Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea

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Understanding the structure and interrelationships of North Sea benthic invertebrate and fish communities and their underlying environmental drivers is an important prerequisite for conservation and spatial ecosystem management on scales relevant to ecological processes. Datasets of North Sea infauna, epifauna, and demersal fish (1999–2002) were compiled and analysed to (i) identify and compare spatial patterns in community structure, and (ii) relate these to environmental variables. The multivariate analyses revealed significantly similar large-scale patterns in all three components with major distinctions between a southern community (Oyster Ground and German Bight), an eastern Channel and southern coastal community, and at least one northern community (>50 m deep). In contrast, species diversity patterns differed between the components with a diversity gradient for infauna and epifauna decreasing from north to south, and diversity hotspots of demersal fish, e.g. near the major inflows of Atlantic water. The large-scale hydrodynamic variables were the main drivers for the structuring of communities, whereas sediment characteristics appeared to be less influential, even for the infauna communities. The delineation of ecologically meaningful ecosystem management units in the North Sea might be based on the structure of the main faunal ecosystem components.

Keywords: benthic assemblages, community structure, demersal fish, ecosystem management, species diversity.

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Introduction

The increasing variety of anthropogenic pressures on the marine environment, such as those arising from commercial fisheries, aquaculture, the demand for sustainable energy, and transport routes, have led to the promotion of holistic ecosystem management approaches, including spatial management strategies to minimize adverse effects on ecosystem structure, function, and processes. Understanding the structure of the biological components and their underlying environmental drivers is an essential prerequisite for the development of spatial management units on scales relevant to biological and ecological processes because usually the delineation of these management units is based solely on administrative boundaries and social, economic, or political factors (Reiss *et al.*, 2009).

Habitat classification schemes in marine ecosystems have been based largely on spatial patterns in abiotic variables, with the underlying presumption that these patterns would have both physical and biological significance (Roff *et al.*, 2003; Gregr and Bodtker, 2007). The linkages between environmental and biological variability have to be known, and the environmental variables used within habitat classification approaches must be capable of discriminating variation in biological patterns (Snelder *et al.*, 2007).

The North Sea is one of the most intensively exploited and studied marine ecosystems in the world. It is a shelf sea characterized

by seasonal fluctuations of environmental variables in the shallower southern parts and less variable environmental conditions in deeper water towards the north. The spatial patterns of the benthic fauna of the North Sea were first studied by Petersen (1914, 1918), principally in Danish waters, who identified the key importance of sediment type as a structuring force. Further insights into causal influences on patterns in North Sea macrofauna communities were provided by Stephen (1923) and Ursin (1960). Glémarec (1973) considered that the thermal stability of the water column, i.e. the occurrence and persistence of stratification, was an important explanatory variable for structuring benthic communities. Water temperature regimes broadly matched the limited information then available on the presence of assemblages in the shallow mixed waters in the south, which were distinct from those in the central North Sea between 50 and 100 m deep, and also from those in the areas deeper than 100 m to the north (Glémarec, 1973). However, it was not until 1986 that a coordinated synoptic survey of the benthic infauna of the entire North Sea was conducted, allowing a more rigorous evaluation of distributional patterns against a range of environmental variables (Heip *et al.*, 1992; Künitzer *et al.*, 1992).

The benthic invertebrate fauna is an important component of marine shallow shelf seas with tight bentho-pelagic coupling, such as the North Sea, where they play a vital role in nutrient cycling, detrital decomposition, and as a food source for higher trophic levels. Infauna communities are especially suited to comparative studies of spatial and temporal changes in benthic ecosystems because many species are of low mobility and relatively long-lived and hence integrate the effects of environmental change (Pearson and Rosenberg, 1978; Gray and Elliott, 2009). In contrast, other faunal components, such as mobile demersal fish or invertebrate epifauna, have the potential to avoid unfavourable environmental conditions, at least on smaller scales, or even benefit from disturbances (Kaiser and Spencer, 1994; Ramsay *et al.*, 1998). Studies of spatial patterns of benthic faunal components in the North Sea have focused on the structure of invertebrate benthos, i.e. infauna (Heip *et al.*, 1992; Künitzer *et al.*, 1992; Heip and Craeymeersch, 1995) and epifauna (Frauenheim *et al.*, 1989; Zühlke *et al.*, 2001; Callaway *et al.*, 2002), whereas less detailed information is available for spatial patterns of demersal fish communities (see, e.g., Daan *et al.*, 1990; Greenstreet and Hall, 1996). Only limited effort has been made to examine any interrelationships in community structure and functional role between these divergent components (infauna, epifauna, and fish). For example, Callaway *et al.* (2002) reported on a qualitative comparison between epifaunal and demersal fish communities in the North Sea. A more detailed comparison between these components, which differ in life-cycle traits, mobility, trophic level, and ecological niches occupied, should allow further insights to be gained into the major causal influences of patterns and processes observed.

Therefore, the objectives of this study are to (i) identify and compare the spatial community patterns of infauna, epifauna, and demersal fish of the North Sea using univariate and multivariate analyses, and (ii) relate spatial patterns of the different ecosystem components to environmental variables to gain an insight into the large-scale driving forces and the functional similarities and differences between them.

Material and methods
Sampling and sample processing
The infauna data were compiled and processed within the framework of the ICES North Sea Benthos Project 2000 (NSBP 2000;

Rees *et al.*, 2007). Although quasi-synoptic sampling was intended for late spring to summer in 2000, several regions of the North Sea could only be covered by including material from adjacent seasons or years (from 1999 to 2002). Most of the infauna sampling for NSBP 2000 was conducted with a 0.1 m^2 van Veen grab; Dutch and Scottish samples were obtained with boxcorers, and English samples mostly with a 0.1 m^2 Day or Hamon grab, depending on the sediment type. Samples were sieved over a mesh of 1 mm, before fixation with 4% formaldehyde, except for parts of the samples from Belgian waters, where they were fixed before sieving (Degraer *et al.*, 2007). All infauna data were standardized to 1 m^2. Generally, two or three replicates per station were taken. In total, 808 stations were occupied in this study. A more detailed description of the methods used for sampling and processing the infauna is given in Rees *et al.* (2007).

The epifauna data were collected at 255 stations in summer 2000 (Callaway *et al.*, 2002). Samples were taken with a 2-m beam trawl with a chain mat attached. The mesh size of the net was 20 mm, and a liner of 4 mm knotless mesh was fitted inside the codend. After contact with the seabed, the beam trawl was towed at ∼1 knot for 5 min. To estimate the towing distance and, therefore, the sampled area, a net probe was fixed to the headline of the trawl to determine the exact point in time when the gear touched and left the bottom. Further details of the gear and the sampling procedure are given in Jennings *et al.* (1999), Zühlke *et al.* (2001), and Callaway *et al.* (2002). From the information on towing distances, all data were standardized to a sampled area of 500 m^2. Colonial organisms, infaunal species, and pelagic fish species were excluded from the quantitative analysis.

The data for the demersal fish fauna were extracted from the ICES International Bottom Trawl Survey (IBTS) database. The main objective of the IBTS is to monitor the distribution and relative abundance of demersal fish species in the North Sea (ICES, 2006). The standard gear used within the IBTS is a Grande Ouverture Verticale (GOV) trawl. The height of the gear's vertical opening was some 4.5–5 m, with a wingspread of ∼20 m depending on water depth. The net was equipped with 20-cm-diameter rubber disc groundgear in the bosom, 10 cm rubber discs in the net wings, with iron discs fixed between them. The codend contained a liner of 20 mm mesh. The standard towing time was 30 min at a target speed of 4 knots over the ground. All catch data were standardized to a tow duration of 60 min (catch per unit effort). The standardization to 60 min has historical reasons because all nations fished for 60 min before 1976 (Heessen *et al.*, 1997). Since 1999, all nations fish for 30 min, so a comparison of species composition and diversity measures is possible, although diversity will be underestimated because of the one-sided raising of abundance values. Detailed characteristics of the standard GOV and of the sampling procedure are given in ICES (2006). Only data collected in summer 2000 (quarter 3) were used; 316 stations in all. Pelagic fish species caught were omitted from the analysis.

