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Diversity and community structure of epibenthic invertebrates and fish in the North Sea

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The structure of North Sea benthic invertebrate and fish communities is an important indicator of anthropogenic and environmental impacts. Although North Sea fish stocks are monitored regularly, benthic fauna are not. Here, we report the results of a survey carried out in 2000, in which five nations sampled the epibenthic and fish fauna at 270 stations throughout the North Sea. The aim of the survey was to investigate the diversity and community structure of epibenthic and fish communities and to identify relationships with environmental factors, including the frequency of commercial otter and beam trawling disturbance. Epibenthic species diversity was lower in the southern North Sea than in central and northern areas. Fish, conversely, were more diverse in the south. The 50 m, 100 m and 200 m depth contours broadly defined the boundaries of benthic and fish communities. The abundance of epibenthos of the southern North Sea was dominated by free-living species, whilst north of the 50 m contour sessile species prevailed. A hybrid area, with sessile species typical of the north and free-living species characteristic of the south, was found off the Norfolk and Flamborough coast stretching towards the Dogger Bank.

Large-scale hydrodynamic phenomena were most likely to be responsible for the main divisions between communities, especially the boundary between mixed and stratified water masses. However, bottom temperature, sediment parameters and beam trawling were closely correlated with species richness and diversity, as well as community patterns, and may modify regional species composition.

Our study shows that effective large-scale sampling of benthic communities can be conducted during existing fisheries surveys. Since annual fisheries surveys are conducted throughout the northeast Atlantic shelf seas, concurrent benthic surveys would allow benthic sampling on unprecedented spatial and temporal scales. The samples would help to monitor the environmental impacts of trawling disturbance, climate change, pollution and other natural and anthropogenic factors.

Keywords: epibenthos, fish, diversity, community structure, fishing effects, North Sea.

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Introduction

Several studies have described the diversity and community structure of epibenthic invertebrates and demersal fish in the North Sea (Petersen, 1914; Dyer *et al.*, 1983; Basford *et al.*, 1989; Frauenheim *et al.*, 1989; Kröncke, 1990; Duineveld *et al*, 1991; Rogers *et al.*, 1998; Rees *et al.*, 1999). However, all the studies of epibenthos used

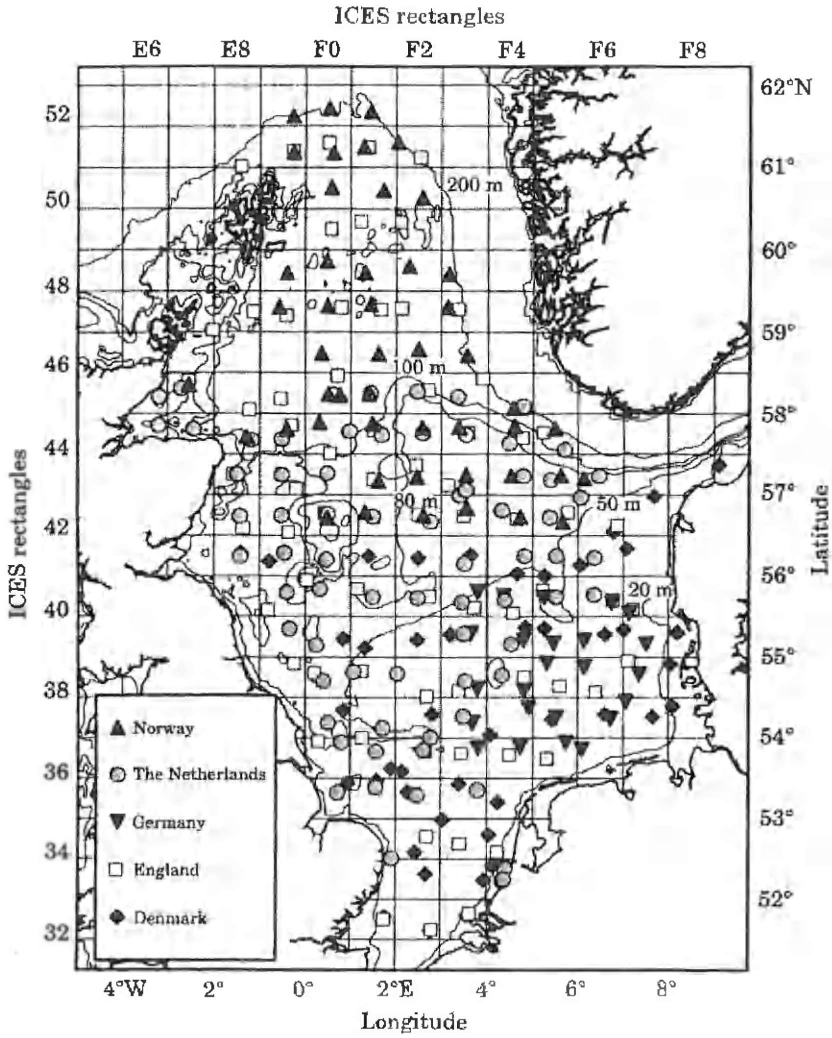


Figure 1. Sampling stations.

different sampling methods and the analyses were often based on a limited number of stations. From 1996 to 1998 a European project standardized the sampling design for epibenthic surveys and implemented invertebrate biodiversity monitoring on national groundfish surveys (GFS), which monitor fish stocks for scientific and management purposes (Jennings *et al.*, 1999; Anon., 2001; Callaway *et al.*, 2002). This greatly extended the geographical coverage with limited financial resources. The first international survey was carried out in 1999 (Zühlke *et al.*, 2001). Here we report the results of the 2000 survey. A 2 m steel beam trawl (Jennings *et al.*, 1999) was deployed during five European 3rd quarter groundfish surveys to sample epibenthos. Diversity of demersal fish communities was assessed from the catches of the 2-m beam trawl as well as the main survey trawl – a Grande Ouverture Verticale (GOV) otter trawl (Anon., 1996). The aims of the present study are to provide a large scale description of epibenthos and fish diversity throughout the North Sea, to identify spatial patterns in fish and benthic community structure and to relate environmental factors, including the frequency of trawling disturbance, to diversity and community structure.

Methods

Epibenthic invertebrates and demersal fish were sampled at 270 stations in the North Sea, covering 139 ICES rectangles (Figure 1). Samples were taken during national 3rd quarter 2000 groundfish surveys (GFS) of five European countries: Germany, The Netherlands, England, Norway and Denmark.

Sampling gear and procedure

Samples were taken with a 2-m beam trawl constructed from galvanized steel. It was fitted with a 20 mm stretched mesh (10 mm knot to knot) and a cod-end liner of 4 mm knotless mesh (2 mm "knot" to "knot"). A chain-mat was attached to minimize the catch of heavy rocks. Details about the equipment and sampling protocol are given in Jennings *et al.* (1999) and Zühlke *et al.* (2001).

Sample treatment

Samples were washed through a 5 mm sieve (internal mesh size) and epibenthic fauna and fish were separated from other material. Species that could not be identified at sea were preserved in 4% formalin solution buffered with 3 g l^{-1} sodium acetate trihydrate for later identification in the laboratory. All animals were identified to the lowest possible taxonomic level. Species names were standardized to the nomenclature of Picton and Howson (1999). Free-living fauna and fish were counted and weighed with a seagoing marine scale (Pols) with an accuracy of 1 g. Sessile animals were recorded as present or absent.

ICES fish data

In addition to the data collected from the 2-m beam trawl samples, species-abundance data for fish caught with the GOV survey otter trawl on the national GFSs (Knijn *et al.*, 1993) were analysed. The data were extracted from the ICES (International Council for the Exploration of the Sea) International Bottom Trawl Survey Database (Copenhagen, DK).

