Abstract

Under the guidance of the ICES Benthos Ecology Working Group, surveys by several institutes in UK, F, B, NL, N and D were performed in 2000 (and a few additional surveys also in 2001) to re-investigate the macro-infaunal assemblages of invertebrates in the North Sea and compare these with earlier descriptions, mainly the survey of 1986.

Altogether, 24 clusters were identified based on Bray-Curtis-similarity and group average linkage after fourth root transformation of the abundance data. These assemblages are distributed according to water depths and sediment conditions and show very similar latitudinal distributional patterns as in earlier investigations, especially in the 1986 North Sea survey. A main separation is seen north of the Dogger Bank near the 50 m depth contour. The assemblages of coarse sand, gravel and stony fields are well separated from such inhabiting finer substrates. While the majority of the assemblages are regarded communities, a few inshore and coarse sand/gravel clusters may be regarded as local expressions (sub-communities) of larger, widely distributed community types.

All identified assemblages are compiled in a table, which also presents information about environmental conditions, internal similarity, densities and species diversity as well as on dominating and characterizing and name-giving species.

Several general trends, e.g. diversity versus latitude and depth, are presented, while abundance is only weekly increasing from the South to the North. When comparing on a community level instead of comparing all stations at once, several differences and trends become more obvious. In a few cases, shifts in the distribution of communities can be shown (e.g. of the mud-inhabiting Nucula-nitidosa-community in the Pleistocene Elbe valley in the German Bight). They are related with shifts of some dominant species, which can partly be explained with the warming in the southern North Sea.

Introduction

Under the guidance of the ICES Benthos Ecology Working Group, surveys by several institutes in UK, F, B, NL, N and D were performed in 2000 (and a few additional surveys also in 2001) to re-investigate the macro-infaunal assemblages of invertebrates in the North Sea and compare these with earlier descriptions, mainly the survey of 1986 (Künitzer et al., 1992; Heip et al. 1992). The specific work was coordinated by the ICES Study Group of the North Sea Benthos Project (SGNSBP).

This contribution describes spatial distribution patterns of North Sea macro-zoobenthos assemblages and general trends in some structural features of the fauna. They allow comparison
with earlier descriptions and provide a renewed baseline for long-term comparison, mainly relating to possible climate-related changes and anthropogenic influences such as eutrophication, pollution, acidification, sand and gravel extraction and fisheries, as well as environmental and nature protection measures and their trends. Last, but not least, they may be generally useful for better ecosystem understanding.

Methods

Although quasi-synoptic sampling was intended for early summer in 2000, several parts of the North Sea could only be covered by including material from adjacent seasons and years (mainly 2001), see contribution A: 18 of E. Vanden Berghe.

Most infauna sampling was performed with grabs of the van Veen type (two grabs of 0.1 m² at most stations), sieving them on screens of 1 mm, and analysing the preserved material in the home laboratories. Specific information, including the areas covered by the different laboratories and the sampling locations is presented in Section 3.1 of the CRR 288.

In the following analysis, a reduced dataset (950 stations, 521 taxa) was employed, after accounting for taxonomic inconsistencies and the exclusion of very rare species. Univariate analyses included diversity derivations from rarefaction to compensate for different sample sizes between stations and clusters (e.g., ES(100) = expected number of species in a hypothetical sample of 100 individuals).

Cluster analyses using the PRIMER 5.0 software package (Clarke and Warwick, 1994) were carried out using the Bray–Curtis similarity measure and group-average linkage. As initial results based on presence/absence and fourth-root transformed abundance data were similar, only the latter were used in subsequent analyses. Clusters were compared with the results of TWINSPAN analyses, and a common grouping derived for comparative analyses. The characteristic species (see Salzwedel et al., 1985) of each main cluster were determined using, among others, the SIMPER tool within the PRIMER work package. For their selection, fidelity in abundance, presence, fidelity in presence, numerical dominance and rank of species contributing to dissimilarity (against all other stations) have been considered. These are defined as follows:

- fidelity in abundance (FA, total individual number of a species within a cluster/total individual number in the survey; highest ranks, >60%),
- presence (P, share of stations within a cluster, where the species was found; highest ranks, >70%),
- fidelity in presence (FP, number of presence stations within a community/total number of presence stations in the survey; highest ranks, >60%),
- numerical dominance (ND, highest ranks, as a rule not less than 3%),
- rank of species contribution to dissimilarity of a cluster group compared with all other stations (RD, ranks 1–5 only considered).