The environmental variables used were depth, sediment characteristics (% mud, sand, and gravel), average water temperature and salinity (winter and summer), stratification of the water column, chlorophyll content of the surface water column, tidal stress, and peak wave stress.

Most NSBP 2000 data contributors collected information on sediment granulometry during the infauna surveys, but procedures were not standardized, so all sediment datasets were collated into a uniform database. The datasets for which fractional

data were available were reprocessed to yield uniformly calculated means, sorting coefficients, and descriptive assessments. The program GRADISTAT, version 4.0 (Blott and Pye, 2001) was used for analyses. The final dataset contains percentages for mud content (grain size <63 μm), sand (63–2000 μm), gravel (>2000 μm), median grain size, and sediment sorting coefficient, except the data for the Dutch continental shelf, for which only median grain size and mud content were available.

Data on temperature and salinity were derived from the hydro-dynamic HAMburg Shelf Ocean Model (HAMSOM), which is a three-dimensional, baroclinic primitive equation for simulations of oceanic and coastal and shelf sea dynamics (Backhaus, 1985). It has a horizontal resolution of 12 min of latitude and 20 min of longitude, and a vertical resolution of a maximum of 19 layers. For details about the specific HAMSOM application, see Pohlmann (1996).

The ECOlogical North Sea Model HAMburg (ECOHAM1) was used to estimate the primary production of the water column. ECOHAM1 is a model that can be used to calculate annual and long-term phytoplankton dynamics, nutrient transport, and primary productivity for shelf seas in a three-dimensional physical environment (Skogen and Moll, 2005). It is based on a simple phosphorus/nitrogen cycle and takes four state variables into account, three pelagic variables [phytoplankton, phosphate (DIP), and nitrogen (DIN)], and one for benthic detritus. The horizontal grid size of the numerical model is 20 × 20 km, the vertical resolution is 5 m for the upper 50 m, and increasing layer thickness below 50 m up to a maximum of 19 layers. The ECOHAM1 model was validated using observed chlorophyll (Moll, 1998), phosphate concentrations (Moll, 2000), and primary production values (Skogen and Moll, 2000).

Tidal parameters were generated using a three-dimensional hydrodynamic model (Davies and Aldridge, 1993), run in depth-integrated form on an ~3.5-km resolution grid covering the European continental shelf. Average and peak wave stress were calculated from a 1-year model run covering the period September 1999 to September 2000, on an ~12-km grid, using the WAM spectral wave model run at the Proudman Oceanographic Laboratory (Osuna and Wolf, 2005). The stratification parameter S was derived from the formulation presented in Pingree and Griffiths (1978), using modelled M2 tidal velocities and measured depths at the benthic stations.

Data analysis

As a measure of diversity, we calculated species number, Shannon–Wiener Index (H'), Hurlbert index (expected number of species in 50 individuals; ES50), and Pielou's evenness (J'). Inverse distance weighted interpolation (ArcGIS 9.0) was used for mapping univariate faunal variables. Interrelationship among the univariate variables of the infauna, epifauna, and fish communities, such as diversity measures and abundance, and between environmental and univariate faunal variables were tested using Pearson product-moment correlation.

To permit direct comparison of the spatial patterns of the different components, the datasets (infauna, epifauna, and fish) were reduced to stations with matching position or at least positions relatively close to each other (Rees *et al.*, 2007). The nearest stations were determined using GIS software (ArcView 3.1), and a dataset was created including only stations up to a maximum distance of 21 nautical miles apart (a total of 130 matching stations). This distance was chosen because most of

the station combinations were below this value, and an extension of the distance would have included stations with a distance above the edge-length of an ICES rectangle (30 nautical miles), which was originally set as the maximum distance. In cases where more than one station was situated within the 21-nautical mile zone, the nearest station was chosen.

Multivariate ordination methods were applied to analyse the community structure of the infauna, epifauna, and demersal fish, and the relationship between community structure and environmental variables. Hierarchical cluster analysis was carried out with the statistical package PRIMER 6 (Clarke and Warwick, 1994), using fourth-root transformed abundance data and the Bray–Curtis similarity index with a group average method of linkage. For the community analyses of infauna, epifauna, and fish, the complete station grids were used. Only stations within clusters of more than five stations or very distinctive clusters with more than three stations were used for further analyses, reducing the number of stations for infauna from 808 to 728, for epifauna from 255 to 217, and for fish from 316 to 303. SIMPER (Primer statistical package) was applied to identify characteristic species of the communities.

The similarity among the community structures was tested using the RELATE routine in PRIMER 6, based on the reduced datasets. Different transformation types were used (presence/absence, fourth-root, and no transformation) to explore the relative importance of abundant or rare species. The relationship between environmental variables and community structure was evaluated by calculating Spearman rank correlations between the similarity matrices, using the BIOENV routine of PRIMER. The similarity matrix for the environmental variables was calculated using normalized Euclidean distance.

Additional multivariate analyses were performed based on abundance data using CANOCO 4.5 (ter Braak and Smilauer, 1998). The gradient length was determined using detrended correspondence analysis. The length of gradient expressed in standard deviation (s.d.) units is a measure of how unimodal the species responses are along an ordination axis. As all values were >3.5 s.d., subsequent analyses were based on unimodal species-response models (Jongman *et al.*, 1995; ter Braak and Smilauer, 1998). Therefore, the relationship between the community structure of the faunal components and environmental variables was analysed further via canonical correspondence analysis (CCA). Forward selection was performed to order the environmental variables according to the amount of variance they captured in the species data (ter Braak and Verdonschot, 1995). Statistical significance was tested using a Monte Carlo permutation test (999 unrestricted permutations).

Results

In all, 489 infauna, 280 free-living epifauna, and 62 demersal fish species were recorded.