Environmental data

Sediment samples were taken at 60 stations during the English survey. The dried sediment samples were sieved through a series of standard sieves from 2000 µm to 63 µm mesh to determine the grain size distribution. Bottom and surface temperature and salinity data were recorded on the survey vessel and provided from a database maintained by CEFAS (Lowestoft, UK).

The latest and most complete international commercial trawling effort data were available for 1998. Six countries contributed to a compilation: The Netherlands, Germany, England, Scotland, Norway and Denmark. Beam trawling and otter trawling effort were separated. All data were recorded as hours fishing by ICES statistical rectangle (boxes 0.5° latitude × 1° longitude), since we did not have sufficiently disaggregated data to account for differences in vessel type, power, towing speed, fishing gear design and other factors that would influence the area impacted by trawls per unit time.

Data analysis

Mean diversity indices and biomass were calculated for each ICES rectangle. Hill's diversity indices N_0 and N_1 were calculated, where N_0 is the total number of species (species richness) and N_1 is an index of the number of abundant species [exp (H), where H is Shannon–Wiener diversity] (Hill, 1973).

Abundance and biomass were standardized to a tow length of 200m (area = 400 m^2). Numbers of species were analysed as numbers of species per haul.

Multivariate community analysis was carried out with the statistical package PRIMER 5 (Clarke and Warwick 1994). Hierarchical cluster analysis was used to separate groups of stations with similar species assemblages. The data matrix for all epibenthic species was presence/absence transformed, because sessile species were recorded as present or absent only. Abundance of fish was double square root transformed. The Bray–Curtis index was calculated between each possible pair of samples. Species which were predominantly responsible for the similarity within clusters and for the separation between clusters, were determined with the PRIMER program SIMPER. This examines the percentage contribution that each species makes to the similarity within the cluster and to the difference between two clusters.

The term "community" is used for groups of stations with similar epibenthic or fish species derived from cluster analysis. Ecological interactions are not implied.

The relationships between environmental factors and univariate diversity indices were analysed by calculating product moment correlation coefficients. Multivariate statistical tools were then used to analyse the epibenthic community structure in relation to environmental factors. The PRIMER program BIO-ENV (Clarke and Warwick, 1994) calculated which set of environmental factors and fishing effort was best correlated with the epibenthic community structure. For each possible combination of environmental factors a dissimilarity matrix based on normalized Euclidean distances was calculated. The agreement between the biotic matrix and matrices of environmental factors was expressed as the Spearman rank correlation coefficient.

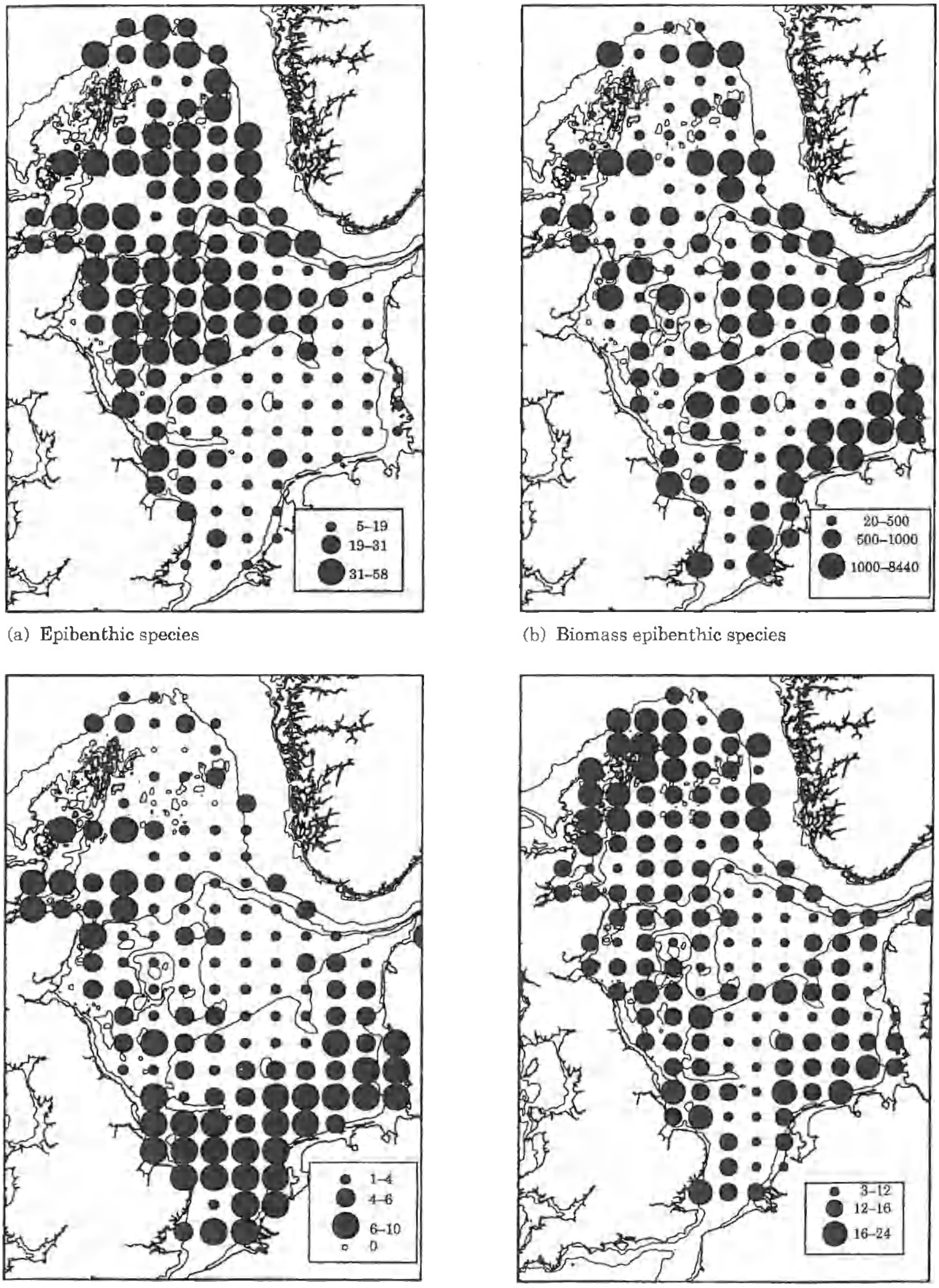
To visualize the relationship between environmental factors and the epibenthic community structure, values of abiotic factors were superimposed onto MDS plots (multi dimensional scaling). MDS plots were based on Bray–Curtis indices of presence/absence transformed epibenthic data.

Results

A total of 456 epibenthic and 64 fish species was recorded at the 270 stations sampled during the surveys.

Diversity pattern of epibenthic species

Numbers of invertebrate species were lower in the southern than in the northern North Sea (Figure 2a).



(a) Epibenthic species

(b) Biomass epibenthic species

(c) Demersal fish (2 m beam trawl)

(d) Fish (otter trawl)

Figure 2. Total number of epibenthic species and fish (ICES rectangle^{-1}) in the North Sea in 2000. (a) Total number of epibenthic species. (b) Mean epibenthic biomass. Numbers are based on wet-weight of free living species. (c) Total number of demersal fish caught with a 2-m beam trawl. (d) Total number of fish species (h trawling^{-1}) caught by otter trawling. Source of data: ICES International Bottom Trawl Survey Database.

The division between areas of low and high numbers of species roughly corresponded with the 50 m contour. In the southern North Sea the mean number of species was 14 ± 6 haul^{-1}, while in the northern North Sea it was 30 ± 10 haul^{-1}. An area off the Humber Estuary and Norfolk coast did not fit the general pattern. Here, numbers of species were comparable to stations in the northern North Sea, although the area was less than 50 m deep.

