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Infauna, epifauna and demersal fish communities in the North Sea: community patterns and underlying processes

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ABSTRACT

In order to provide a broad ecosystem context for the interpretation of the infauna community data revealed during the ‘North Sea Benthos Project 2000’, the data were analysed in conjunction with epifaunal and demersal fish assemblage data collected under other (EU and ICES) auspices. The objectives were to compare the spatial community patterns of all three faunal components and to relate the spatial patterns in the different faunal components to environmental parameters to get insights into their functional similarities and differences.

Patterns in the distribution of infaunal, epifaunal and fish assemblage types determined from cluster analyses were very similar, with major distinctions between the southern (<50 m), central (50-100 m) and northern (100-200 m) North Sea. The degree of similarity was quantitatively assessed for a subset of matching stations. The (multivariate) similarity matrices of all three components were significantly correlated. This supports visual assessments of the disposition of assemblage types across the North Sea, and leads to the conclusion that there appears to be a broad level of consistency in the responses of the infauna, epifauna and demersal fish to widely-operating environmental forces. This was further re-inforced by the outcome of an analysis of inter-relationships with a range of environmental variables, with hydrographic influences being especially important for the community structure. However, their influence on smaller spatial scales appeared to be more variable across the faunal components.

INTRODUCTION

Until now, studies of North Sea faunal communities have focused mainly on the spatial structure of single faunal components such as the infauna (e.g. Heip et al. 1992; Künitzer et al. 1992) and epifauna (Glémarec 1973; Frauenheim et al. 1989; Zühlke et al. 2001; Callaway et al. 2002), whereas less detailed information has been available for spatial patterns in fish communities (Daan et al. 1990; Greenstreet and Hall 1996).

Because of differences in the life-cycle traits and the mobility of the three faunal components, ranging from relatively sessile infaunal species to highly mobile demersal fish species, the community structures as well as the responses to environmental parameters are expected to differ among these faunal groups. Callaway *et al*. (2002) reported on a qualitative comparison of epifaunal and demersal fish communities in the North Sea and found contrary diversity patterns. The linkages and functional relationships between different faunal components of marine ecosystems are particularly important in the light of future marine management strategies, which need to implement an ecosystem approach for the evaluation of anthropogenic impacts across all ecosystem components.

Thus, the main objectives of this paper are (i) to analyse and compare the spatial community patterns of the infauna, epifauna, and demersal fish and (ii) to relate the spatial patterns in the different faunal components to environmental parameters in order to get insights into their functional similarities and differences.

MATERIAL AND METHODS

The community structure of all three faunal components within a spatial range covering the entire North Sea was analysed. Therefore, different datasets had to be used and were provided by several sources.

Infauna

The infauna data were provided by several European Research institutes within the framework of the ‘ICES North Sea Benthos Project 2000’. A detailed description of methods used for sampling and processing the infauna is given in ICES (2007).

Epifauna

The epifauna data were collected in summer 2000 as part of the EU project “Monitoring biodiversity of epibenthos and demersal fish in the North Sea and Skagerrak”. 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 approximately 1 knot for 5 min. 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. Modular organisms, infaunal species, and pelagic fish species were excluded from the quantitative analysis.

Demersal fish

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, *inter alia*, to monitor the distribution and relative abundance of all demersal fish species in the North Sea (ICES 2006). The standard gear used in the IBTS is a Grande Ouverture Verticale (GOV). The height of the gear's vertical opening is approximately 4.5 to 5 m, with a wingspread of around 20 m depending on the water depth. The net is equipped with 20-cm diameter rubber disk groundgear in the bosom and 10-cm rubber disks in the net wings with iron disks fixed between them. The codend has a fine mesh liner of 20-mm mesh opening. The standard towing time is 30 min at a target speed of 4 knots over ground. Detailed characteristics of the standard GOV and the sampling procedure are given in ICES (2006). Only data collected in summer 2000 (quarter 3) were used. Pelagic fish species were omitted prior to analyses.

Environmental parameters

The environmental parameters were compiled from a variety of sources within the framework of the 'ICES North Sea Benthos Project 2000'. The sediment granulometry was measured during the sampling of infauna by the NSBP partners, whereas data on salinity, temperature, chlorophyll, tidal stress and wave stress were derived from computer models. Water temperature and salinity of the entire water column were modelled using the hydrodynamic **HAM**burg **S**helf **O**cean **M**odel (HAMSOM) (Pohlmann 1991) and the **ECO**logical North Sea Model **HAM**burg (ECOHAM1) was used for modelling the primary production (Moll 1998). Tidal parameters were generated using a three-dimensional hydrodynamic model (Davies and Aldridge 1993) and wave stress was modelled using the WAM spectral wave model (Osuna and Wolf 2004). Further details about the environmental parameters are given in van den Berghe (2007).