Abundance and diversity patterns

High values of abundance for all three ecosystem components were found in the coastal areas of the southern North Sea (Figure 1a–c). A contrasting pattern was found for fish and epifauna abundance, with the highest values in the eastern parts for epifauna, and in the western parts for demersal fish (Figure 1). There was no significant correlation for the abundances of infauna, epifauna, and demersal fish (Table 1).
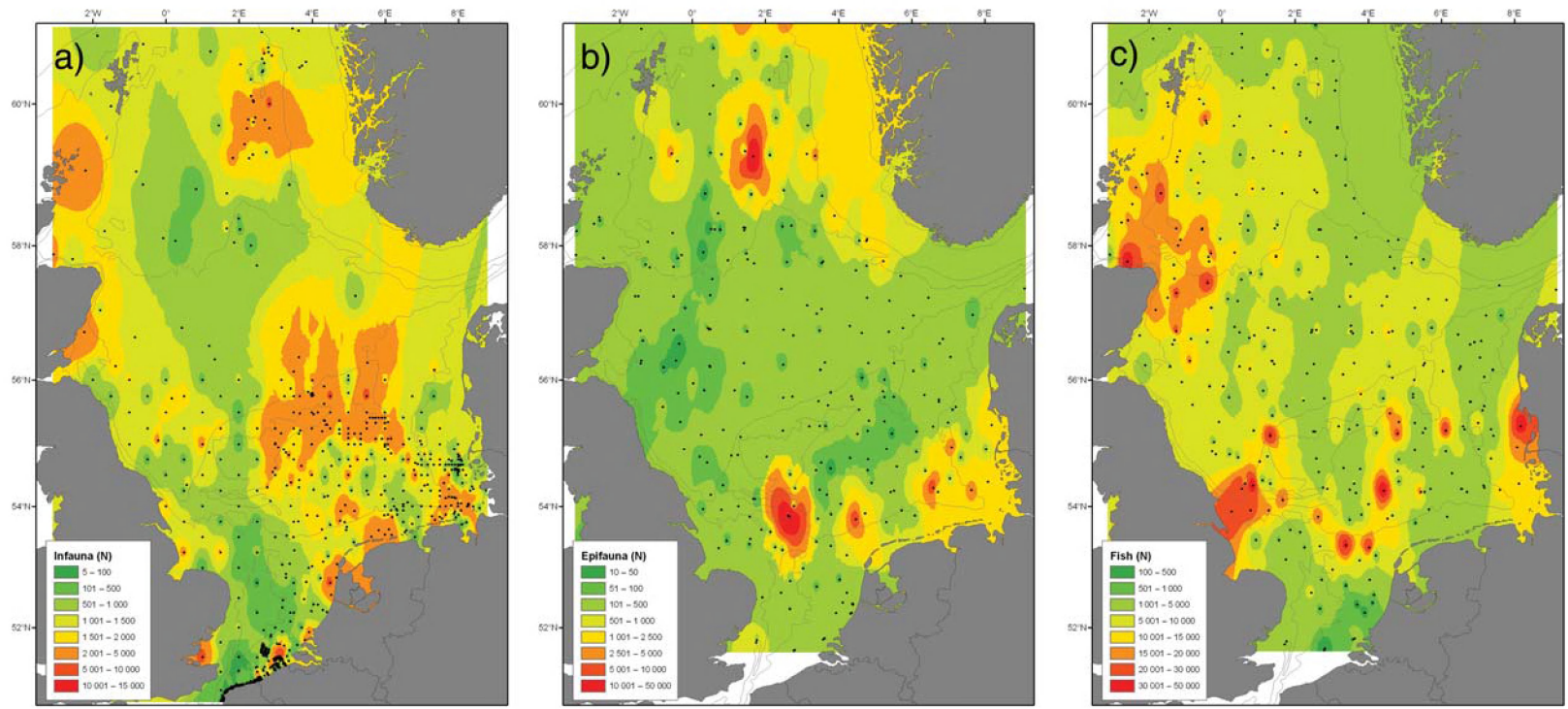
Figure 1. Abundance of (a) infauna (ind. m^{-2}), (b) epifauna (ind. 500 m^{-2}), and (c) demersal fish (catch rate, catch per unit effort).

Table 1. Correlation coefficients relating univariate parameters of infauna, epifauna, and fish.

Parameter	Infauna vs. epifauna	Infauna vs. fish	Epifauna vs. fish
Abundance	−0.070	−0.068	0.099
Species number	**0.302****	0.092	0.153
Shannon–Wiener Index (H')	−0.092	−0.100	0.153
ES50	0.060	−0.127	**0.181***
Evenness (J')	−0.120	−0.095	0.010

Statistically significant correlations are emboldened (**$p < 0.01$ and *$p < 0.05$).

Species number of infauna showed a clear gradient, increasing from the southern towards the northern North Sea (Figure 2a). The same gradient was found for epifauna species numbers, whereas maximum numbers of fish species were found in the southwestern North Sea, along the English coast, and around the Shetlands (Figure 2b and c). The comparison of species numbers of the different faunal components revealed a significant positive correlation between infauna and epifauna species numbers, but no significant correlation between the other combinations (Table 1). Values of diversity indices, such as the expected number of species per 50 individuals (ES50) for the infauna and epifauna, were also lower in the southern than in the northern North Sea (Figure 3a and b). In contrast, the demersal fish fauna showed a maximum ES50 in the central North Sea between the 50- and the 100-m depth contours, and around the Shetlands (Figure 3c). There was a significant positive correlation between the ES50 of epifauna and fish, but no significant relationship for other diversity indices (Table 1). The results therefore indicate more similar patterns in diversity measures between infauna and epifauna than between epifauna and demersal fish or between infauna and demersal fish.

The results of the comparison with diversity variables should be interpreted with care, because of the species–area dependence of most diversity indices (except of ES50) and species numbers. The standardization of the sampled area, as described above, would especially have led to erroneous diversity results, if the realized sampled area had varied strongly between the samples. However, owing to the consistent sampling procedure for all faunal components, this was rarely the case (see above).

Community structure

For all faunal components, a separation of station clusters between the southern North Sea (<50 m) and the northern North Sea (>50 m) was found (Figures 4 and 5). The distinction between communities separated by the 100-m depth contour was evident for epifauna and demersal fish, but less pronounced for infauna. Within the southern cluster, a further separation between the eastern Channel and the southeastern North Sea was obvious for epifauna and fish. There, the infauna community consisted of a mixture of distinct assemblage types, especially near the English Channel and along the English east coast (Figure 5a). This high community diversity also prevailed along the coast of the southeastern North Sea, although one community (cluster C1) was dominant. As the coastal areas are not well represented in the station grids for epifauna and demersal fish, comparable patterns could not be identified. In the northern North Sea, there was a distinct cluster of stations north of the Shetlands. In contrast to the

infauna and epifauna communities, a distinct cluster of stations situated along the Norwegian Trench was additionally found for the demersal fish fauna.

The characteristics of the main clusters/communities are listed in Tables 2–4. Despite the relatively clear distinction between the clusters of the demersal fish communities, there was a high degree of similarity between all samples (similarity between 20 and 40%; Figure 4). This indicates that the distinctions between the clusters are mainly caused by differences in the abundance of the dominant species. In contrast, the distinctions between infauna and epifauna clusters were caused mainly by variation in the distributions and densities of a wide array of characterizing species, resulting in rather low levels of similarity.

The comparison among similarity matrices of the infauna, epifauna, and fish datasets revealed that the spatial community patterns of all components were significantly correlated with each other (Table 5).

Relationship between faunal patterns and environmental variables

The relationships between diversity measures (species number, ES50) of infauna and epifauna with the environmental variables were significant usually, but not for tidal stress, stratification (epifauna), and mean grain size (infauna and epifauna). The weak correlation between infauna species number and mud content and between epifauna ES50 and depth was not significant after Bonferroni correction ($p > 0.0042$). The highest values of r were found for hydrographic variables such as temperature and salinity, as well as for water depth (Table 6). In contrast, only few weak correlations were found for diversity measures of demersal fish, which were not significant after Bonferroni correction ($p > 0.0042$).

The relationship between infauna abundance and environmental variables showed significant correlations only with hydrographic variables such as tidal stress and stratification (Table 6). Epifauna abundance and the demersal fish abundance showed no significant linkages with environmental variables (Table 6). However, these correlation analyses can only provide a rough estimate of the relative importance of environmental variables, rather than precisely reflecting the relationships.

The significant relationships between the similarity matrices of all three faunal components (Table 5) suggest that the community patterns may be triggered by the same underlying environmental variables. This is supported by the BIOENV results revealing comparable relationships between the similarity matrices of the faunal components and the environmental variables for all three components. In general, highest values of r were found for the main hydrographic variables such as summer bottom water temperature, stratification, and salinity, whereas the lowest values of r were found for the relationship with sediment variables such as mud content, as well as with the chlorophyll content of the water column (Table 7). Differences among the faunal components in their relationship with the environmental variables were mainly found for tidal stress and stratification, with a relatively low value of r for epifauna, and high values for infauna and demersal fish (Table 7).