Biomass was high along the continental coast, in central parts of the North Sea and at several stations in the northern North Sea (Figure 2b). A limited number of free-living species was responsible for this pattern. In shallow parts of the North Sea along the continental coast, the starfish *Asterias rubens* and the brittle stars *Ophiura albida* and *Ophiura ophiura* were abundant. The hermit crab *Pagurus bernhardus* and the starfish *Astropecten irregularis* were responsible for high biomass at stations in the central North Sea, while in the northern North Sea *Echinus* spp. and hermit crabs contributed to the high biomass recorded. This is partly reflected in the distribution patterns of the more abundant species (Figure 3).

Diversity pattern of fish species

Most of the fish caught with the 2-m beam trawl were small demersal (bottom dwelling) species. The spatial pattern of species richness opposed that of the epibenthos (Figure 2c), with the highest numbers of species in the southern North Sea and low numbers in the north (with the exception of areas around the Scottish coast). The numbers of fish caught by otter trawling (source: ICES database) were high in the far north, at some stations along the continental and English coast and at a few stations in the central North Sea (Figure 2d).

Epibenthic community structure

Cluster analysis based on presence/absence transformed data divided the fauna into two main clusters, which could be further subdivided into seven clusters (Figure 4a, Table 1). The 50 m depth contour divided the two main clusters (Figure 4b). Four sub-clusters were situated in the southern North Sea, at depths less than 50 m, and three in the central and northern North Sea. The largest community in the southern North Sea (Figure 4, ■) was characterized by *P. bernhardus* (Figure 3a), *A. rubens* (Figure 3b), *A. irregularis*, *Corystes cassivelaunus* (Figure 3c), *Liocarcinus holsatus*, *O. ophiura*, *O. albida* (Figure 3d) and *Psammechinus miliaris*. The majority of ICES rectangles along the continental coast formed a group (Figure 4, ●), which was a species-poor version of the afore mentioned community. The scarcity of *C. cassivelaunus*, *P. miliaris* and *Aphrodita aculeata*, as well as the absence of *Hydrallmania falcata*, contributed to their separation. The cluster in the southern-most area of the North Sea towards the English Channel (Figure 4, ▲) was characterized by the regular presence of the shrimps *Crangon crangon*, *Crangon allmanni* and *Philoceras trispinosus*, while *C. cassivelaunus* and *A. irregularis* were less abundant. Although sessile species played a minor role in the southern North Sea, one region shallower than 50 m depth, stretching from Norfolk up to the Dogger Bank, was an exception (Figure 4, ◆). This cluster was separated from the others by the regular presence of bryozoans such as *Alcyonidium diaphanum* (Figure 3j), *Alcyonidium parasiticum*, *Eucratea loricata* and *Flustra foliacea* as well as hydrozoans such as *H. falcata* (Figure 3i) and *Halecium halecium*. In this respect this cluster was similar to the northern North Sea cluster, although the free-living fauna were typical southern North Sea species.

Clusters in the northern North Sea were located between the depth contours 50–100 m and 100–200 m, but their separation was less conspicuous than between clusters in the south (Figure 4). A large range of species found between the 50 m and 100 m depth (Figure 4, ○), were not recorded in the shallower southern North Sea. Species contributing predominantly to the separation of this cluster from the ones to the south were whelks such as *Neptunea antiqua* (Figure 3f) and *Colus gracilis*, the hermit crabs *Pagurus pubescens* and *Anapagurus laevis* (Figure 3g) as well as species such as *Hydroides norvegica*, *Hyas coarctatus* (Figure 3e), *F. foliacea* and *Epizoanthus papillosus* (formerly *E. incrustatus*). The cluster between the 100 m and 200 m depth line (Figure 4, ◇) was characterized by *A. irregularis*, *Hyalinoecia tubicula* (Figure 3h), *Hormathia digitata* (Figure 3k) and *Echinus* spp. Many species occurring regularly in the 50–100 m community were less frequently found between 100 m and 200 m (e.g. *A. digitatum*, *F. foliacea* and *Tubularia indivisa*), a factor contributing to the separation of the clusters.

A small cluster was formed by the ICES rectangles north of 61°N latitude (Figure 4, □). These stations were characterized by the presence of the hexacoral *Caryophyllia smithii* (Figure 3l) but otherwise by the absence of several species found further south.

Fish community structure

Fish communities were divided into two main groups located south and north of the 50 m depth line. This was true for fish caught with the 2-m beam trawl and otter trawl. Cluster analysis based on fish species caught with the 2-m beam trawl separated one cluster for the southern North Sea and three for the north (Figure 5a & b, Table 2).

The community of the southern North Sea (Figure 5b, ■) was characterized by small, non-commercial species. Most common were *Buglossidium luteum*

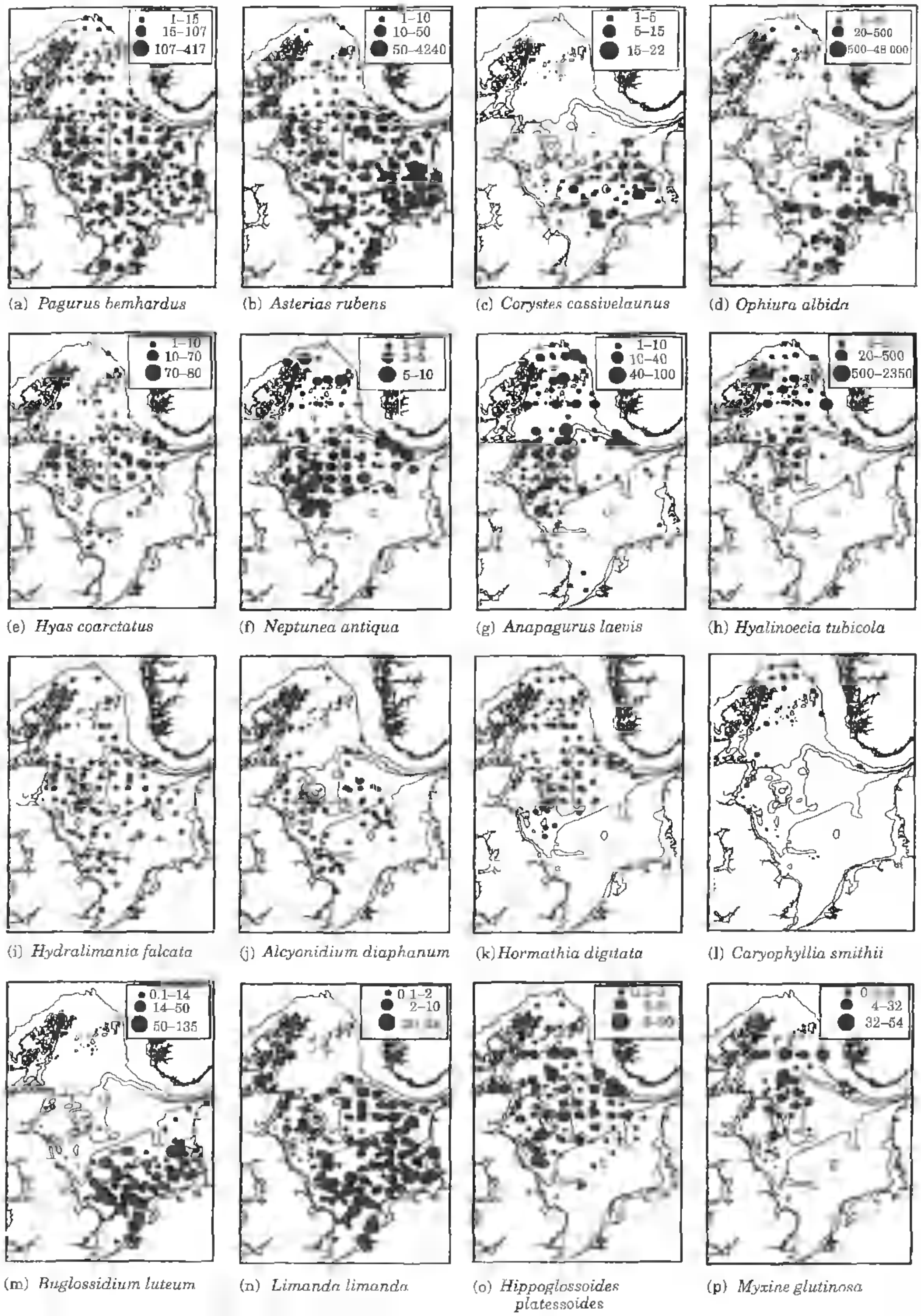


Figure 3. Distribution of species characteristic for epibenthic and fish communities. The size of bubbles indicates abundance. Species were recorded as present or absent if no legend is shown.

