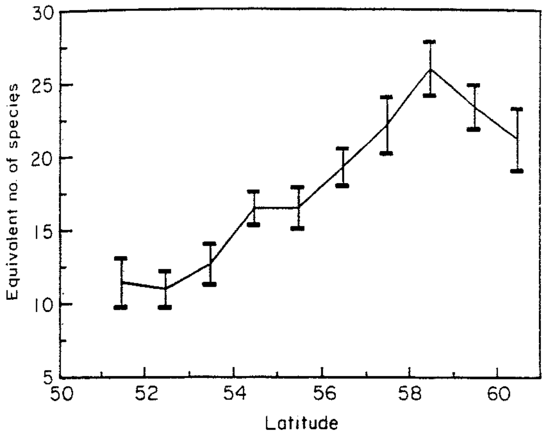


Figure 23 Diversity (Hill number N_1 expressed in equivalent number of species) as a function of latitude.

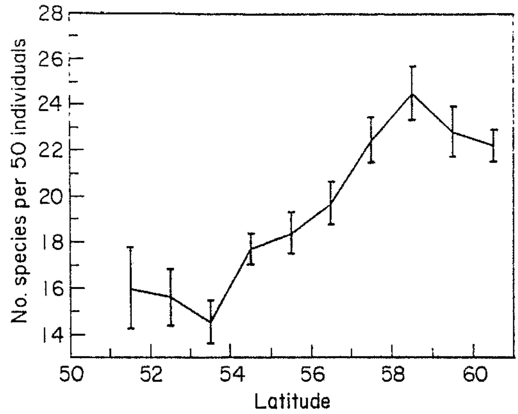


Figure 24 Diversity (number of species per 50 individuals) as a function of latitude.

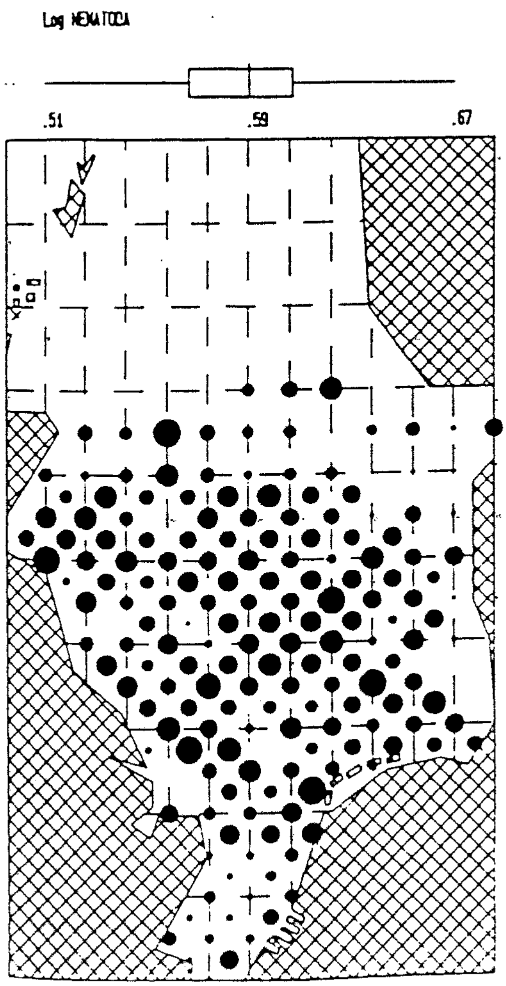


Figure 25 Log of total density of Nematoda in the North Sea.

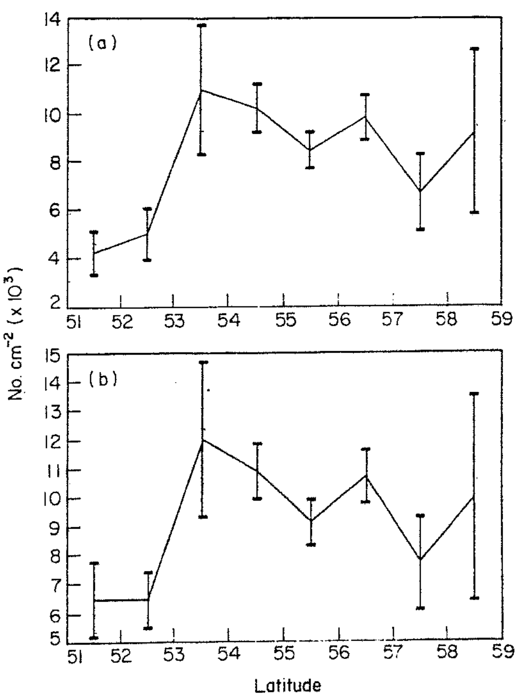


Figure 26 Trend of total density with latitude. (a) Nematoda. (b) Total meiobenthos.