The more detailed results of the CCA also suggest some differences among the faunal components concerning the linkages with the environmental variables. The CCA with environmental variables revealed that the first two canonical axes explained only 12%, 6% (but both significant at $p < 0.05$), and 5% of the variance in the fourth-root transformed abundance data of infauna,
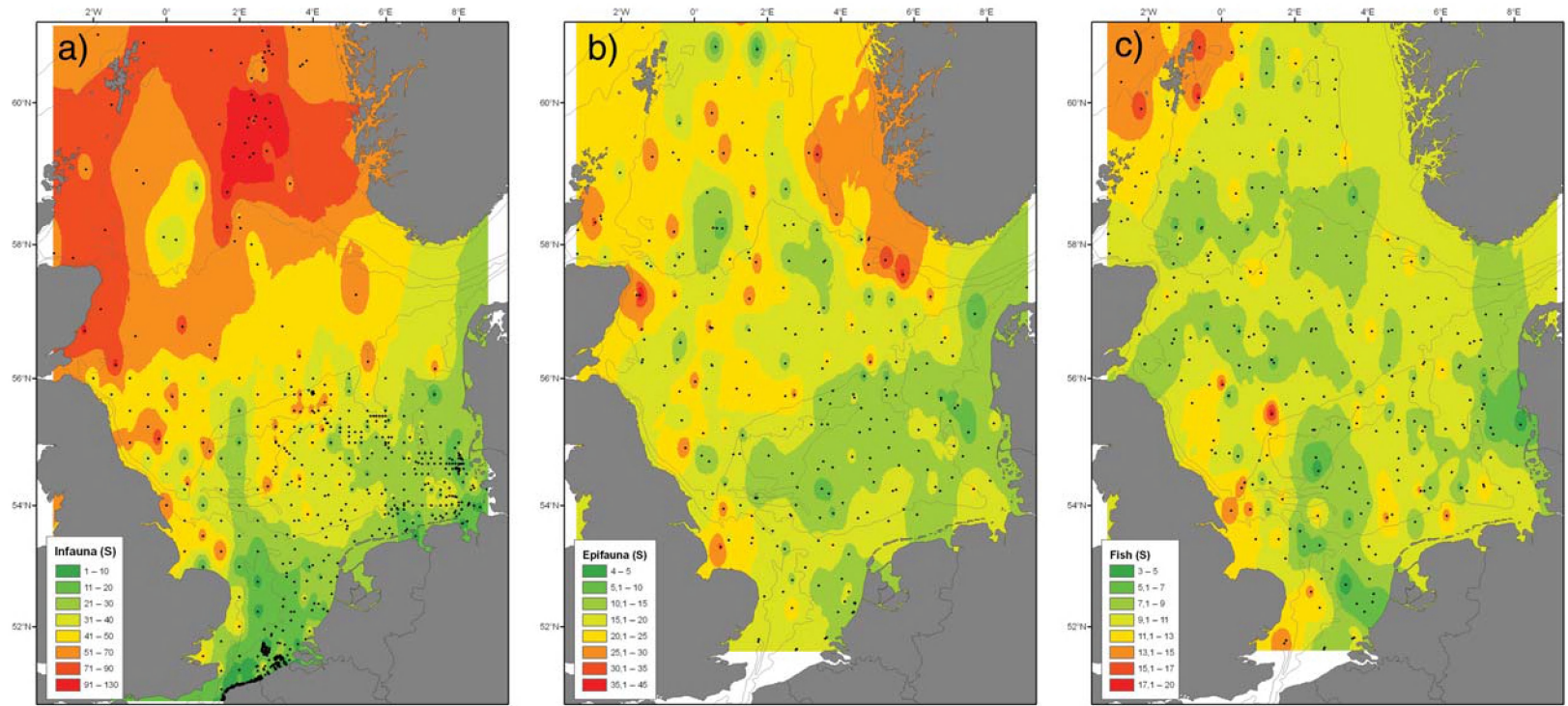
Figure 2. Species number of (a) infauna (S sample^{-1}), (b) epifauna (S haul^{-1}), and (c) demersal fish (S haul^{-1}).
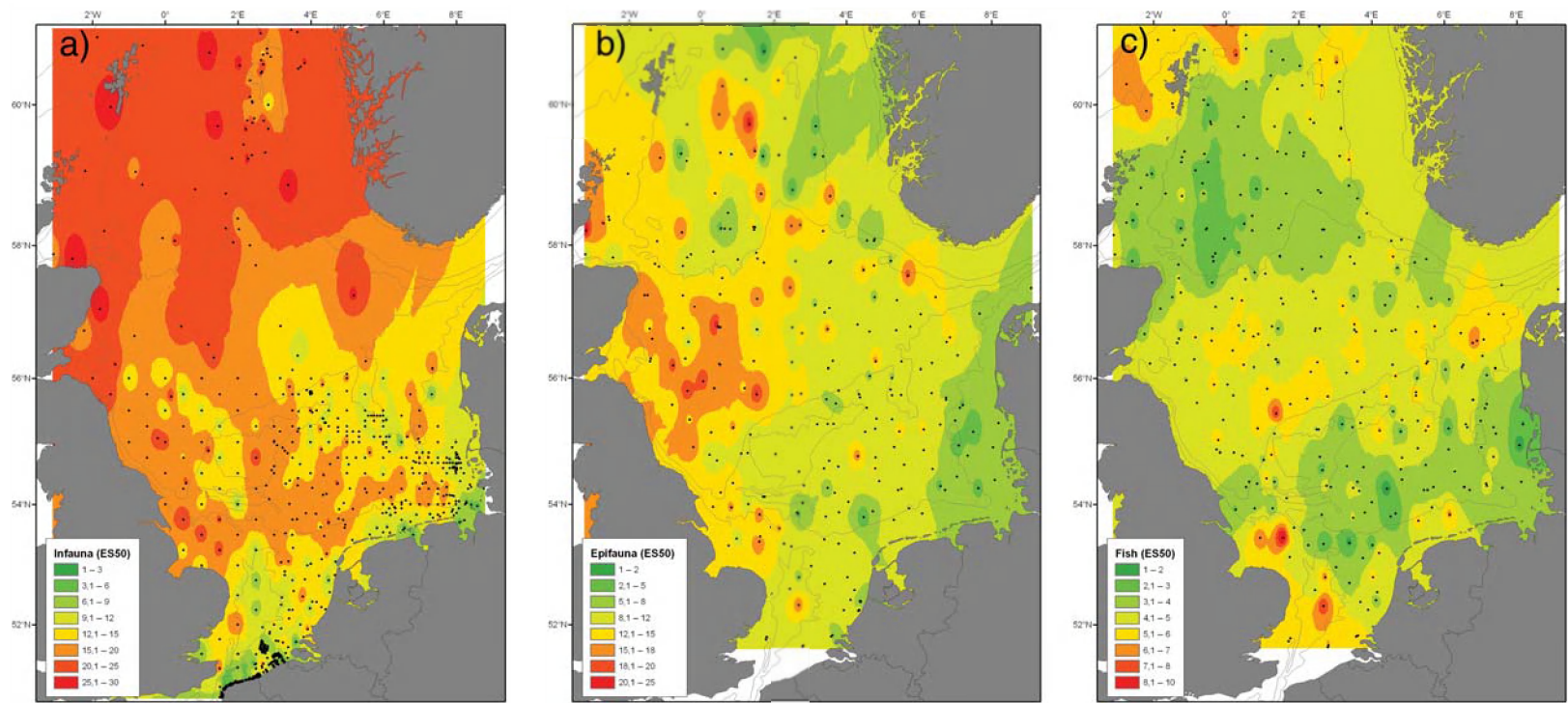
Figure 3. Hurlbert Index ES50 of (a) infauna, (b) epifauna, and (c) demersal fish.
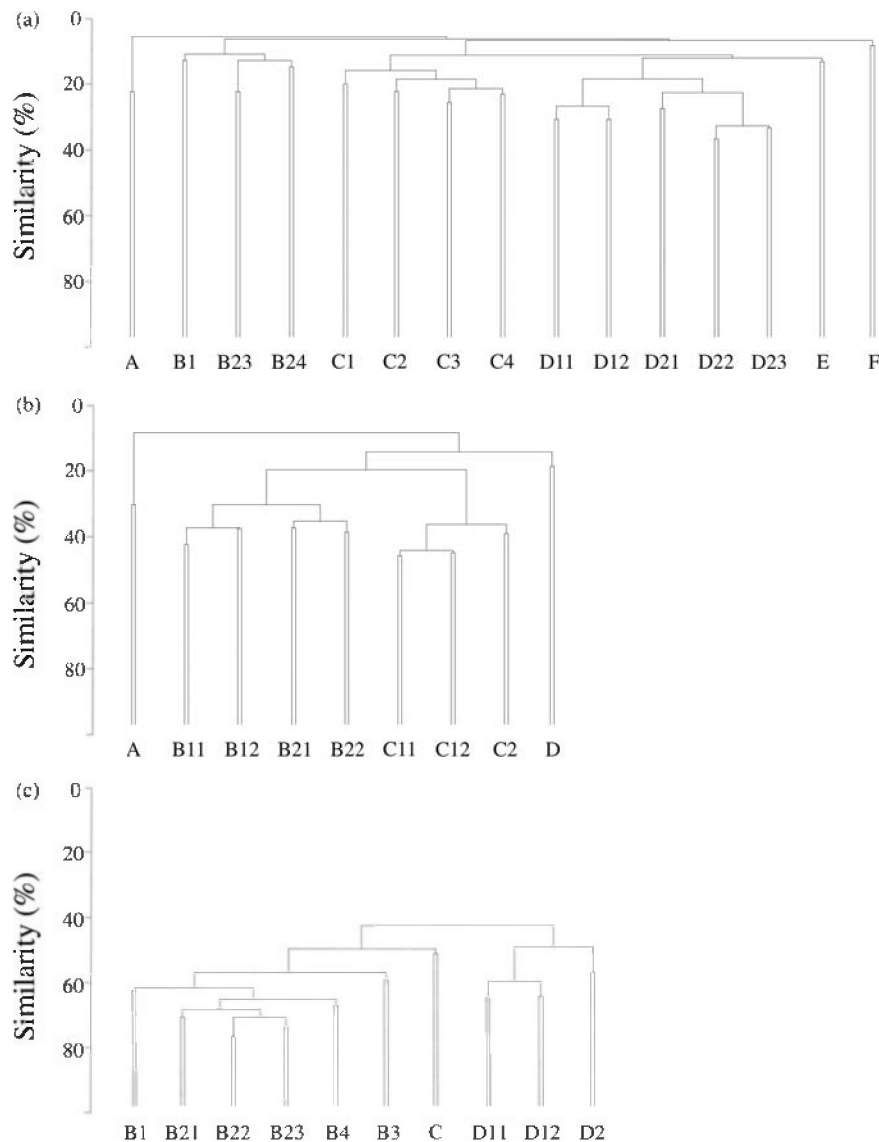
Figure 4. Schematic cluster dendrogram and groupings shown in Figure 5 revealed with fourth-root transformed abundance data of (a) infauna ($n = 808$), (b) epifauna ($n = 255$), and (c) demersal fish ($n = 316$).