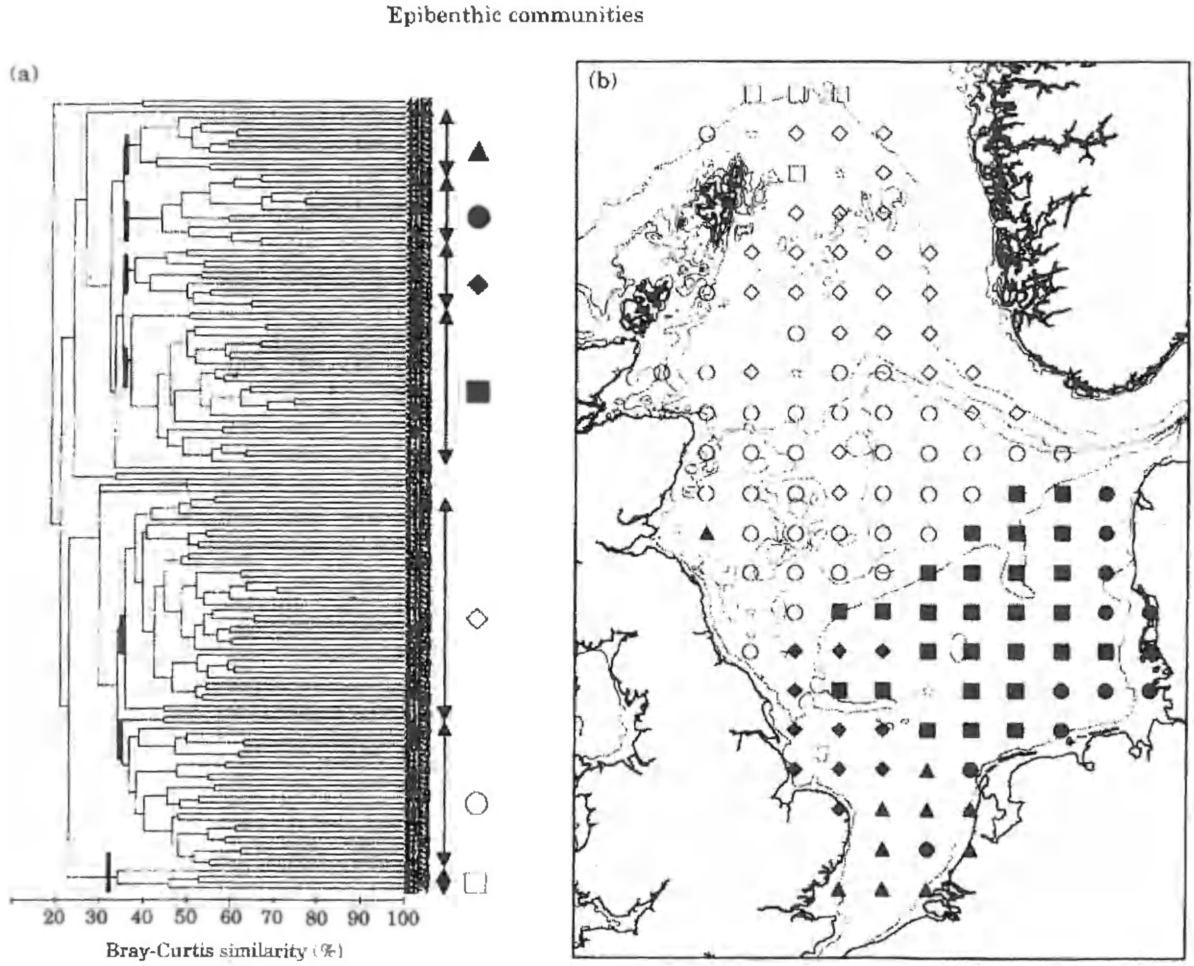


Figure 4. Epibenthic communities in the North Sea in 2000. (a) Hierarchical classification analysis based on presence/absence transformed data. Vertical bars indicate the main groupings. (b) Location of clusters identified by hierarchical classification analysis (☆ outliers).

(solenette, Figure 3m), *Limanda limanda* (dab, Figure 3n) and *Callionymus lyra* (dragonet). *Arnoglossus laterna* (scaldfish) were regularly recorded, but in low numbers.

In the central and northern North Sea one cluster ranged from 50–100 m and another from 100–200 m. Between 50 m and 100 m (Figure 5b, △) fewer of the small, non-commercial species were found. Numbers of *L. limanda* were higher than in the south and *Hippoglossoides platessoides* (long rough dab, Figure 3o) were recorded regularly. In waters deeper than 100 m (Figure 5b, ○), *H. platessoides* was the characterizing species for the community, together with *Myxine glutinosa* (hagfish, Figure 3p). Some ICES rectangles in the far north (Figure 5b, ◇), around the 200 m depth line, were grouped as a third cluster based on the paucity of demersal fish in this area.

For fish caught with the GOV trawl during the survey (source: ICES database) cluster analysis formed three clusters in the south, one in the central and one in the northern North Sea (Figure 5c & d, Table 3).

In the southern North Sea two of the three clusters were spatially dominating, but they were intermixed rather than geographically discrete (Figure 5d, ■●). Both clusters were characterized by a similar range of species, including *Merlangius merlangus* (whiting), *Eutrigla gurnardus* (grey gurnard), *L. limanda* and *Trachurus trachurus* (scad). Differences in abundance of these species were responsible for the separations into two clusters. A third smaller cluster was formed in the far south between the English and Dutch coast (Figure 5d, ▲). Higher numbers of *T. trachurus* and *Scomber scombrus* (mackerel) were recorded in this area.

As with the analysis based on the 2-m beam-trawl samples, there was a division between communities from 50–100 m depth (Figure 5d, ○) and 100–200m depth (Figure 5d, □). The area between the 50 m and 100 m contour was numerically dominated by *Melanogrammus aeglefinus* (haddock), *M. merlangus*, *Clupea harengus* (herring) and *Pleuronectes platessa* (plaice). Between

Table 1. Epibenthic species which account for most of the similarity within the clusters identified by cluster analysis. The symbols for clusters follow Figure 4. "Mean similarity" is the mean similarity within the cluster and "contribution" is the contribution of individual species to the total similarity within the group. Species contributing altogether 60% of the similarity or the six species contributing most to the similarity are shown.