Data analyses

Multivariate community analyses were carried out with the statistical package PRIMER 5 (Clarke and Warwick 1994). Hierarchical cluster analysis was carried out using double square-root transformed abundance data and the Bray–Curtis similarity index.

For the community analyses of epifauna and fish, the complete datasets were used. Additionally, all datasets (infauna, epifauna, and fish) were reduced to stations close to each other, to compare the spatial patterns in univariate measures and multivariate outputs. 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 40 km apart (yielding a total of 130 matching stations; Figure 5).

The relationship among the univariate faunal parameters and between environmental and univariate faunal parameters was determined by a Spearman rank correlation.

The relationship between environmental parameters and community structure was determined by calculating Spearman rank correlations between the similarity matrices using the RELATE and BIOENV routines of PRIMER. The similarity matrix for the environmental parameters was calculated using normalized Euclidean distance.

RESULTS

The analyses are divided into two main sections. In the first section, all available stations in each dataset are used in the analyses. Because the infaunal communities have already been described in detail by Rachor et al. (this volume: ICES CM/A:17), only the epifauna and the fish fauna are analysed here. In the second part, infauna, epifauna, and fish are compared, using the matching stations.

Epifauna and fish communities

Abundance and diversity

The highest abundance of epifauna was found in the coastal areas of the southern North Sea and the northeastern North Sea especially along the Norwegian Trench (Fig. 1a). A somewhat different pattern was found for fish abundances with the highest values in the northwestern North Sea and the area between the Dogger Bank and the English coast (Fig. 1b). However, for the epifauna, high mean abundances of small demersal fish species were found in shallower parts of the southern North Sea.

Highest numbers of epifaunal species were found north of the 50-m depth contour, whereas the southeastern North Sea was characterized by low species numbers (4–17 species per haul). Again, the pattern of species numbers of fish differed from the epifauna pattern. Highest values were found in the northern North Sea around the Shetlands and in the southern North Sea and the Dogger Bank area (Fig. 1d). However, species numbers and species richness (Margalef d) were significantly correlated with latitude for epifauna and demersal fish, whereas no significant relationship with latitude was found for other univariate parameters except for evenness (J’) of fish and latitude (Table 1).

Values of diversity indices such as the Shannon–Wiener index and the expected number of species per 50 individuals (ES(50)) for the epifauna were lower in the southern than in the northern North Sea (Fig. 2a and c). In contrast, values of both measures for the demersal fish fauna show a maximum in the central North Sea between the 50- and 100-m depth contour and around the Shetlands (Fig. 2a and c).

Community structure

The cluster dendrograms and the distribution of the epifauna and demersal fish communities are shown in Figure 4a and 4b, respectively. For both faunal components, a clear separation of station clusters between the southern North Sea (<50 m), the central North Sea (50–100 m), and the northern North Sea (100–200 m) was found (Fig. 4). Within the southern cluster, a further separation between the eastern Channel area and the southeastern North Sea was obvious. In the northern North Sea, a distinct cluster was found for stations north of the Shetlands. In contrast to the 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 shown in Table 2 and Table 3. Despite the clear distinction between the clusters of the demersal fish communities, there was a high degree of similarity between all the samples. 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 the epifauna clusters were mainly caused by variation in the distribution and densities of a wide array of characterizing species.

Comparing infauna, epifauna, and fish communities

The station grid on which the comparison of infauna, epifauna, and fish was based is shown in Figure 5. In all, 130 stations were used for the comparison.

Abundance and diversity

The comparison of the univariate measures of the different faunal components revealed a significant positive correlation for species number and species richness (d) as well as a negative correlation for evenness (J') between infauna and epifauna (Table 4). No significant relationship was found between the infauna and demersal fish. Between the epifauna and fish, only the correlation of expected number of species per 50 individuals was significant.

The results of the comparison with univariate parameters should be interpreted with care, because of the species–area dependency of most diversity indices, species number, and species richness. However, the results indicate more similar patterns in diversity between infauna and epifauna compared with epifauna and fish or infauna and fish.

Community structure

In order to compare the spatial community patterns of the different faunal components in the North Sea, the similarity matrices of the infauna, epifauna, and fish datasets were compared by Spearman rank correlation within the RELATE routine of PRIMER. The patterns of all faunal components were significantly correlated with each other. Surprisingly, the highest R value, as an indication of the magnitude of the similarity between the patterns, was found for fish and infauna communities.