epifauna, and fish, respectively. The forward selection showed that most variables significantly explained the variance in the infauna abundance data as sole predictors (marginal effects) and were also significantly stepwise included in the CCA model (conditional effects; Table 8). In contrast, just depth, mud content, and summer temperature were significantly included in the model for epifauna abundance, and only winter temperature for demersal fish abundance (Table 8).

Discussion

We have compared the spatial patterns of infauna, epifauna, and demersal fish community structure and linked the patterns with environmental factors. The multivariate analyses revealed the presence of similar large-scale patterns of infauna, epifauna, and demersal fish community structure, with major distinctions between a southern community (including the Oyster Ground and the German Bight), an eastern Channel and southern coastal community, and at least one northern community

(>50 m deep), evident in all three components. Also, the direct (multivariate) comparison of the community structure revealed a significant similarity among infauna, epifauna, and demersal fish, suggesting that similar underlying environmental variables may be influencing the community patterns. However, the relationships between community patterns and available environmental variables differed appreciably among components and were always relatively weak for fish community structure.

Species diversity

The intercomparison of univariate measures such as abundance and diversity measures for the different faunal components generally revealed no significant correlations. Only the patterns of species numbers between the infauna and epifauna were highly significantly correlated. However, because of differences in the sampling procedures within the infaunal dataset (Rees *et al.*, 2007), the low and partly unknown catch efficiency of the 2-m beam trawl and the GOV (Ehrich *et al.*, 2004; Reiss *et al.*, 2006), and the area
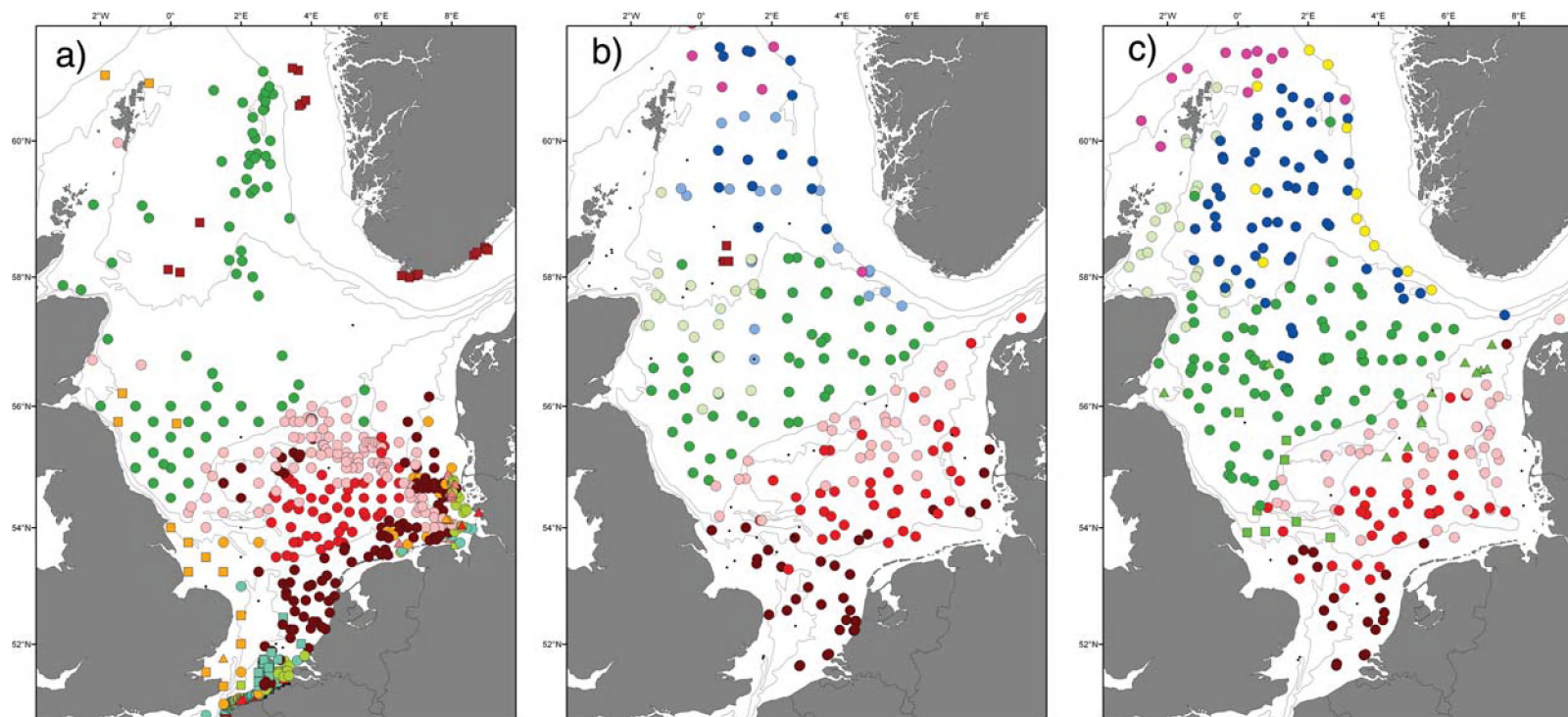
Figure 5. Distribution of (a) infauna, (b) epifauna, and (c) fish assemblages in the North Sea according to cluster analyses with fourth-root transformed abundance data (Figure 4). For further details concerning the infauna community, see Rachor *et al.* (2007).