For a characteristic species, at least three of the criteria have to be fulfilled, with ND as a rule not less than 3% and FP not less than 40%. The characterizing species are presented in Table 1.

Results

Some general trends revealed by univariate analyses

Note: In the graphical outputs to accompany the following account, we have colour-coded the data points to highlight the different data sources used in the NSBP 2000 and how they relate to the overall trends that were identified.
Diversity

Increasing trends in ES (100) values with latitude north of 51°N (Figure 1) are shown by the rarefraction analysis. This is in accordance with the results from 1986 (Heip et al., 1992). South of 53°, elevated diversities in the eastern English Channel (Newell) and also along parts of the SE English coast (Rees) which were not so effectively sampled in 1986, can be accounted for by the generally coarser substrata, which present greater small-scale heterogeneity. Biogeographical trends (with increasing species numbers to the West) additionally explain elevated values in the Channel area. (Figures 1 and 3). The high values of the Aberdeen samples (Robertson) may be explained by the use of a large (0.25 m²) corer for collection which, because of deeper penetration than smaller cores or grabs, appear to be intrinsically more “biodiverse” than elsewhere at comparable latitudes. Finally, the depressed ES (100) values for the blue sub-cluster (inshore German waters; Nehring) can be accounted for by estuarine influences.

![Figure 1. Diversities (rarefaction: ES 100, for single grabs) vs. latitude.](image-url)
Similarly, diversity generally increases with depth (Figure 2), which may be explained by increasing environmental stability (e.g. decreased wave-induced or tidal turbulence and reduced temperature extremes) and the stronger influence of Atlantic inflow to the North. It is therefore clear that latitudinal gradients are matched by gradients in a number of influential environmental variables. Also notable are the depressed diversities of some of the deep-water Norwegian samples (Oug, >350 m).

Figure 2. Diversities (rarefaction: ES 100) vs. water depths, all data from individual grabs.

Figure 3. Diversities (rarefaction: ES 100, for single grabs) vs. longitude.
Also, a longitudinal trend in diversity exists (Figure 3), with a decrease towards the eastern North Sea, where less saline water and more continental (climatic) influences prevail and species adapted to warmer waters are rare. As expected, the lowest values were found in the estuaries there (Nehring’s data).

**Abundance**

Figure 4 shows increases from the Channel to the southeastern North Sea and slight increases from the southern to the central North Sea. The variability in these parts of the North Sea is high. From the central up to the northern North Sea, abundances are more or less stable, mostly at a relatively high level.

![Figure 4](image)

**Figure 4.** Abundances (ind. per m²; for single grabs) vs. latitude.

**Assemblages** identified by multivariate analyses

Both, TWINSPAN and PRIMER analyses employing fourth-root transformed abundance data produced similar results. Nevertheless, a number of stations in nearshore areas and several in transitional parts of the North Sea, such as in the vicinity of the Dogger Bank, were not assigned to the same groups by either method (Figure 5). Figure 6 shows the results of group-average clustering only.
Figure 5. Common communities from clustering and TWINSPAN.
Figure 6. Distribution of macro-zoobenthos assemblages in the North Sea in 2000 according to group-average cluster analysis.
The main groups identified by the different methods are related to water depths and distances from the shore (especially from South to North); differences between coarse and fine substrate types are also influential (assemblages B1 and B2).

The quality of this clustering was also checked by looking at subsets of data which (from previous analyses) represented discrete communities – in particular from a survey near the Belgian coast which revealed well-defined trench and sandbank communities (see Degraer et al., 2003, 2006) and from surveys in the German Bight (Rachor and Nehmer, 2003; Rachor, 2006).

The following descriptions relate to the outcome of clustering using group-average linkage (Figure 6).

In the cluster dendrogram (not shown here, but, see Rachor et al. 2007) a clear separation of station groups in mainly shallow inshore waters in the south from the French up to the German coastal-zones, in the Channel, as well as adjacent to the eastern and southeastern English coasts, from those in deeper waters north of the Dogger Bank. In between, the offshore assemblages of the sandy and muddy areas are also well distinguished, including the Oyster Ground and the sandy Dogger Bank and its slopes, which are inhabited by the same assemblage (D 23) as is found in the Pleistocene Elbe valley extending from the inner German Bight to the East of the sandbank.

The main separation of the deep-water cluster group (D 21) is found near the 50 m depth contour north of the Dogger Bank, where it borders the assemblage D 23.