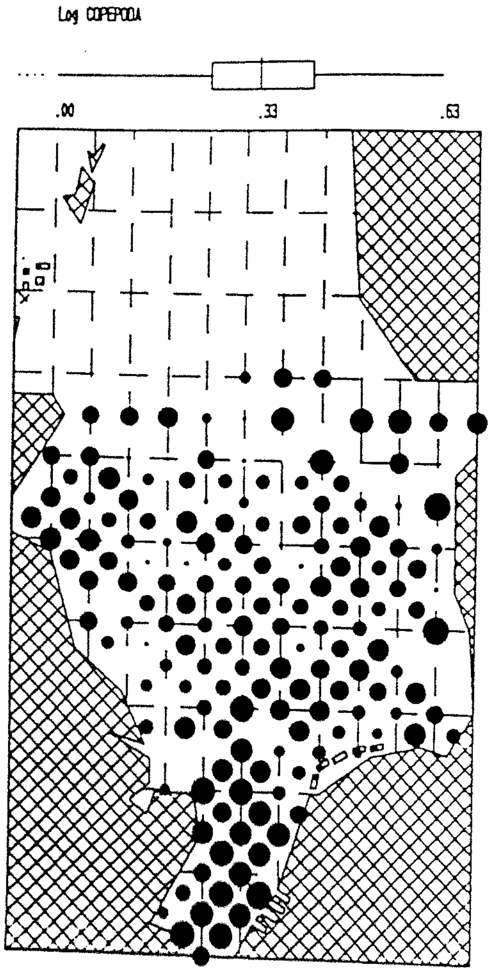


Figure 27 Log of total density of Copepoda in the North Sea.

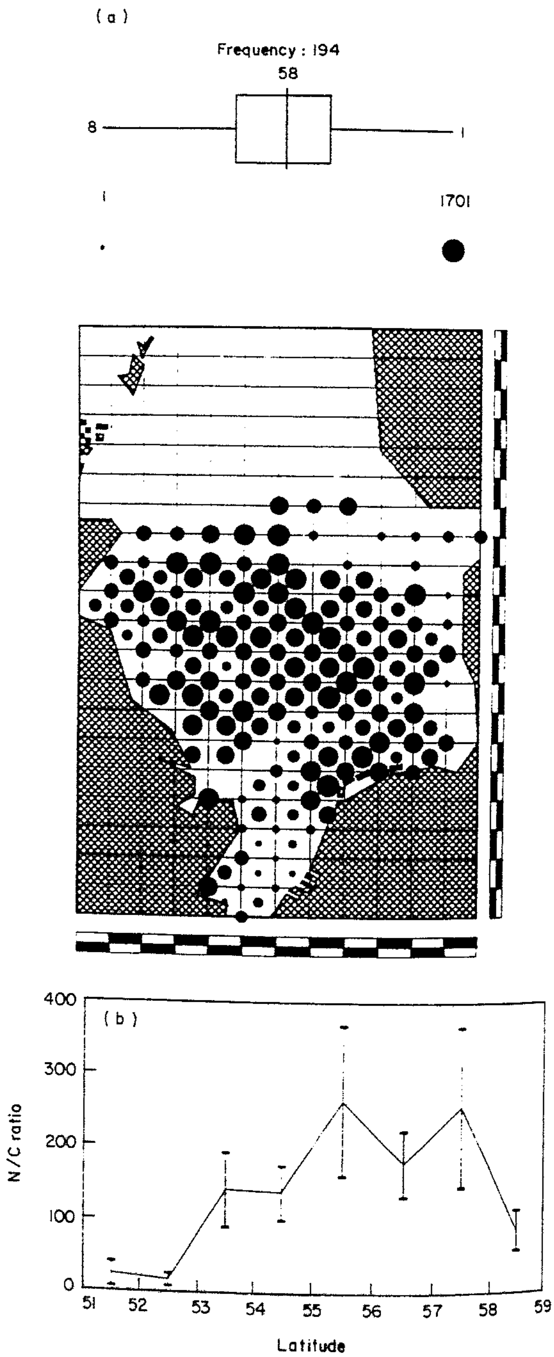


Figure 28 (a) Log of nematode:copepod ratio in the North Sea. (b) Trend of nematode:copepod ratio with latitude.