Table 2. Main infauna assemblages in the North Sea with information on the area, mean water depth (range of water depth), average similarity of each cluster, characterizing and dominant species (identified with SIMPER), and the number of stations in each cluster (for detail, see Figures 4a and 5a).

Cluster	Area	Water depth (m)	Average similarity (%)	Dominant and characteristic species	Stations
A	Norway, Fladen Ground	235 (50–454)	37.6	*Heteromastus filiformis, Paramphinome jeffreysii, Thyasira equalis, Eriopisa elongate*	20
B1	Southern North Sea	30 (17–60)	19.8	*Aonides paucibranchiata, Echinocyamus pusillus, Branchiostoma lanceolatum*	26
B23	Western North Sea and north of Shetlands	48 (21–136)	29.3	*Glycera lapidum, Polycirrus* spp., *Sabellaria spinulosa*	14
B24	Helgoland deep trench and outer Thames	43 (20–56)	26.2	*Scalibregma inflatum, Cerianthus lloydii, Gattyana cirrhosa*	4
C1	Southeastern North Sea	12 (8–21)	30.6	*Nephtys cirrosa, Spisula solida, Ophelia borealis, Tellina tenuis*	28
C2, C3, and F	Southern North Sea	14 (3–41)	29-37	*Nephtys cirrosa, Gastrosaccus spinifer, Magelona johnstoni, Urothoe brevicornis*	75
C4	Inshore southern North Sea	14 (3–32)	13.9	*Nephtys caeca*	7
D11	Offshore southern North Sea, Dogger Bank	22 (4–43)	35.8	*Magelona johnstoni, Spiophanes bombyx, Urothoe poseidonis*	128
D12	Coastal southern North Sea	13 (3–29)	36.7	*Abra alba, Spiophanes bombyx, Magelona johnstoni*	118
D21	Northern and central North Sea	96 (40–185)	36.6	*Myriochele* spp., *Amphiura filiformis, Spiophanes* spp., *Paramphinome jefreysii*	74
D22	Oysterground	43 (31–51)	42.3	*Amphiura filiformis, Corbula gibba, Mysella bidentata*	55
D23	Around Dogger Bank and pleistocean Elbe valley	43 (24–125)	39.3	*Spiophanes bombyx, Amphiura filiformis, Mysella bidentata, Magelona filiformis*	121
E	Inshore North Sea	9 (2–20)	24.6	*Chaetozone* spp., *Abra alba, Nephtys hombergii*	58

Table 3. Main epifauna assemblages in the North Sea with information on the area, mean water depth (range of water depth), average similarity of each cluster, characterizing and dominant species (identified with SIMPER), and the number of stations in each cluster (for detail, see Figures 4b and 5b).

Cluster	Area	Water depth (m)	Average similarity (%)	Characteristic species	Stations
A	Fladen Ground	152 (149–158)	37.40	*Nephrops norvegicus, Pandalus borealis, Myxine glutinosa*	3
B11	Northwestern North Sea	91 (72–118)	44.94	*Pagurus prideaux, Pagurus bernhardus, Anapagurus laevis, Asterias rubens, Hyalinoecia tubicola*	20
B12	Central North Sea	72 (54–112)	43.71	*Pagurus bernhardus, Astropecten irregularis, Asterias rubens, Buccinum undatum, Colus gracilis*	48
B21	Northern North Sea	128 (93–165)	45.88	*Astropecten irregularis, Crangon allmanni, Echinus* spp., *Anapagurus laevis, Hyalinoecia tubicola*	20
B22	Northern North Sea	145 (105–243)	41.15	*Echinus* spp., *Astropecten irregularis, Hyalinoecia tubicola, Luidia sarsi, Anapagurus laevis, Scaphander lignarius*	16
C11	Oyster Ground	44 (21–77)	53.05	*Astropecten irregularis, Asterias rubens, Buglossidium luteum, Pagurus bernhardus*	28
C12	Dogger Bank and area around 50 m contour southern North Sea	46 (34–69)	47.44	*Astropecten irregularis, Pagurus bernhardus, Asterias rubens, Limanda limanda, Corystes cassivelaunus*	39
C2	Southwestern North Sea and eastern Channel	30 (16–68)	46.77	*Liocarcinus holsatus, Ophiura ophiura, Buglossidium luteum, Pagurus bernhardus, Ophiura albida*	36
D	Northern North Sea north of Shetlands	167 (112–205)	25.22	*Echinus* spp., *Anapagurus laevis, Pagurus prideaux, Pagurus bernhardus, Colus gracilis*	7

dependence of diversity measures, a station-by-station comparison is expected to be relatively inaccurate (see also Greenstreet and Piet, 2008). For example, the relationship between sampled area and epifaunal species numbers differs depending on the region within the North Sea (HR, unpublished data). Nevertheless, the lower species number and richness in the southern than in the northern North Sea found for infauna and epifauna was consistent with the results of previous studies (e.g. Frauenheim *et al.*, 1989; Heip

et al., 1992; Callaway *et al.*, 2002). This gradient was even more conspicuous for the diversity of sessile epibenthic species (Callaway *et al.*, 2002), which were excluded from the present study. However, the north–south gradient was not found for demersal fish, with maximum species number near major Atlantic inflows such as the Fair Isles and East Shetland in the north, and the English Channel in the south. This pattern indicates that immigration from adjacent regions into the North Sea is an important

Table 4. Main fish assemblages in the North Sea with information on the area, the mean water depth (range of water depth), the average similarity of each cluster, characterizing and dominant species (identified with SIMPER), and number of stations in the cluster (details see Figures 4c and 5c).

Cluster	Area	Water depth (m)	Average similarity (%)	Characteristic species	Stations
B1	Western central North Sea	75 (51–94)	66.61	*Merlangius merlangus, Melanogrammus aeglefinus, Limanda limanda, Eutrigla gurnardus*	8
B21	Northwestern North Sea	92 (50–120)	75.92	*Melanogrammus aeglefinus, Merlangius merlangus, Microstomus kitt, Limanda limanda*	22
B22	Central North Sea	75 (43–111)	87.86	*Melanogrammus aeglefinus, Merlangius merlangus, Limanda limanda, Hippoglossus platessoides*	82
B23	East of Dogger Bank around 50 m contour	45 (37–58)	76.92	*Limanda limanda, Merlangius merlangus, Melanogrammus aeglefinus, Eutrigla gurnardus*	12
B3	Northern North Sea mainly >100 m	122 (85–153)	71.07	*Melanogrammus aeglefinus, Merlangius merlangus, Hippoglossus platessoides, Gadus morhua*	60
B4	Northern North Sea, Shetlands	150 (96–209)	65.11	*Melanogrammus aeglefinus, Hippoglossus platessoides, Eutrigla gurnardus, Merlangius merlangus*	13
C	Mainly near Norwegian Trench	157 (132–228)	62.22	*Melanogrammus aeglefinus, Pollachius virens, Hippoglossus platessoides, Merlangius merlangus*	12
D11	Oysterground and southwestern North Sea	42 (36–48)	68.16	*Merlangius merlangus, Limanda limanda, Eutrigla gurnardus, Pleuronectes platessa*	35
D12	Dogger Bank and coastal southeastern North Sea	35 (21–58)	65.80	*Limanda limanda, Eutrigla gurnardus, Merlangius merlangus, Pleuronectes platessa*	40
D2	Southwestern North Sea and Channel	32 (24–39)	60.19	*Merlangius merlangus, Limanda limanda, Trachinus vipera, Pleuronectes platessa*	19

Table 5. Correlation coefficients relating the similarity matrices of infauna, epifauna, and demersal fish communities for different transformation types (RELATE).