In general, the lowest (but still significant) R values were found using untransformed abundance data, whereas the highest R values were found with fourth-root transformed abundance data, indicating the important influence of less abundant species for determining the similarity of the spatial patterns.

However, despite the significance of the relationships between the community patterns, scatterplots of the Bray–Curtis similarities revealed a rather high variability (not shown).

Relationship between faunal patterns and environmental parameters

The relationship between environmental parameters and the univariate faunal attributes is shown in Table 6. Significant correlations between the infaunal and epifaunal diversity measures and the environmental parameters were found in most cases except for mud content (epifauna) and median grain size (infauna and epifauna). In contrast, no significant correlations were found for the demersal fish. The relationship between abundance and environmental parameters was somewhat less pronounced for the infauna and epifauna, as indicated by the comparatively low R values (Table 6). Only the infaunal attributes and fish abundances were significantly correlated with the mud content.

The significant relationships between the similarity matrices of all three faunal components (Table 5) suggested that the community patterns may be triggered by the same underlying environmental parameters. This is supported by the finding that the relationships between the similarity matrices and the environmental parameters were comparable for all three components. In general, highest R values were found for the main hydrographic parameters such as bottom water temperature and salinity and, in particular, summer bottom water temperature (Table 7), whereas the lowest R values were found for the relationship with sediment parameters (mud content). Differences between the faunal components included the relationship between tidal stress and community structure, with the second highest R value for the infauna (0.515) and much lower values for the epifauna (0.141) and fish fauna (0.381).

DISCUSSION

The objective of this section was to compare the community structure of different faunal components of the North Sea ecosystem and to relate these patterns to the environmental parameters.

The multivariate analyses revealed the presence of large-scale patterns in the infaunal, epifaunal, and demersal fish data with major distinctions between a southern community (including the Oyster Ground and German Bight), an eastern Channel and southern coastal community, and at least two northern communities (50–100-m depth and >100-m depth) evident in all three components (see also Rachor et al. 2007). Similar results were found in previous studies of infaunal communities (Heip et al. 1992; Künitzer et al. 1992), epifaunal communities (Jennings et al. 1999; Callaway et al. 2002) , and fish communities (Daan et al. 1990; Greenstreet and Hall 1996).

Furthermore, the results of the direct (multivariate) comparison of the community structure in Table 5, showed a significant similarity between the infauna, epifauna, and demersal fish, suggesting that the same underlying environmental parameters may be influencing the community patterns. On a North Sea-wide scale, the most influential of these appear to be hydrographic parameters such as bottom water temperature, bottom water salinity, and tidal stress (in the case of the infauna). Sediment characteristics expressed as mud content appeared to be less influential, even for the infauna communities, which would be expected to be more closely dependant than the more mobile epifaunal and demersal fish fauna. However, this relationship seems to be valid on a North Sea-wide scale, but less so on a smaller spatial scale. Sediment characteristics were the most important parameter affecting infaunal community structure in the southwestern North Sea (Schratzberger et al. 2006) and epifaunal community structure in the southern North Sea (Rees et al. 1999; Callaway et al. 2002). Furthermore, 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).

Sediment type deduced from the same 0.1-m^2 grab sample used for collecting the infauna should provide an adequate habitat descriptor for the organisms in that sample. However, it must be cautioned that it may be partly or wholly inadequate to describe the sedimentary environment along the entirety of epifaunal or fish trawl tows. Therefore, while it seems biologically plausible to expect a reduced dependency of motile epifaunal and fish species on substratum type, sediment descriptors from the NSBP 2000 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, and hence may link more closely with measures such as tidal stress, which was an influential variable in our study (see also Rees et al. 1999).

The intercomparison of univariate measures such as abundance and diversity for the different faunal components revealed no significant correlations in most cases. Only the patterns of species number and species richness between the infauna and epifauna were highly significantly correlated. However, because of the differences in the sampling procedures within the infaunal dataset (see Section 3), 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 dependency of diversity measures, a station-by-station comparison is expected to be relatively inaccurate. For example, the relationship between sampled area and epifaunal species number differs depending on the region within the North Sea (Reiss, unpublished data). Also, for the expected number of species (ES(50)), which is less dependent on sample size, no significant correlation for the comparison between the infauna and epifauna and the infauna and fish was found. Indeed, only a weak significant correlation between the epifauna and fish was found (Table 4). Thus, the processes influencing diversity patterns on one hand and community structure on the other might be different. This is also indicated by the results of the correlation between environmental parameters and univariate faunal parameters, which showed contrary results for infaunal and fish diversity (Table 6).