Cluster ▲ Mean similarity: 44.84	Cumulative contribution to similarity (%)	Cluster ● Mean similarity: 49.90	Cumulative contribution to similarity (%)
Pagurus bernhardus	10.30	*Pagurus bernhardus*	23.08
Liocarcinus holsatus	20.59	*Liocarcinus holsatus*	46.16
Crangon allmanni	30.89	*Asterias rubens*	69.24
Ophiura albida	39.63	*Ophiura ophiura*	77.52
Asterias rubens	47.79		
Crangon crangon	54.39		
Cluster ◆ Mean similarity: 42.10		Cluster ■ Mean similarity: 45.08	
Ophiura ophiura	6.29	*Pagurus bernhardus*	9.29
Pagurus bernhardus	12.57	*Asterias rubens*	18.57
Liocarcinus holsatus	18.86	*Astropecten irregularis*	27.86
Alcyonidium diaphanum	25.14	*Corystes cassivelaunus*	36.69
Electra pilosa	30.35	*Liocarcinus holsatus*	43.63
Hydrallmania falcata	35.50	*Ophiura ophiura*	49.43
Cluster ◇ Mean similarity: 42.12		Cluster ○ Mean similarity: 39.85	
Pagurus bernhardus	4.73	*Astropecten irregularis*	5.37
Neptunea antiqua	9.19	*Hyalinoecia tubicola*	10.22
Asterias rubens	13.33	*Hormathia digitata*	14.89
Colus gracilis	17.28	*Echinus* sp.	19.44
Hyas coarctatus	20.96	*Anapagurus laevis*	23.93
Hydractinia echinata	24.59	*Pagurus pubescens*	27.84
Cluster □ Mean similarity: 41.15			
Epizoanthus papillosus	10.14		
Echinus sp.	20.28		
Anapagurus laevis	30.42		
Adamsia carciniopados	40.56		
Caryophyllia smithii	46.07		
Pandalus montagui	51.50		

100 m and 200 m *Trisopterus esmarkii* (Norway pout) was the dominant species in the community.

Environmental factors and fishing effort

Environmental factors were significantly correlated, both positively and negatively, with univariate diversity indices of the epibenthic fauna or fish (Table 4). Numbers of epibenthic species were negatively correlated with bottom temperature and beam trawling effort (Table 4, Figure 6), while they were positively correlated with bottom salinity.

Fewer correlations with environmental factors were found when analysing the southern North Sea (<50 m depth) and central-northern North Sea (>50 m depth) separately, possibly due to lower numbers of samples reducing the power to detect statistical differences. In the southern North Sea numbers of sessile benthic species were negatively correlated with beam trawling effort, but there were no other significant correlations for the benthos. In the northern North Sea numbers of epibenthic species were correlated with several sediment parameters and beam trawling effort (Table 1).

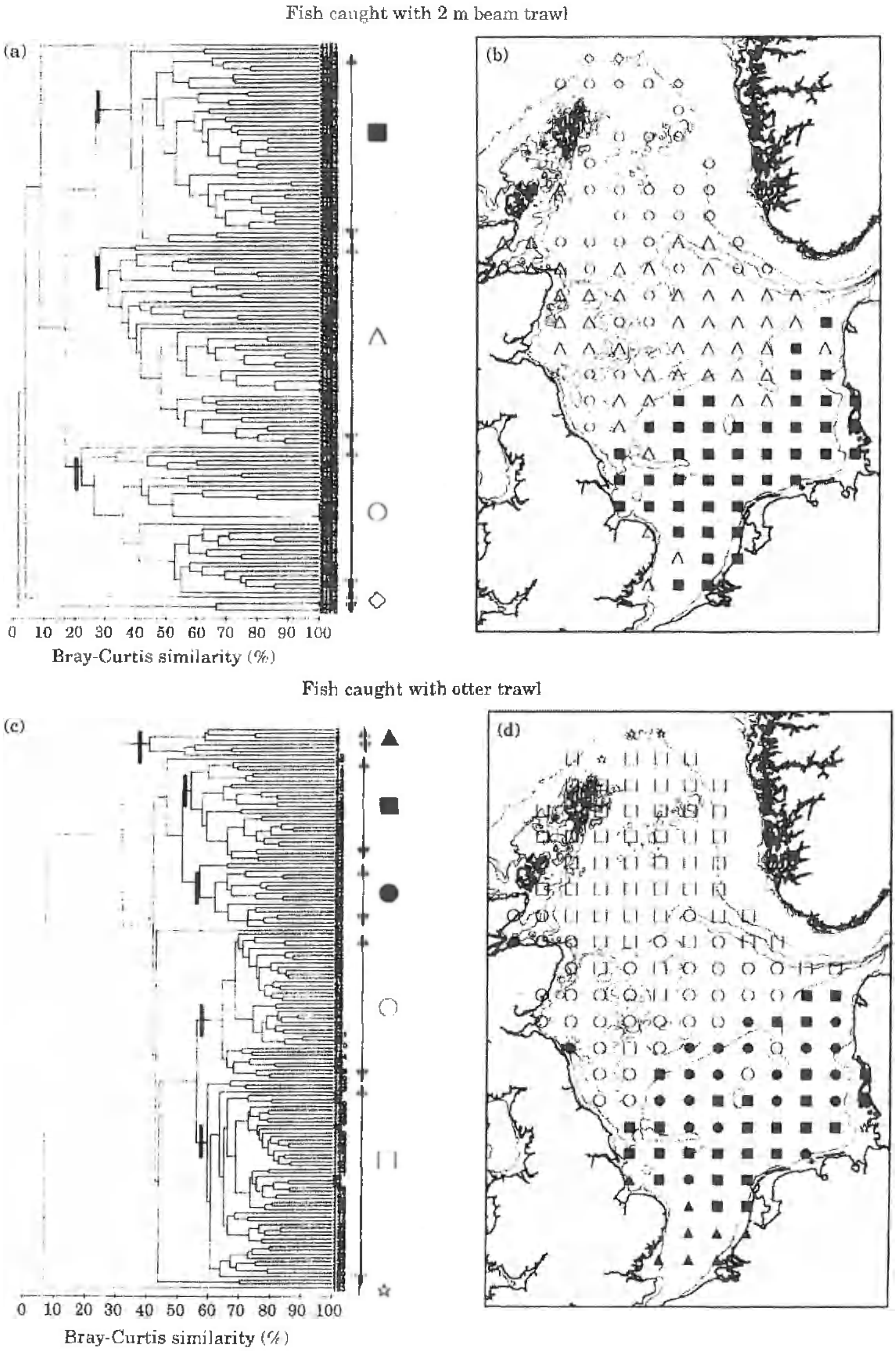


Figure 5. Fish communities in the North Sea in 2000. (a) Hierarchical classification analysis based on 4th root transformed data of fish caught with a 2-m beam trawl. Vertical bars indicate main groupings. (b) Location of fish communities indicated by dendrogram (a). (c) Hierarchical classfication analysis based on 4th root transformed data of fish caught by otter trawling during groundfish surveys (source of data: ICES database). (d) Location of fish communities indicated by dendrogram (c).

Table 2. Fish species caught with the 2-m beam trawl, which accounted for most of the similarity within the clusters identified by cluster analysis. The symbols for clusters follow Figure 5. "Mean similarity" is the mean similarity within the cluster and "contribution" is the contribution of individual species to the total similarity within the group. Species contributing altogether 70% of the similarity are shown.

Cluster ■ Mean similarity: 46.36	Cumulative contribution to similarity (%)	Cluster ○ Mean similarity: 36.05	Cumulative contribution to similarity (%)
Buglossidium luteum	27.47	*Hippoglossoides platessoides*	58.54
Limanda limanda	47.09	*Myxine glutinosa*	71.86
Callionymus lyra	59.48		
Pomatoschistus minutus	70.28		
Cluster △ Mean similarity: 37.88		Cluster ◇ Mean similarity: 35.93	
Limanda limanda	48.16	*Gadiculus argenteus*	100.00
Hippoglossoides platessoides	72.18		

Table 3. Fish species, caught by otter trawling (main groundfish survey), which accounted for most of the similarity within the clusters identified by cluster analysis. The symbols for clusters follow Figure 5. "Mean similarity" is the mean similarity within the cluster and "contribution" is the contribution of individual species to the total similarity within the group. Species contributing to altogether 70% of the similarity are shown.