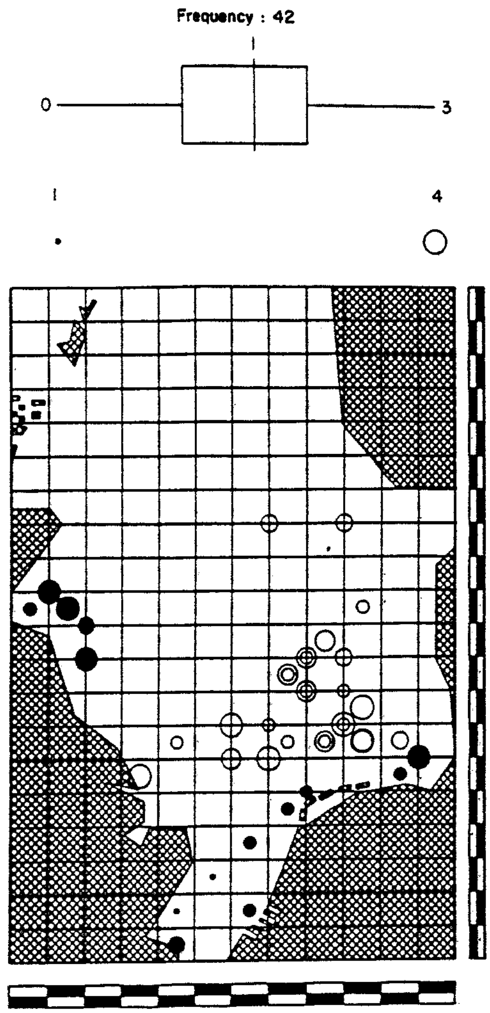


Figure 29 Log of total density of Kinorhyncha in the North Sea. Empty circles denote mud-dwelling genera; filled circles denote sand-inhabiting genera.

Figure 30 Copepoda. Trend of density, calculated on the total sample, with latitude. Per degree of latitude, the density of all stations falling within the zone is averaged. Error bars indicate standard errors of the mean.

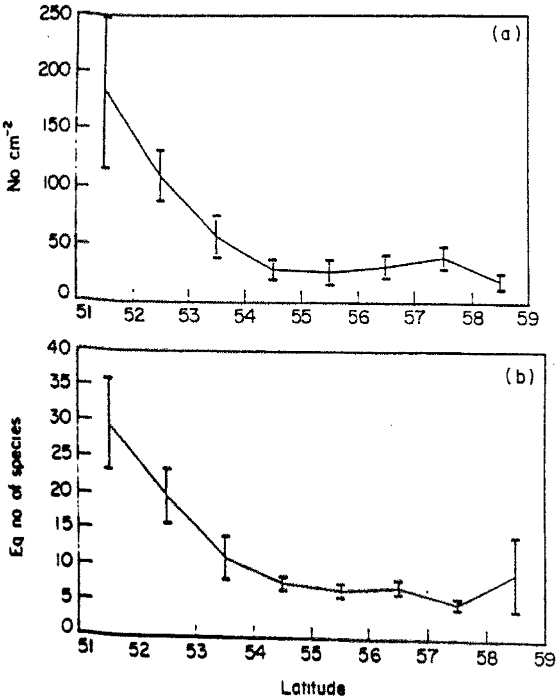


Figure 31 Copepoda. Trend of diversity N_1 with latitude. Per degree of latitude, diversity of all stations falling within the zone is averaged. Error bars indicate standard errors of the mean.

Figure 32 Copepoda. Trend of total biomass with latitude. Per degree of latitude, the biomass of all stations falling within the zone is averaged. Error bars indicate standard errors of the mean.