B24 is a very specific cluster in the gravely-to-muddy Helgoland Deep Trench, where faunal elements from the northern North Sea have their discrete outpost. These stations are similar to one outlier off the Thames mouth.

The characterizing features of each assemblage type identified from cluster analyses are shown in Table 1. In some cases, very similar clusters are shown together.
Table 1. Assemblages of macro-zoobenthos in the North Sea in 2000 with information on the area, the sediments/habitats, water depths, dominating and characterizing species as well as structural descriptors.

<table>
<thead>
<tr>
<th>CLUSTER</th>
<th>AREA</th>
<th>PREDOMINANT WATER DEPTHS (M)</th>
<th>PREDOMINANT SEDIMENTS</th>
<th>ASSEMBLAGE TYPE (NAME GIVING SPECIES)</th>
<th>DOMINANTS</th>
<th>CHARACTERIZING SPECIES (PRELIMINARY)</th>
<th>AV. SIM.</th>
<th>AV. DIVERSITY ES(50)</th>
<th>AV. DENSITY AND SD</th>
<th>NO. OF STATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Near Norway and Fladen Ground</td>
<td>mainly &gt;100</td>
<td>Mud to muddy sand</td>
<td><em>Thyasira equalis</em></td>
<td><em>Heteromastus filiformis</em></td>
<td><em>Paramphinome jeffreysi</em></td>
<td><em>Thyasira equalis</em></td>
<td>Eriopisa elongata</td>
<td>37.6</td>
<td>18.6</td>
</tr>
<tr>
<td>D 21</td>
<td>Northern and central NS</td>
<td>&gt;50</td>
<td>Muddy sand and fine sand</td>
<td><em>Amphiura</em> with <em>Paramphinome</em></td>
<td><em>Myriochele</em> spp.</td>
<td><em>Amphiura filiformis</em></td>
<td><em>Paramphinome jeffreysi</em></td>
<td>36.6</td>
<td>19.4</td>
<td>1536</td>
</tr>
<tr>
<td>D 23 and D2x</td>
<td>Around Dogger Bank and in the Pleistocene Elbe valley (PEV)</td>
<td>35–50</td>
<td>Slightly muddy sand</td>
<td><em>Amphiura</em> with <em>Spiophanes</em></td>
<td><em>Spiophanes bombyx</em></td>
<td><em>Amphiura filiformis</em></td>
<td><em>Magelona filiformis</em></td>
<td>39.3 (24.0)</td>
<td>14.1</td>
<td>2276</td>
</tr>
<tr>
<td>D 22</td>
<td>Oyster Ground and outer part of the PEV</td>
<td>35–50</td>
<td>Muddy sand</td>
<td><em>Amphiura</em> with <em>Corbula</em></td>
<td><em>Amphiura filiformis</em></td>
<td><em>Corbula gibba</em></td>
<td><em>Myselfa bidentata</em></td>
<td>42.3</td>
<td>15.1</td>
<td>1520</td>
</tr>
<tr>
<td>D 11</td>
<td>Offshore sand areas in the southern NS (SNS) and Dogger Bank</td>
<td>15–35</td>
<td>Fine sand</td>
<td><em>Tellina fabula</em> with <em>Urothoe poseidonis</em></td>
<td><em>Magelona johnstoni</em></td>
<td><em>Spiophanes bombyx</em></td>
<td><em>Urothoe poseidonis</em></td>
<td>35.8</td>
<td>12.5</td>
<td>1177</td>
</tr>
<tr>
<td>D 12</td>
<td>Sand areas nearer to coast in the SNS</td>
<td>10–20</td>
<td>Fine to medium sand</td>
<td><em>Tellina fabula</em> with <em>Abra alba</em></td>
<td><em>Spiophanes bombyx</em></td>
<td><em>Abra alba</em></td>
<td><em>Magelona johnstoni</em></td>
<td>None</td>
<td>36.7</td>
<td>10.9</td>
</tr>
<tr>
<td>E</td>
<td>Inshore S NS</td>
<td>2–20</td>
<td>Sandy mud to muddy sand</td>
<td><em>Nephtys hombergii</em> with <em>Abra alba</em></td>
<td><em>Chaetozone</em> spp.</td>
<td><em>Abra alba</em></td>
<td><em>Nephtys hombergii</em></td>
<td>None</td>
<td>24.6</td>
<td>7.1</td>
</tr>
<tr>
<td>Cluster</td>
<td>Area</td>
<td>Predominant Water Depths (m)</td>
<td>Predominant Sediments</td>