Because the data for the infauna, epifauna, and demersal fish were collected on different occasions and under separate programmes, no congruent station grid for all faunal components was available. Therefore, it was necessary to select a subset of matching stations to allow a direct quantitative comparison of faunal patterns, which further limited the scope of the analyses. Future research and development and monitoring programmes should aim at an integrated sampling of these faunal components to enable a comprehensive analysis of the faunal patterns and the underlying processes. These data are particularly important because future marine management strategies need to implement an ecosystem approach for the evaluation of anthropogenic impacts across all components.

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Table 1. Correlation coefficients between latitude and univariate measures for the epifauna and fish. Statistical significance is indicated (**p <0.01 and *p <0.05).

	Epifauna	**Fish**
Abundance	0.007	–0.021
Species number	**0.321****	**0.182****
Species richness (d)	**0.367****	**0.140***
Shannon–Wiener index (H’)	–0.047	0.022
ES(50)	0.045	0.009
Evenness (J’)	**–0.153***	–0.060

Table 2. Main epifauna communities in the North Sea with information on the area, the mean and range of water depth, the average similarity of each cluster, characterizing species, and number of stations in the cluster.

Cluster	**Area**	**Water depth (m)**	**Av. Similarity (%)**	**Characteristic species**	**Stations**
A	Fladen Ground	152 (149–158)	37.40	*N. norvegicus, P. borealis, M. glutinosa*	3
B11	Northwestern NS	91 (72–118)	44.94	*P. prideaux, P. bernhardus, A. laevis, A. rubens, H tubicola*	20
B12	Central NS	72 (54–112)	43.71	*P. bernhardus, A. irregularis , A. rubens B. undatum, C. gracilis*	48
B21	Northern NS	128 (93–165)	45.88	*A. irregularis, C. allmanni, Echinus* spp., *A. laevis, H. tubicola*	20
B22	Northern NS	145 (105–243)	41.15	*Echinus, A. irregularis, H. tubicola, L. sarsi, A. laevis, S. lignarius*	16
C11	Oyster Ground	44 (21–77)	53.05	*A. irregularis, A. rubens, B. luteum, P. bernhardus*	28
C12	Dogger Bank and area around 50-m contour southern NS	46 (34–69)	47.44	*A. irregularis, P. bernhardus, A. rubens, L. limanda, C. cassivelaunus*	39
C2	Southwestern NS & eastern Channel	30 (16–68)	46.77	*L. holsatus, O. ophiura, B. luteum, P. bernhardus, O. albida*	36
D	Northern NS north of Shetlands	167 (112–205)	25.22	*Echinus spp., A. laevis, P. prideaux, P. bernhardus, C. gracilis*	7

Table 3. Main demersal fish communities in the North Sea with information on the area, the mean and range of water depth, the average similarity of each cluster, characterizing species, and number of stations in the cluster.

Cluster	**Area**	**Water depth (m)**	**Av. Similarity (%)**	**Characteristic species**	**Stations**
B1	Western central NS	75 (51–94)	66.61	*M. merlangus, M. aeglefinus, L. limnda, E. gurnardus*	8
B21	Northwestern NS	92 (50–120)	75.92	*M. aeglefinus, M. merlangus, M. kitt, L. limanda*	22
B22	Central NS	75(43–111)	87.86	*M. aeglefinus, M. merlangus, L. limanda, H. platessoides*	82
B23	East of Dogger Bank around 50-m contour	45 (37–58)	76.92	*L. limanda, M. merlangus, M. aeglefinus, E. gurnardus*	12
B3	Northern NS mainly >100 m	122 (85–153)	71.07	*M. aeglefinus, M. merlangus, H. platessoides, G. morhua*	60
B4	Northern NS, Shetlands	150 (96–209)	65.11	*M. aeglefinus, H. platessoides, E. gurnardus, M. merlangus*	13
C	Mainly near Norwegian Trench	157 (132–228)	62.22	*M. aeglefinus, P. virens, H. platessoides, M. merlangus*	12
D11	Oyster Ground and southwestern NS	42 (36–48)	68.16	*M. merlangus, L. limanda, E. gurnardus, P. platessa*	35
D12	Dogger Bank and coastal southeastern NS	35 (21–58)	65.80	*L. limanda, E. gurnardus, M. merlangus, P. platessa*	40
D2	Southwestern NS & Channel	32 (24–39)	60.19	*M. merlangus, L. limanda, T. vipera, P. platessa*	19

Table 4. Correlation coefficients relating univariate measures for infauna, epifauna, and fish. Statistical significance is indicated (**p <0.01 and *p <0.05).