Cluster ▲ Mean similarity: 47.72	Cumulative contribution to similarity (%)	Cluster ■ Mean similarity: 59.55	Cumulative contribution to similarity (%)
Merlangius merlangus	19.58	*Sprattus sprattus*	19.94
Trachurus trachurus	32.73	*Merlangius merlangus*	37.09
Limanda limanda	43.95	*Limanda limanda*	48.11
Scomber scombrus	51.68	*Clupea harengus*	58.21
Pleuronectes platessa	59.12	*Trachurus trachurus*	64.15
Echiichthys vipera	65.75	*Eutrigla gurnardus*	69.57
Cluster ● Mean similarity: 58.31		Cluster ○ Mean similarity: 69.51	
Limanda limanda	19.66	*Melanogrammus aeglefinus*	20.39
Merlangius merlangus	34.21	*Merlangius merlangus*	34.66
Eutrigla gurnardus	47.40	*Limanda limanda*	47.44
Trachurus trachurus	56.48	*Pleuronectes platessa*	56.56
Scomber scombrus	64.46	*Clupea harengus*	65.05
Pleuronectes platessa	72.31	*Eutrigla gurnardus*	72.99
Cluster □ Mean similarity: 65.57			
Trisopterus esmarkii	22.63		
Melanogrammus aeglefinus	39.64		
Merlangius merlangus	50.52		
Clupea harengus	59.67		
Pleuronectes platessa	67.72		
Microstomus kitt	71.99		

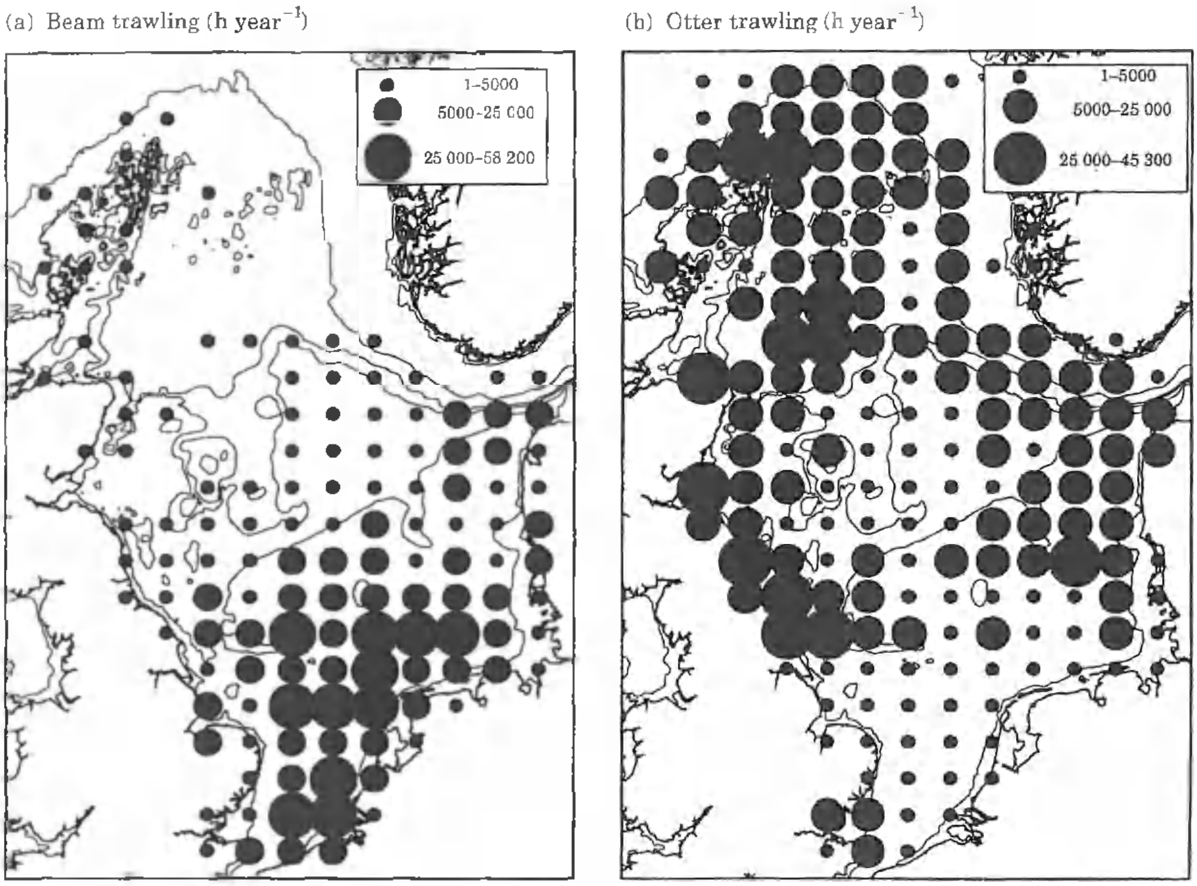


Figure 6. Beam and otter trawling effort 1998 (h ICES rectangle^{-1} year^{-1}). Cumulated data of Germany, The Netherlands, England, Denmark, Norway and Scotland.

The BIO-ENV procedure (Clark and Warwick, 1994) was used to find the combination of abiotic factors which best accounted for the epibenthic community structure (Table 5, Figure 7). In the entire North Sea and in the northern North Sea, bottom temperature, the mud content of the sediment and beam trawling provided the best explanation of epibenthic community structure (Figure 7, Table 5). In the southern North Sea the patterns in community structure were best explained by other sediment parameters, beam trawling effort and otter trawling effort (Table 5).

This analysis was compromized by several inter-correlations between environmental factors. Negative correlations were found for beam trawling and otter trawling, bottom temperature and the amount of mud in the sediment, the 250 μm and 125 μm sediment fraction for stations in less than 50 m depth and bottom temperature and bottom salinity for stations deeper than 50 m. Positive correlations occurred between bottom temperature and beam trawling and beam trawling and the amount of fine sand in the southern North Sea. Clarke and Warwick (1994) suggested substituting correlated factors by just one of them. However, we decided to include all factors in the analysis because the inter-correlations between environmental factors were not consistent for all the spatial areas analysed.

Discussion

The fauna of the southern North Sea was dominated by free-living invertebrates and small demersal fish, while in the north sessile species played a greater role. A hybrid area, with a sessile fauna typical for the northern North Sea and free-living species characteristic for the south, was found off the coast of Norfolk and Flamborough stretching towards the Dogger Bank.

The most conspicuous boundary for North Sea fish and epibenthic communities was the 50 m depth line which separates the southern and central-northern North Sea. The 100 m and 200 m contours can also be viewed as faunal boundaries, but they are less clearly defined than the boundary at 50 m depth. These boundaries are similar to those noted by Künitzer *et al.* (1992) in their study of infauna communities.

Table 4. Significant positive and negative correlations (product moment correlation coefficient (r), $p<0.05$) between univariate indices of the fauna and environmental factors (sediment fraction 1000 μm, 500 μm, 250 μm, 63 μm, <63 μm, bottom temperature, bottom salinity, otter trawling, beam trawling). Correlation analysis was carried out for stations of the entire North Sea (A), for stations shallower than 50 m (B) and deeper than 50 m (C). If an environmental factor is not listed no significant relationship was found. Numbers of fish species were derived from 2-m beam trawl samples. The analysis was based on samples of the English survey.