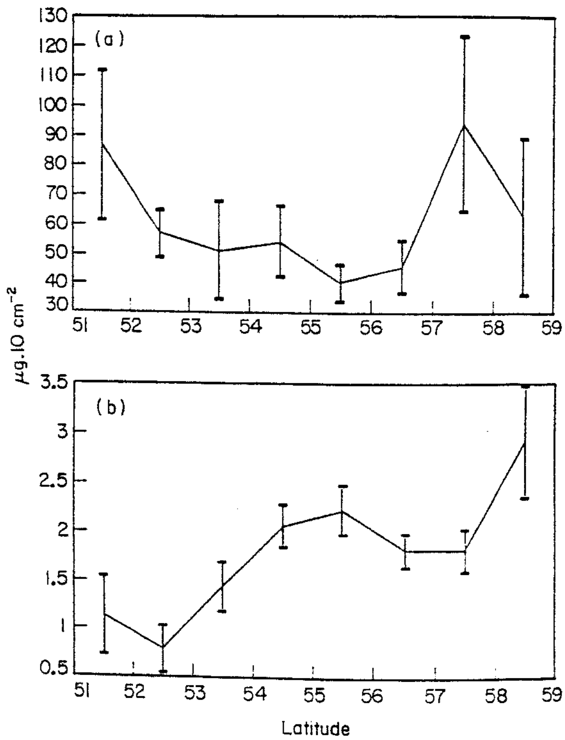


Figure 33 Copepoda. Trend of mean individual ash free dry weight with latitude. Per degree of latitude, the individual AFDW of all stations falling within the zone is averaged. Error bars indicate standard errors of the mean.

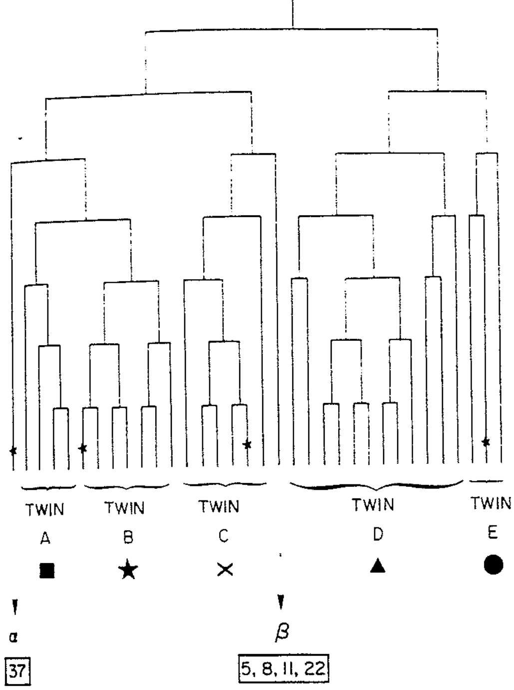
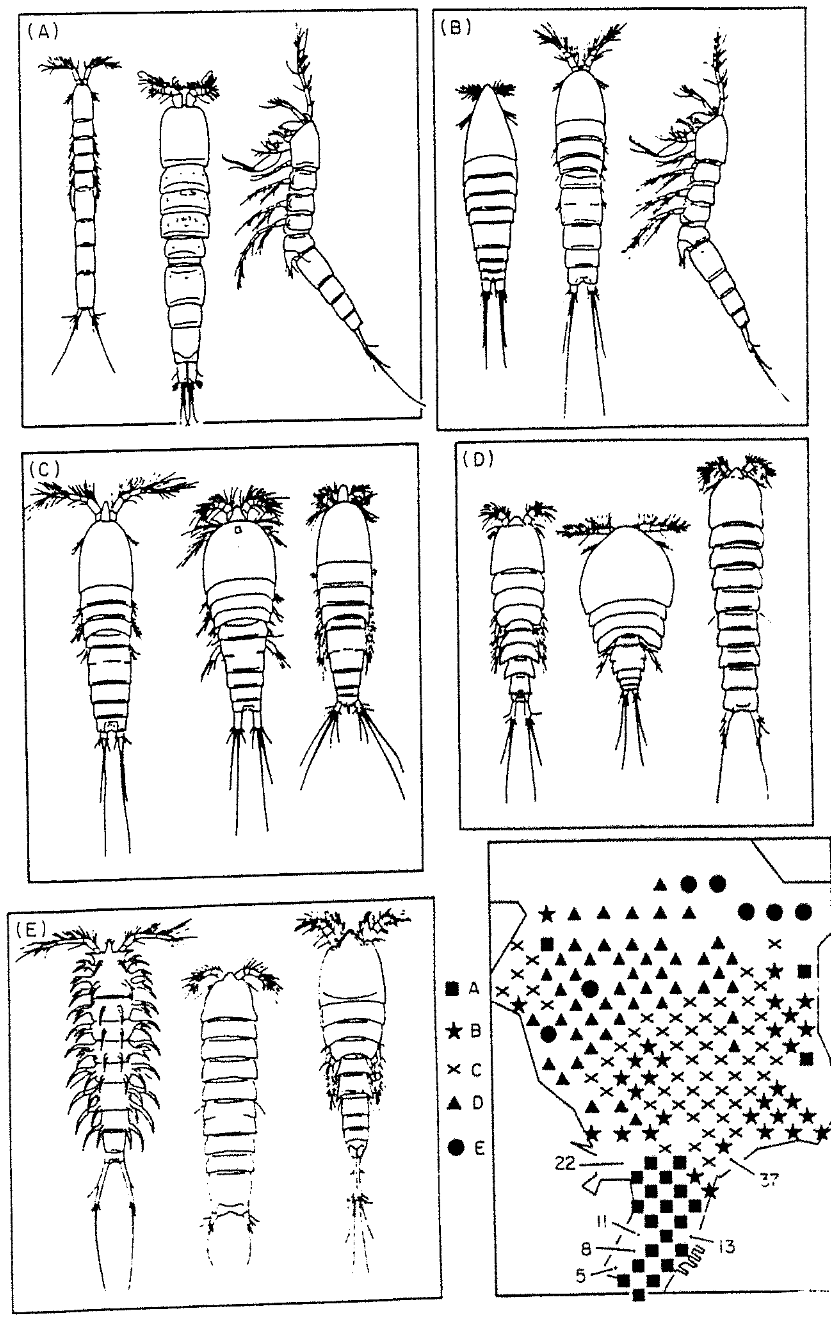