	Infauna vs. Epifauna	**Infauna vs. Fish**	**Epifauna vs. Fish**
Abundance	–0.070	–0.066	0.099
Species number	**0.279****	0.098	0.158
Species richness (d)	**0.358****	0.019	0.133
Shannon–Wiener Index (H’)	–0.099	–0.141	0.159
ES(50)	0.049	–0.11	**0.179***
Evenness (J’)	**–0.177***	–0.097	0.159

Table 5. Correlation coefficients (Spearman rank) relating the similarity matrices of the infauna, epifauna, and demersal fish communities for different transformation types (RELATE). Statistical significance is indicated (**p <0.01).

	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****

Table 6. Correlation coefficients relating univariate community attributes and environmental parameters. Number of stations compared is in parentheses. Statistical significance is indicated (**p <0.01 and *p <0.05).

	Species number			Abundance			ES(50)		
	Infauna	**Epifauna**	**Fish**	**Infauna**	**Epifauna**	**Fish**	**Infauna**	**Epifauna**	**Fish**
Tidal stress (130)	__–0.453__**	0.052	–0.02	__0.289__**	0.148	–0.02	__0.225__**	0.088	–0.058
Wave stress (130)	__–0.464__**	__–0.419__**	–0.09	__0.202__*	0.150	–0.08	__0.442__**	__–0.349__**	–0.093
Bottom salinity winter (129)	__0.730__**	__0.363__**	0.107	0.11	__–0.216__*	__0.175__*	__0.564__**	__0.360__**	0.051
Bottom salinity summer (129)	__0.697__**	__0.373__**	0.135	0.12	__–0.212__*	0.17	__0.526__**	__0.373__**	0.081
Bottom temp. winter (129)	__0.611__**	__0.334__**	0.073	0.01	__–0.202__*	0.13	__0.461__**	__0.338__**	0.114
Bottom temp. summer (129)	__–0.754__**	__–0.339__**	–0.154	–0.13	__0.248__**	__–0.237__**	__–0.589__**	__–0.347__**	–0.042
Mean grain size (72)	0.122	0.143	0.144	–0.050	–0.109	–0.117	0.132	0.135	0.184
Mud content (96)	__0.516__**	0.113	0.00	__0.238__*	–0.04*	__0.248__	__0.434__**	0.030	–0.152
Chlorophyll (129)	__–0.434__**	__–0.368__**	–0.020	0.16	__0.257__**	–0.05	__–0.325__**	__–0.406__**	–0.170

Table 7. Correlation coefficients (R) relating community structure (abundance data) and the environmental parameters (99 stations compared).

	Infauna (R)	**Epifauna (R)**	**Fish (R)**
Tidal stress	0.515	0.141	0.381
Wave stress	0.352	0.290	0.431
Chlorophyll	0.290	0.358	0.361
Bottom salinity winter	0.470	0.424	0.531
Bottom salinity summer	0.434	0.416	0.487
Bottom temp. winter	0.405	0.462	0.481
Bottom temp. summer	0.526	0.582	0.631
Mud content	0.163	0.204	0.038