Transformation	Infauna vs. epifauna	Infauna vs. fish	Epifauna vs. fish
Fourth-root	0.410**	0.568**	0.495**
Presence/absence	0.386**	0.502**	0.369**
No transformation	0.252**	0.332**	0.250**

Statistically significant correlations are emboldened (**$p < 0.01$).

factor in structuring fish diversity (Greenstreet and Piet, 2008). Additionally, high fish species diversity in terms of ES50 was found across the central North Sea between 50 and 100 m deep, similar to the patterns found by Greenstreet and Piet (2008) based on diversity indices N1 and N2. The greater diversity in the central North Sea, situated between the two main communities in the south and the north, might be attributable to an overlap of distributions of the northern and southern fish species there. However, the differences in the patterns of species diversity between the three ecosystem components, in contrast to the significant match in terms of community structure, indicate that different processes may be influencing species diversity patterns on the one hand and community structure on the other. This is also shown by the correlations between environmental variables and univariate faunal parameters, which identified contrasting results for infauna and fish diversity (Table 6).

Community structure

The spatial patterns we observed in infaunal community structure largely match the results of earlier studies. The main division of the infauna in the North Sea was between the deeper northern and shallower southern parts (Glémarec, 1973; Künitzer et al., 1992; Heip and Craeymeersch, 1995), with the 50-m contour as a

boundary for both epifauna and demersal fish (Figure 5). Therefore, this boundary in the central North Sea seems to exist for the majority of benthic ecosystem components (see also Daan et al., 1990; Greenstreet and Hall, 1996; Callaway et al., 2002; Reiss et al., 2003; Fraser et al., 2008; Neumann et al., 2008; Ehrich et al., 2009), as well as for planktonic components (Fransz et al., 1991; Williams et al., 1993; Krause et al., 1995). Another distinct community evident in all three benthic components was found near the Dover Strait and along the eastern English coast. However, for the infauna, that community was characterized by several divergent assemblages, most likely reflecting the relatively heterogeneous seabed substrata in the area. Rachor et al. (2007) showed that the infauna communities farther south in the eastern English Channel are distinct from all other communities in the North Sea. For epifauna and demersal fish, a clear separation between communities in the central North Sea and north of the 100-m contour was evident. This differentiation in the northern North Sea was also found in previous infauna studies, but was not so clear for the infauna in this study, perhaps because of the relatively few sampling stations in the northern North Sea compared with previous studies (Figure 5). However, differentiation of infauna communities was evident at lower similarity levels as well as using Twinspan analysis (Rachor et al., 2007). A distinct community near the Shetlands, for epifauna and demersal fish, was also not apparent in the infauna data, which might have been caused by the inadequate number of infauna stations sampled there (Figure 5).

In some previous analyses (e.g. of epifauna; Callaway et al., 2002), presence/absence transformation was used, which ignores the abundance of species. In this study, the fourth-root transformation was chosen to include both abundant and rare species. However, especially in terms of demersal fish fauna, a few species are dominant, and less abundant species hardly contribute to the assemblage structure. Therefore, the abundant fish species are still the most important for the assemblage patterns found here.

Table 6. Correlation coefficients relating univariate community attributes and environmental variables.

Parameter	Abundance			Species number			ES50		
	Infauna	Epifauna	Fish	Infauna	Epifauna	Fish	Infauna	Epifauna	Fish
Depth (130)	−0.075	−0.001	−0.008	**0.646****	**0.354****	0.034	**0.634****	**0.187*** [b]	0.006
Tidal stress (130)	**−0.265****	−0.009	−0.042	**−0.369****	0.064	−0.042	**−0.321****	0.039	**0.241****[b]
Mean wave stress (130)	0.092	−0.009	0.039	**−0.418****	**−0.322****	−0.148	**−0.382****	**−0.329****	**−0.185***[b]
Peak wave stress (130)	0.153	−0.031	0.031	**−0.404****	**−0.384****	−0.108	**−0.390****	**−0.352****	−0.158
Salinity winter (129)	0.145	−0.011	0.063	**0.676****	**0.316****	0.164	**0.543****	**0.356****	0.081
Salinity summer (129)	0.118	−0.027	0.083	**0.660****	**0.351****	0.155	**0.517****	**0.382****	0.095
Temperature winter (129)	0.066	−0.041	−0.025	**0.560****	**0.333****	0.115	**0.418****	**0.375****	**0.178***[b]
Temperature summer (129)	−0.114	0.033	−0.105	**−0.751****	**−0.344****	−0.170	**−0.630****	**−0.329****	−0.027
Stratification coefficient (130)	**0.268****	−0.040	0.036	**0.433****	−0.028	0.027	**0.353****	0.065	−0.150
Mean grain size (72)	0.091	−0.027	−0.124	−0.010	0.032	**−0.313****	0.016	−0.001	0.079
Mud content (96)	0.029	−0.064	0.128	**0.221***[b]	0.092	0.128	**0.293****	0.059	**−0.223***[b]
Chlorophyll (129)	0.087	0.043	−0.075	**−0.452****	**−0.371****	−0.077	**−0.325****	**−0.412****	**−0.245****[b]

The number of stations compared is shown in parenthesis. Statistically significant correlations are emboldened (**p < 0.01 and *p < 0.05; [b]not significant after Bonferroni correction, *p* < 0.00417).

Table 7. Correlation coefficients (*r*) relating community structure (abundance data) and the environmental variables revealed with BIOENV (99 stations compared).

Parameter	Infauna (*r*)	Epifauna (*r*)	Fish (*r*)
Depth	0.409	0.700	0.505
Tidal stress	0.515	0.141	0.381
Mean wave stress	0.352	0.290	0.431
Peak wave stress	0.220	0.180	0.266
Stratification	0.537	0.135	0.410
Salinity winter	0.470	0.424	0.531
Salinity summer	0.434	0.416	0.487
Temperature winter	0.405	0.462	0.481
Temperature summer	0.526	0.582	0.631
Chlorophyll	0.290	0.358	0.361
Mud	0.163	0.204	0.038

Spatial patterns related to external environmental drivers

For community structures on the scale of the whole North Sea, the most influential environmental variables appeared to be hydrographic variables such as bottom water temperature, bottom water salinity, and tidal stress (for the infauna). In particular, bottom water temperature has a strong influence on the community structure of all three faunal components, as indicated by the results of the BIOENV and CCA analysis. Although the stratification parameter was not significantly correlated with the community structure, it is nevertheless expected to be an important determinant of spatial variation in bottom temperature (see also Heip and Craeymeersch, 1995; Callaway *et al.*, 2002). Therefore, the main boundary between the faunal communities along the 50-m contour also reflects the boundary between the thermally stratified waters to the north and the more or less permanently mixed waters to the south (Brown *et al.*, 1999). The influence of different water masses in the North Sea may also determine the faunal community structures. The main inflow of Atlantic water into the northern North Sea is via the Fair Isle current to the west, and the East Shetland and the Norwegian Trench inflow to the east (Turrell, 1992). The community patterns of epifauna and demersal fish in the northern North Sea closely mirror this current regime, with a separation approximately along the 100-m contour into an eastern and a western community