Figure 34 TWINSPAN dendrogram based on the species composition of the Copepoda.

Figure 35 Distribution of the five main TWINSPAN station-groups in the North Sea. For each TWIN group the most important ecotypes are illustrated.



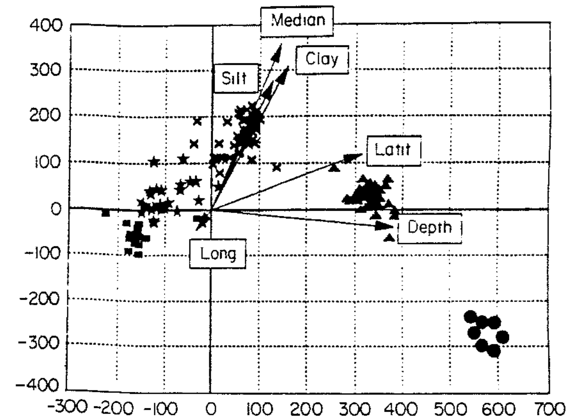


Figure 36 Canonical correspondence analysis (CCA) ordination diagram of the five major TWIN groups based on copepod composition.

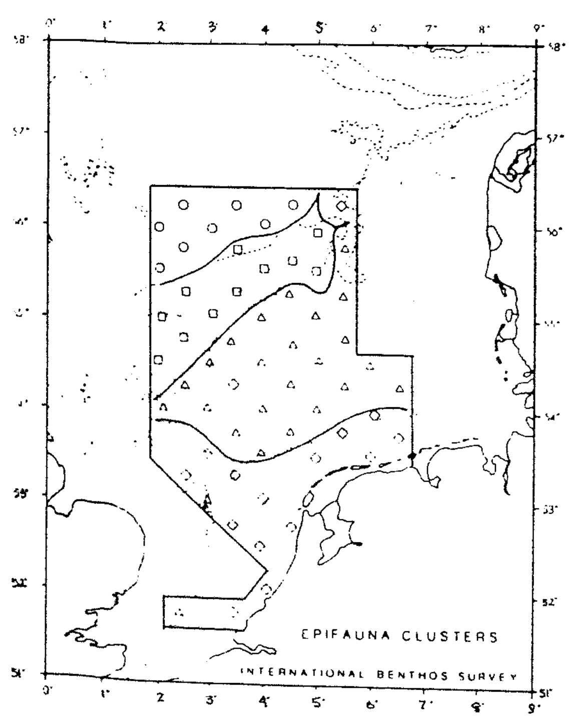


Figure 37 Distribution of the major epifauna station-groups in the Dutch, German and Danish sectors of the North Sea.