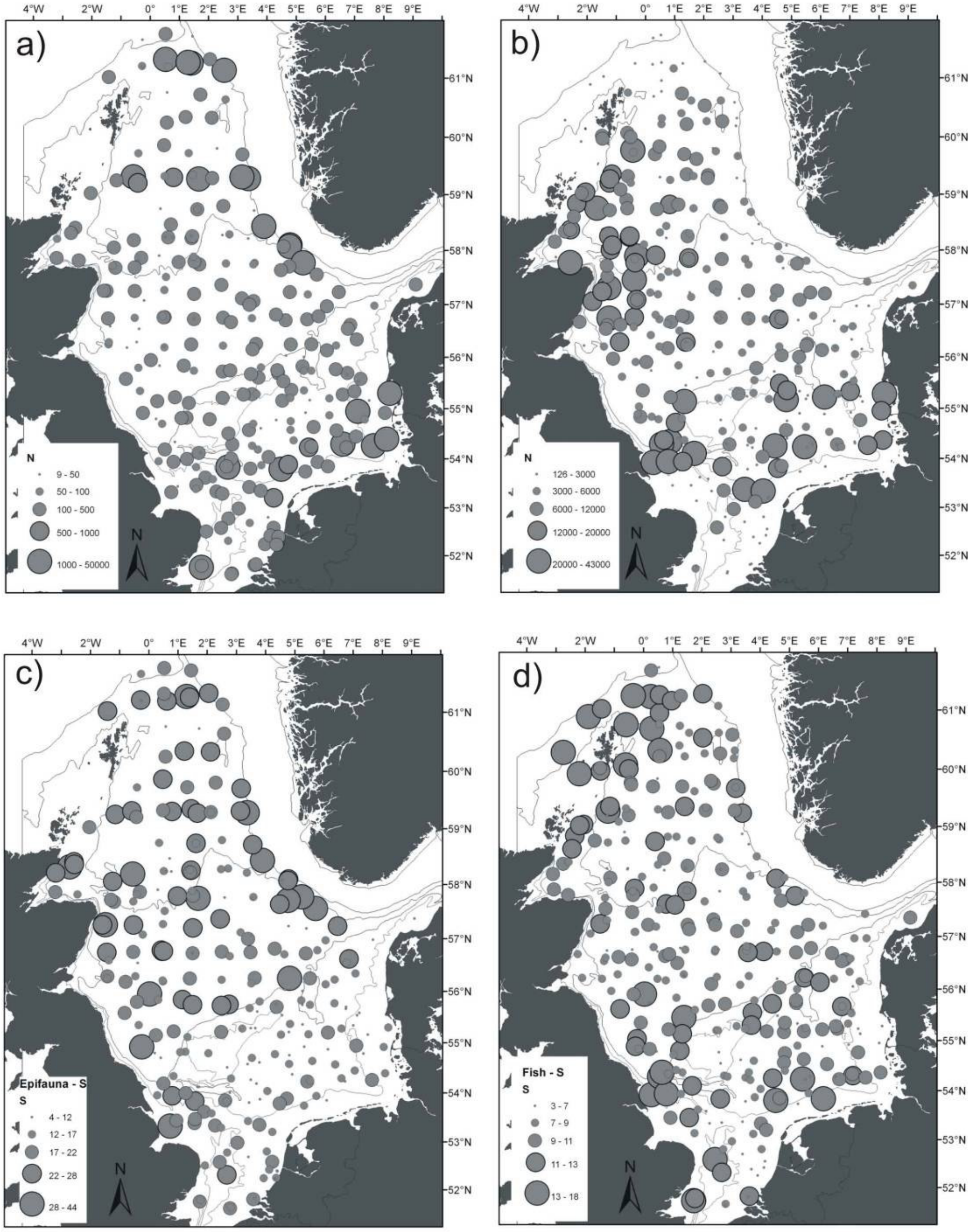

Figure 1. Abundance of (a) epifauna (500 ind/m²) and (b) demersal fish (cpue); and species number of (c) epifauna and (d) demersal fish (S/haul) in 2000.