(Figure 5). Distinct communities were also found near the eastern English Channel, corresponding to the inflow of Atlantic water to the south. Significant linkages between the different water masses and the fish community patterns in the North Sea were found by Ehrich *et al.* (2009) across different mesoscale areas in the North Sea. In contrast, sediment characteristics expressed as mud content appeared to be less influential, even for the infauna communities, which would be expected to be more closely dependent on them than the more mobile epifaunal and demersal fish fauna. It is also important to recognize practical constraints on the facility to quantify environmental variability so as to represent realistically the habitats within or over which the faunal components are sampled. For example, sediment type deduced from a 0.1-m^2 grab sample used for collecting the infauna should provide a realistic habitat descriptor for all the organisms in that sample. However, it may be completely inadequate to describe the sedimentary environment along the entirety of epifaunal or fish trawl tows. Therefore, although it seems biologically plausible to anticipate a reduced dependence of motile epifaunal and fish species on substratum type, sediment descriptors from the infauna survey alone are too narrowly defined to demonstrate this, other than in homogeneous areas. Also, other measures such as sorting coefficients may better describe the dynamic nature of the seabed environment, so may link more closely with measures such as tidal stress, which was an influential variable in this study (see also Rees *et al.*, 1999).

The relative influence of environmental factors on the structure of communities depends on the spatial scale and the environmental gradients under consideration (Menge and Olson, 1990; McArdle *et al.*, 1997; Thrush *et al.*, 1997). Therefore, the relationship we observed between environmental variables and faunal structure seems to be valid on a North Sea-wide scale, but less so on a smaller spatial scale. Sediment characteristics were the most important variables affecting infaunal community structure in the southwestern North Sea (van Hoey *et al.*, 2004; Schratzberger *et al.*, 2006), and epifaunal community structure in the southern North Sea (Rees *et al.*, 1999; Callaway *et al.*, 2002). Moreover, in the southwestern North Sea, the influence of sediment characteristics on community structure was less pronounced or even absent for the epifauna and fish fauna, compared with the infauna (Schratzberger *et al.*, 2006). Hence, on a regional or local spatial scale, the community structure of

Table 8. Results of CCA for infauna, epifauna, and demersal fish based on fourth-root transformed abundance data.

Parameter	Axis 1	Axis 2	Axis 3
Infauna			
Eigenvalue	0.490	0.397	0.253
Species-environment correlation	0.966	0.881	0.901
Cumulative % variance			
of species data	6.6	11.9	15.3
of species environmental relationship	23.7	42.9	55.1
Epifauna			
Eigenvalue	0.305	0.225	0.163
Species-environment correlation	0.716	0.741	0.702
Cumulative % variance			
of species data	3.7	6.3	8.3
of species environmental relationship	24.3	42.1	55.1
Fish			
Eigenvalue	0.079	0.041	0.027
Species-environment correlation	0.520	0.477	0.363
Cumulative % variance			
of species data	3.5	5.3	6.5
of species environmental relationship	34.3	52.1	63.7

	Marginal		Conditional	
	λ_1	*p*-value	λ_a	*p*-value
Infauna				
Temperature summer	0.44	0.001	0.44	0.001
Depth	0.42	0.001	0.18	0.001
Salinity winter	0.41	0.001	0.13	0.001
Temperature winter	0.41	0.001	0.14	0.001
Stratification	0.40	0.001	0.38	0.001
Salinity summer	0.40	0.001	0.09	0.094
Tidal stress	0.37	0.001	0.15	0.001
Chlorophyll	0.37	0.001	0.11	0.002
Mean wave stress	0.36	0.001	0.13	0.002
Mud	0.27	0.001	0.21	0.001
Peak wave stress	0.26	0.001	0.11	0.013
Epifauna				
Depth	0.26	0.001	0.26	0.001
Mud	0.21	0.001	0.15	0.004
Temperature summer	0.20	0.001	0.16	0.003
Temperature winter	0.20	0.001	0.08	0.553
Chlorophyll	0.18	0.001	0.06	0.851
Salinity winter	0.18	0.001	0.11	0.153
Salinity summer	0.17	0.001	0.09	0.396
Mean wave stress	0.15	0.009	0.09	0.585
Peak wave stress	0.12	0.097	0.08	0.469
Stratification	0.11	0.090	0.09	0.385
Tidal stress	0.10	0.298	0.09	0.383
Fish				
Temperature winter	0.04	0.040	0.04	0.040
Temperature summer	0.04	0.046	0.02	0.694
Salinity summer	0.04	0.067	0.02	0.539
Depth	0.04	0.140	0.02	0.810
Salinity winter	0.03	0.198	0.03	0.391
Mean wave stress	0.03	0.213	0.01	0.879
Chlorophyll	0.03	0.257	0.01	0.757
Peak wave stress	0.03	0.244	0.01	0.867
Stratification	0.02	0.739	0.01	0.665
Tidal stress	0.01	0.786	0.04	0.144
Mud	0.01	0.934	0.02	0.649

The marginal effects represent the percentage variance explained by each variable as the sole predictor variable. The conditional effects represent the percentage variance explained by each environmental variable with the variables already selected treated as covariables, based on forward selection.

benthic ecosystem components seems to be influenced mainly by physical habitat characteristics (e.g. bottom topography and substratum type) and biological interactions (e.g. predator–prey relationships, interspecific competition for space, and food supply), whereas on larger scales, community structure seems to be more influenced by hydroclimatic variability. The relative importance of the major influencing factors will vary not only with the spatial scale, but also with the characteristics of the ecosystem component, e.g. between mobile demersal fish and sedentary infauna. This anticipated difference between the ecosystem components was not evident on the scale of the whole North Sea because community structure was similar between all three faunal components.

Implications for ecosystem management

Although each dataset used in this study constitutes the most comprehensive contemporary data available for the North Sea benthic ecosystem components, the data were collected on different occasions and under separate programmes, so no congruent station grid was available. It was therefore necessary to select a subset of stations to allow direct comparison of faunal patterns, which limited the scope and the level of detail of the analyses. To permit a more comprehensive analysis of the faunal patterns and hypothesis formulation for the underlying processes, future monitoring programmes should (e.g. IBTS) aim if feasible to integrate sampling of these faunal components. Such an integrated approach, as promoted by the ICES Transition Group on Integrated Surveys for the Ecosystem Approach (TGISURV), is particularly important because future marine management needs to implement an integrated approach towards the evaluation of anthropogenic impacts across all ecosystem components.

Our study further has provided a glimpse of the possible delineation of biologically relevant spatial management units in the North Sea, going beyond existing administrative and sectoral boundaries (e.g. Douvere *et al.*, 2007; Reiss *et al.*, 2009). To date, spatially defined management units have been based mainly on administrative boundaries and social, economic, or political factors and, at most, on the abiotic characteristics such as hydrographic features or seabed structure among the ecosystem properties (Zacharias *et al.*, 1998; Roff *et al.*, 2003). In fact, the latter criteria should only be used as a proxy for the biological structure if tightly linked to the biological units at the relevant spatial scale (Roff *et al.*, 2003; Snelder *et al.*, 2007; McBreen *et al.*, 2008). When delineating management units, the spatial differentiation directly from spatially and ecologically wide-scale biological data, as presented here, should be considered superior to the use of abiotic proxies alone.

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