A. all sampling stations; n=59, r0.05(2),57=0.256	Total number of epibenthic species	Number of sessile epibenthic species	Number of free-living epibenthic species	Hill's N_1 (based on free-living epibenthos)	Number of fish species
Sediment <63 μm (g)		− 0.31			
Bottom temperature (°C)	− 0.67	− 0.50	− 0.67	− 0.54	+ 0.43
Bottom salinity (‰)	+ 0.50	+ 0.37	+ 0.50		− 0.26
Beam trawling (h y^{-1})	− 0.55	− 0.50	− 0.45	− 0.41	
B. stations <50 m depth; n=21, r0.05(2),19=0.433					
Sediment 1000 μm (g)			+ 0.56		
Bottom temperature (°C)					+ 0.44
Beam trawling (h y^{-1})		− 0.44			
C. stations >50 m depth; n=38, r0.05(2),36=0.320					
Sediment <63 μm (g)	− 0.47	− 0.64			
Sediment 63 μm (g)		− 0.60			
Sediment 125 μm (g)		+ 0.43			
Sediment 250 μm (g)	+ 0.38	+ 0.51			
Bottom temperature (°C)					− 0.47
Beam trawling (h y^{-1})	− 0.32			− 0.33	

Epibenthos

The lower epibenthic diversity and species richness in the southern than northern North Sea was consistent with the results of previous studies (Frauenheim *et al.*, 1989; Jennings *et al.*, 1999; Zühlke *et al.*, 2001). However, previous authors did not separate the epibenthos of the south into different communities, mainly due to the constraints imposed by low levels of sample replication and the statistical tools available at that time. We differentiated four communities in the southern North Sea. Their separation was based on the rich sessile fauna off the Norfolk and Flamborough coasts, high numbers of shrimp and prawn species in the far south and the overall scarcity of species along the continental coast.

Several species were ubiquitous in all four communities, such as the brittle star *Ophiura ophiura*, the starfish *Asterias rubens*, the hermit crab *Pagurus bernhardus* and the swimming crab *Liocarcinus holsatus*. Their ubiquity was consistent with patterns described in previous years (e.g. Frauenheim *et al.*, 1989; Jennings *et al.*, 1999; Rees *et al.*, 1999).

We identified three epibenthic communities in the central-northern North Sea, and again, the locations of these communities are broadly consistent with those described in previous reports (Dyer *et al.*, 1983; Basford *et al.*, 1989; Frauenheim *et al.*, 1989; Jennings *et al.*, 1999). The 50 m, 100 m and 200 m boundaries also coincide with the concept of three infaunal étages developed by Glemarec (1973), as confirmed and differentiated by Künitzer *et al.* (1992).

The 50 m depth contour was the southern distribution border for many sessile and free-living species. However, the abundance of free-living fauna in the 50–100 m community was dominated by species which were also found in the south, namely *P. bernhardus*, *A. rubens* and *A. irregularis*. This was in accordance with the results of Dyer *et al.* (1983), who stated that many species which were common at the southern stations were caught in the north. Most conspicuous in the community found at depths of 50–100 m was the diverse sessile fauna, with numerous hydrozoans, bryozoans and tube-dwelling polychaetes. Basford *et al.* (1989) found matching distribution patterns for several of the most common sessile species (e.g. *Alcyonidium digitatum*, *Flustra foliacea*,

Table 5. Relationship between environmental factors and the community structure. The combination of environmental factors, which showed the highest correlation [Spearman rank correlation (ρ)] with the epibenthic community structure are listed. Results are based on multivariate data analysis.

	Entire North Sea	<50 m depth (south)	>50 m depth (north)
All epibenthic species	• Bottom temperature • <63 μm sediment fraction • Beam trawling ρ=0.67	• 250 μm sediment fraction • 125 μm sediment fraction • Beam trawling • Otter trawling ρ=0.50	• Bottom temperature • Bottom salinity • 125 μm sediment fraction • <63 μm sediment fraction • Beam trawling ρ=0.58
Free-living species	• Bottom temperature • <63 μm sediment fraction • Beam trawling ρ=0.61	• 1000 μm sediment fraction • 500 μm sediment fraction • 250 μm sediment fraction • Bottom salinity • Otter trawling ρ=0.56	• 500 μm sediment fraction • 63 μm sediment fraction • Bottom temperature • Bottom salinity • Beam trawling ρ=0.52
Sessile species	• Bottom temperature • <63 μm sediment fraction • Beam trawling ρ=0.60	• 250 μm sediment fraction • 125 μm sediment fraction • Beam trawling • Otter trawling ρ=0.33	• Bottom temperature • Bottom salinity • 63 μm sediment fraction • <63 μm sediment fraction • Beam trawling ρ=0.58

Bolocera tuediae) in this area between 1980 and 1985. North of the 100 m contour, *Echinus* spp. were highly abundant at several stations, as also reported by Dyer *et al.* (1983).

Our results were also consistent with those of previous studies when viewed at a smaller spatial scale. Thus Duineveld *et al.* (1991) separated an epibenthic community situated along the continental coast from an offshore community and other authors found a species rich sessile epifauna off the Norfolk coast (Hamond, 1969; Rees *et al.*, 1999). The presence of the sessile bryozoan *A. diaphanum* in the Dogger Bank area was mentioned by Duineveld *et al.* (1991) and Dyer *et al.* (1983) (both authors used the previous name *A. gelatinosum*).

For the area north of the 100 m contour there are some differences between our results and those of previous authors. For example, Dyer *et al.* (1983) and Basford *et al.* (1989) allocate their northern samples to rather different clusters. An examination of individual species distributions suggests that these differences between clusters do not reflect changes in the spatial distribution of epibenthic communities over time. Rather, they are likely to be the result of different sampling methods and data analysis. Standardization of epibenthic sampling techniques was attempted only recently (Jennings *et al.*, 1999; Callaway *et al.*, 2002).

Fish

Although the two sampling methods, the 2-m beam and otter trawl, would have selected for fish of different sizes and different species, the reported spatial distributions of fish communities are remarkably similar. As with the epibenthic communities, the spatial distribution of fish communities was closely related to the <50 m, 50–100 m and 100–200 m depth bands.

However, because the two types of trawl were catching different species in the community, patterns of species richness were different. With the 2-m beam trawl, which catches small species closely associated with the seabed, we recorded high species-richness in shallow areas of the southern North Sea and along the English and Scottish coast and low species richness in the northern North Sea. With the GOV otter trawl, which most effectively catches demersal species more loosely associated with the seabed (Sparholt, 1990), species richness was highest in the far north, in scattered areas along the English and continental coast, and in the central North Sea. This emphasizes the necessity to integrate results from different survey methods in order to gain a comprehensive picture of the fish fauna.

The fish community patterns were consistent with those described by Rogers *et al.* (1998), who collected samples with a 4-m beam trawl. Rees *et al.* (1999) included fish caught with a 2-m beam trawl into their multivariate analysis of benthic community structure and showed that small flatfish characterized the southern North Sea benthic assemblage. The small flatfish that dominate the southern North Sea bottom dwelling fish community are significant consumers of benthic infaunal production (Braber & de Groot, 1973; Connell and Anderson 1999).