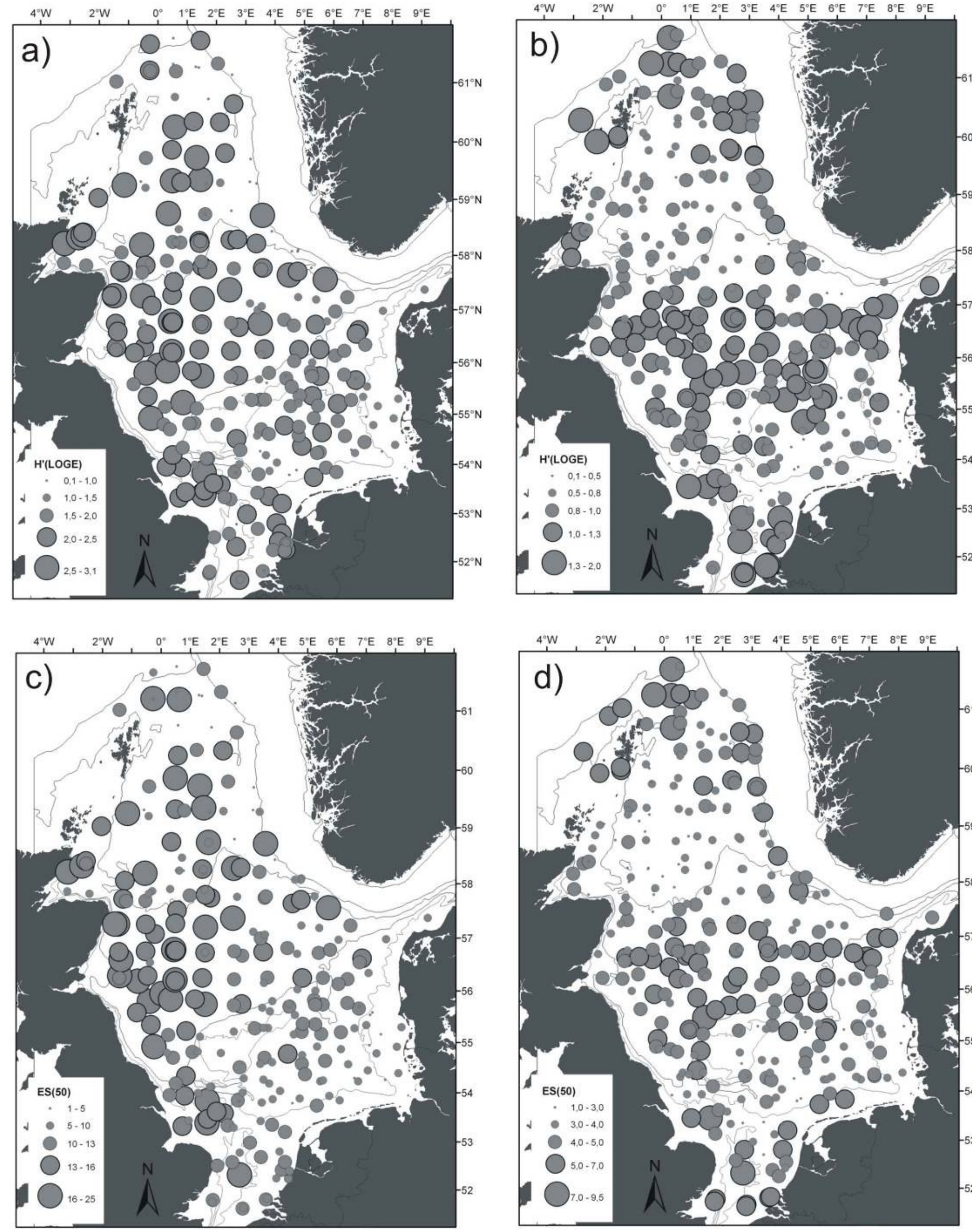

Figure 2 Shannon–Wiener index (H'loge) of (a) epifauna and (b) demersal fish; and the expected number of species per 50 individuals (ES(50)) of (c) epifauna and (d) demersal fish in 2000.