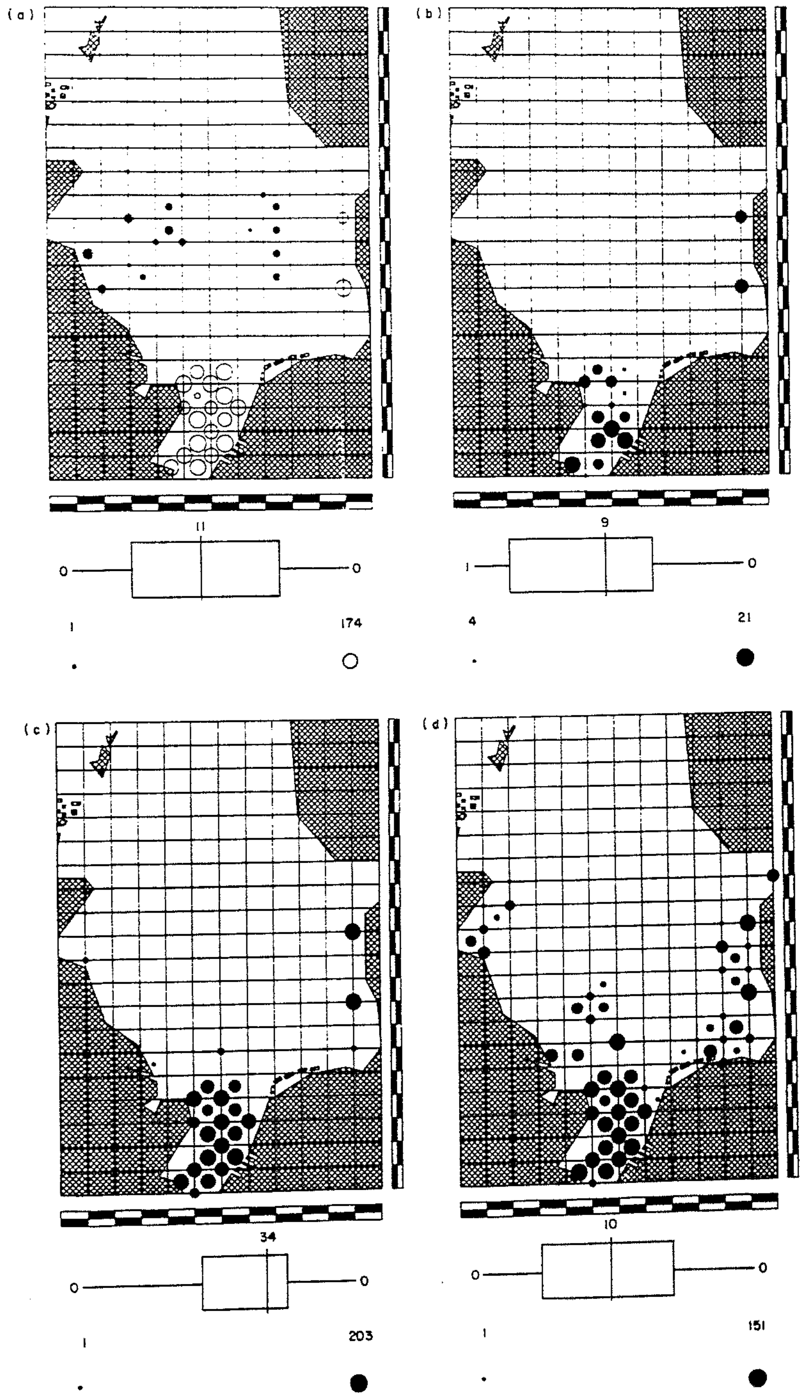


Figure 38 Log of total density of the major interstitial families of the Copepoda in the North Sea. (a) Paramesochridae. (b) Cyclopinidae. (c) Cylindropsyllidae. (d) Leptastacidae.