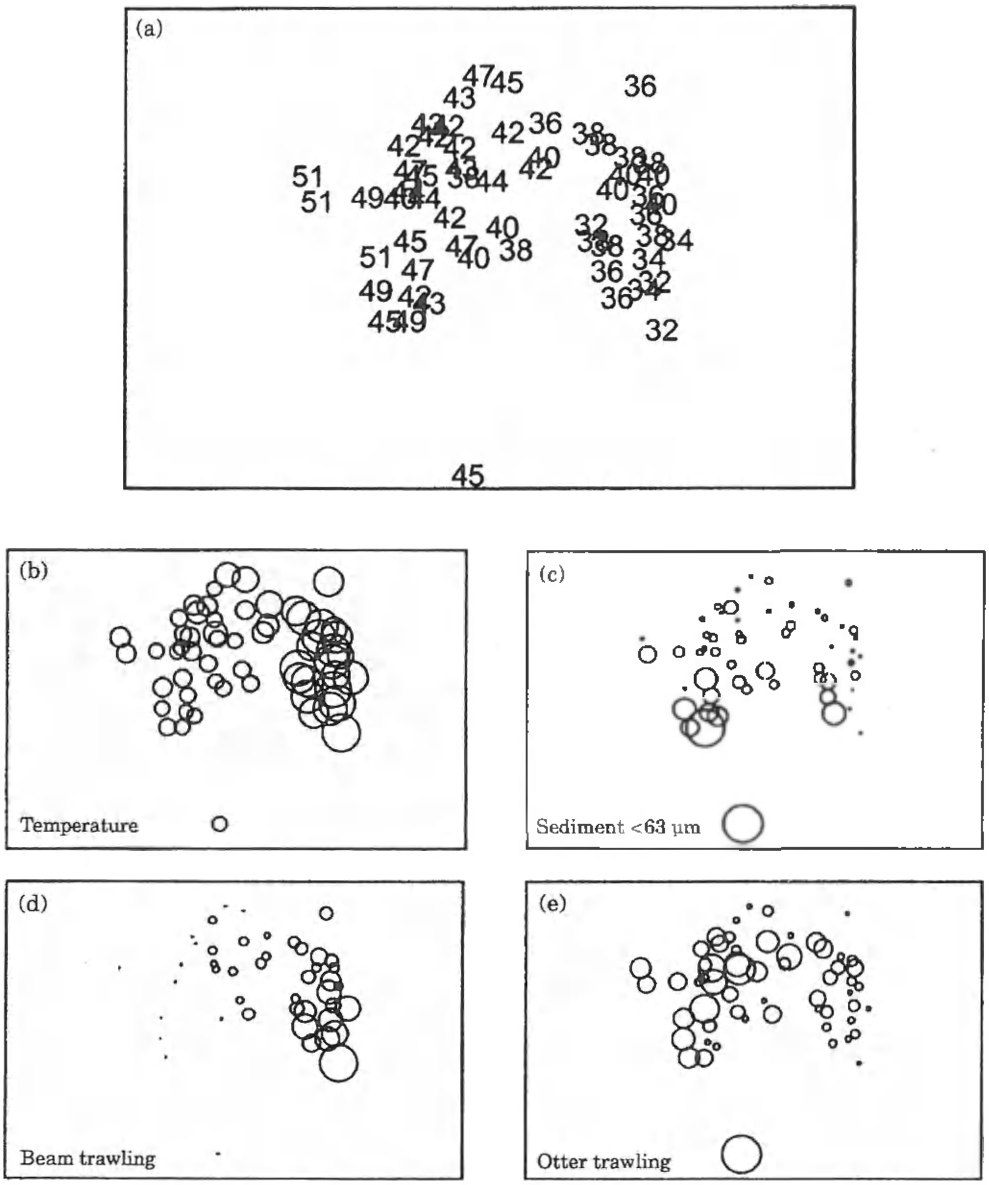


Figure 7. Environmental variables linked to the epibenthic community structure. (a) MDS of epibenthic data, English survey data, presence/absence data transformation, stress 0.18. Numbers show the ICES line a sample was taken; b–e, environmental factors superimposed on MDS. Factors b–d, best explained the ordination (BIOENV correlation analysis).

Environmental factors

Sediment parameters, bottom temperature and fishing effort were all closely correlated with species richness, diversity and community patterns.

Sediment properties are widely regarded as factors influencing the benthic fauna (Basford *et al.*, 1990; Kühne and Rachor, 1996; Rees *et al.*, 1999), although the relationship is clearer for infauna than for epifauna (Basford *et al.*, 1990; Duineveld *et al.*, 1991). The small grab used to sample sediment may provide an impression of habitat type that compromises our attempts to relate sediment properties to the composition of faunal samples taken with 2-m beam trawls. There are two reasons for this. First, the grab does not effectively sample hard substratum such as gravel, rocks or dead shell, which is essential as attachment material for sessile species. Second, the scales at which the beam trawl samples are collected, and the scales at which epibenthic species are likely to "perceive" habitat, are orders of magnitude larger than the scale at which grab samples are taken. To better relate habitat structure to epibenthic and fish samples taken with a 2-m beam trawl requires habitat descriptions that integrate small-scale heterogeneity. Acoustic methods may provide a means by which to achieve this goal. Bottom temperature has a powerful influence on the distribution, abundance and production of benthic fauna (e.g. Duineveld *et al.*, 1991; Brey, 1999). Annual variation in bottom water temperature is most likely to be responsible for the distinctive boundary between communities found south and north of 50 m depth. This depth closely matches the boundary between the thermally stratified waters of the northern North Sea and the permanently vertically mixed waters of the southern North Sea (Brown *et al.*, 1999). Tidal currents maintain a turbulent regime in the southern North Sea, while in the northern North Sea the mixing is weaker and the water column stratifies in response to seasonal heating (Simpson, 1994). This causes higher seasonal fluctuations in bottom water temperature in the south than in the north.

Currents may also determine boundaries between benthic invertebrate and fish communities. Long-term circulation of the North Sea is anticlockwise (Simpson, 1994). However, this is not a basin-wide circulation. In the northern North Sea, the anticlockwise flow takes the form of a well-defined current, the Dooley Current, which follows the 100 m contour (Turrell *et al.*, 1992). Another inflow from the Atlantic enters the North Sea from north of Shetland and follows the 200 m contour along the western edge of the Norwegian Deeps (Dooley, 1974). These currents may influence production, larval and post-larval distribution and may account for some of the community patterns we observe.

Beam trawling is a source of widespread and chronic disturbance in the North Sea. Experimental studies and comparisons between areas subject to different frequencies of trawling disturbance have shown that beam trawling leads to significant mortality of benthic fauna (Bergman and van Santbrick, 2000), reductions in the abundance of species with large body size (Rumohr and Kujawski, 2000) and reductions in production (Jennings *et al.*, 2001). These impacts are reflected in changes in community structure (e.g. Bergman and Hup, 1992; Frid and Hall, 1999; Frid *et al.*, 2000; Lindeboom and DeGroot, 1998). Sessile species are particularly vulnerable to the impacts of trawling (e.g. Collie *et al.*, 1997; Kaiser *et al.*, 1998, 2000; Freese *et al.*, 1999). Our results suggest that beam trawling effort was consistently correlated with benthic community structure, species richness and diversity. However, while Frid *et al.* (2000) and Rumohr and Kujawski (2000) have shown that long-term increases in the frequency of trawling disturbance have accounted for temporal changes in the structure of North Sea benthic communities, the results of our spatial comparisons among benthic communities in areas subject to different levels of trawling disturbance are more difficult to interpret. This is because large-scale patterns of beam trawling effort in the North Sea reflect the availability of substrata that are suitable for beam trawling (e.g. Rijnsdorp *et al.*, 1998). Such substrata are likely to be relatively mobile sediments that do not necessarily provide good environments for the development of a species rich and abundant sessile fauna. Moreover, the natural disturbance that results from wave and tidal action on mobile sediments will favour communities dominated by free-living rather than sessile species. Disentangling the relative roles of fishing, habitat type and natural disturbance in influencing the large-scale structure of benthic communities will require spatial and temporal comparisons among communities in similar physical environments that are subject to different levels of trawling disturbance. To date, such comparisons have involved trade-offs between spatial scale, temporal scale and replication within habitat types. Now that we have shown that large-scale benthic surveys can be run in conjunction with the existing annual fisheries surveys, the annual collection of additional benthic samples within habitat types would allow us to examine the effects of trawling on unprecedented spatial and temporal scales.

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