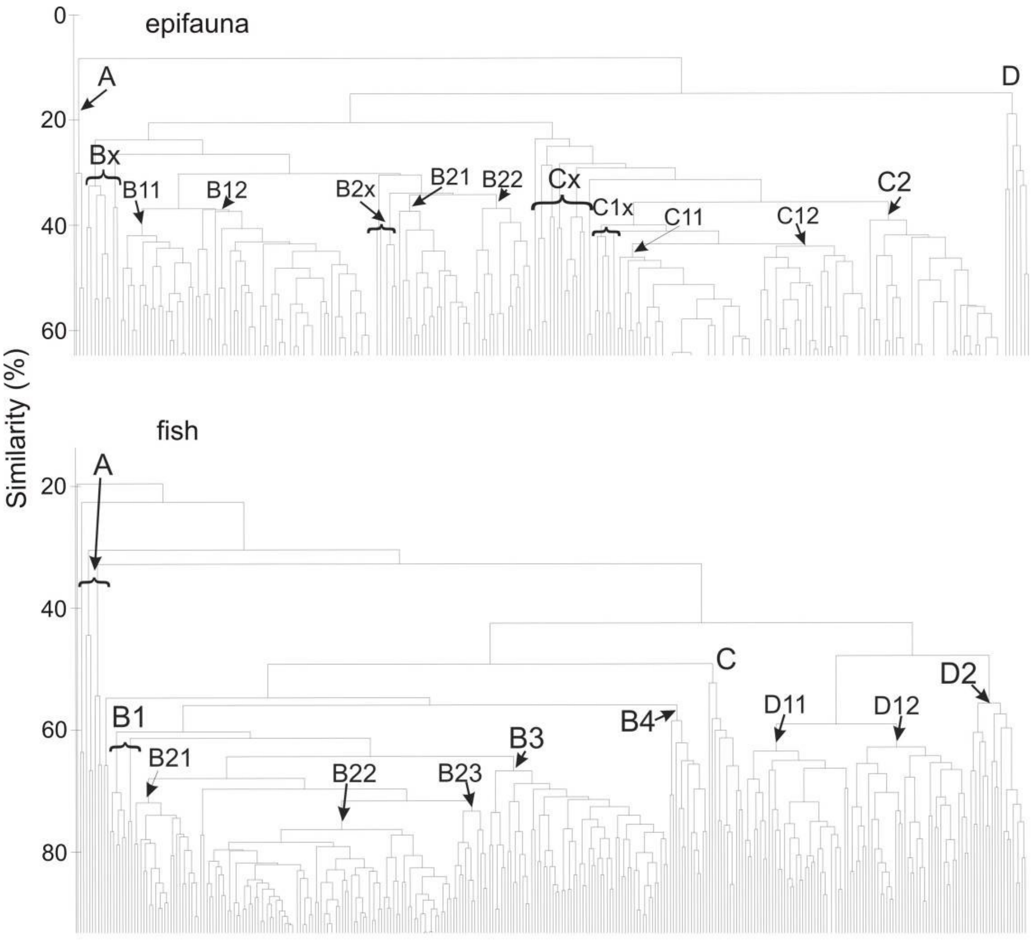

Figure 3 Dendrograms and groupings (shown in Figure) from cluster analysis of fourth-root transformed abundance data for the epifauna (top) and demersal fish (bottom).

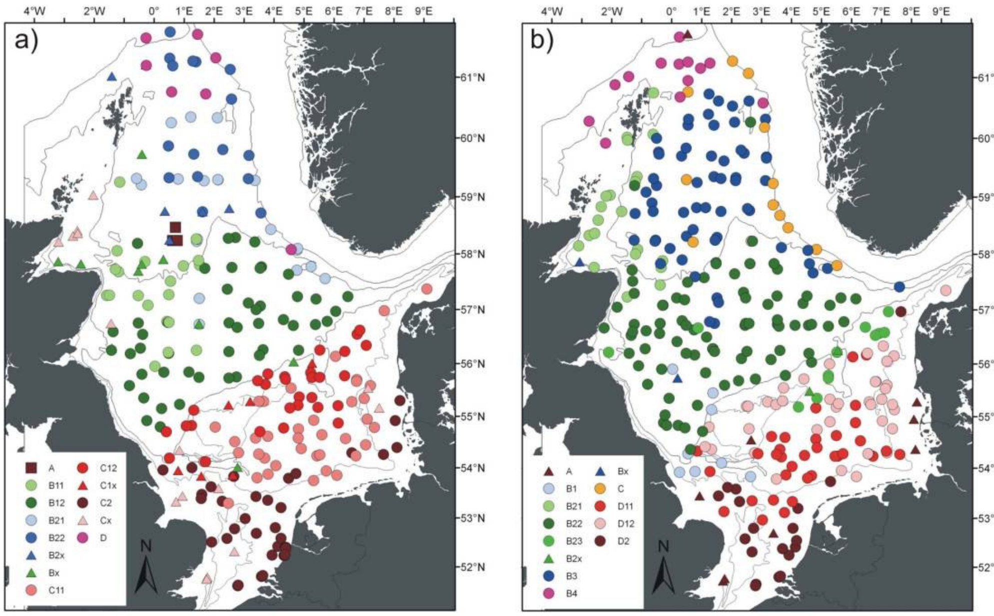

Figure 4. Distribution of (a) epifauna and (b) fish assemblages in the North Sea according to the outputs from cluster analyses of fourth-root transformed abundance data.

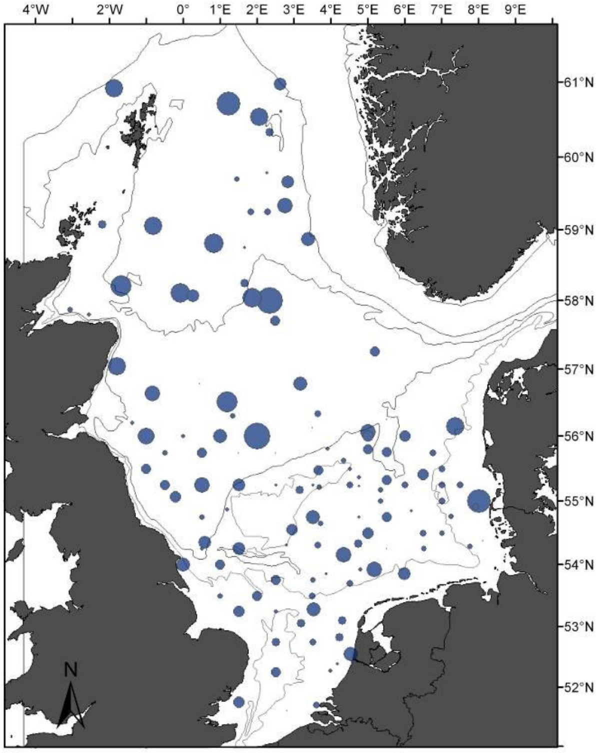

Figure 5. Positions of the nearest matching stations with distances to the nearest station superimposed (m).