<td>Assemblage Type (Name Giving Species)</td>
<td>Dominants</td>
<td>Characterizing Species (Preliminary)</td>
<td>Av. Sim.</td>
<td>Av. Diversity EN(50)</td>
<td>Av. Density and SD</td>
<td>No. of Stations</td>
</tr>
<tr>
<td>---------</td>
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</tr>
<tr>
<td>B 1</td>
<td>Banks with coarse sands (SNS)</td>
<td>15–35</td>
<td>Coarse sand, partly gravelly</td>
<td>Branchiostoma with Echinocyamus</td>
<td>Aonides paucibranchiata Echinocyamus pusillus Branchiostoma lanceolatum</td>
<td>Branchiostoma lanceolatum</td>
<td>19.8</td>
<td>13.2</td>
<td>828 705</td>
<td>26</td>
</tr>
<tr>
<td>C 1</td>
<td>SE-NS banks with medium sands</td>
<td>15</td>
<td>Medium (with coarse) sand, partly gravelly</td>
<td>Spisula with Ophelia</td>
<td>Nephys cirrosa Spisula solida Ophelia borealis</td>
<td>Spisula solida Tellina tenus</td>
<td>30.3</td>
<td>10.0</td>
<td>169 138</td>
<td>28</td>
</tr>
<tr>
<td>C2, C3 and F</td>
<td>Southwestern NS; SNS</td>
<td>&lt;40</td>
<td>Sand</td>
<td>Nephys cirrosa</td>
<td>Nephys cirrosa</td>
<td>Gastroascus spinifer Urothoe brevicornis</td>
<td>29-37</td>
<td>6.6, 8.5</td>
<td>209, 430 291, 280</td>
<td>75, 88</td>
</tr>
<tr>
<td>C4</td>
<td>Inshore SNS mainly &lt;20</td>
<td>Sand</td>
<td>Nephys caeca</td>
<td>Nephys caeca</td>
<td>Nephys caeca</td>
<td>13.9</td>
<td>7.1</td>
<td>72 52</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>B 23</td>
<td>Western NS and north of Shetlands</td>
<td>21–136</td>
<td>Coarse to med. sands</td>
<td>Sabellaria with Polycirrus</td>
<td>Glycera lapidum Polycirrus spp Sabellaria spinulosa</td>
<td>Sabellaria spinulosa Polycirrus spp</td>
<td>29.3</td>
<td>19.7</td>
<td>1648 1394</td>
<td>14</td>
</tr>
<tr>
<td>B 24</td>
<td>Helgoland Deep Trench and Outer Thames</td>
<td>35–60</td>
<td>Sand, gravel, mud and shells</td>
<td>Cerianthus (formerly Nucula nucleus)</td>
<td>Scalibregma inflatum Cerianthus lloydii Gattyana cirrosa</td>
<td>Gattyana cirrosa Cerianthus lloydii</td>
<td>26.2</td>
<td>12.5</td>
<td>2–3000</td>
<td>3–4</td>
</tr>
<tr>
<td>B 21 and B 22</td>
<td>Restricted to eastern English Channel</td>
<td>41–68</td>
<td>Sand to gravel</td>
<td>(Small polychaetes)</td>
<td>Prionospio multibranchiata Aonides paucibranchiata</td>
<td>Prionospio multibranchiata Aonides paucibranchiata</td>
<td>51.1</td>
<td>24.0</td>
<td>823 283</td>
<td>91</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hesionura elongata Aonides paucicirca</td>
<td>Hesionura elongata Eurydice spinigera</td>
<td>50.7</td>
<td>12.1</td>
<td>536 295</td>
<td>12</td>
</tr>
</tbody>
</table>
Differences in diversity and densities of the assemblages are shown in Figure 8.

The average macrobenthic density and diversity per cluster group (assemblage) ranged from about 35 to 3500 ind./m² and ES(50) from 2.7 to 24.0, respectively. More information is presented in the contribution of Willems et al. (A:08; see e.g. Figures 5.3.5 and 5.3.10 in the CRR 288). Groups C1–C3 and Cx are characterized by a combination of low density and moderate diversity. High densities and diversities were found in groups D12 to D23 and also in A, B23, B24. Generally, several coarse sand to gravel assemblages had the highest diversities. Group C4 had both the lowest density and diversity (neglecting the outliers of “x”).

**Discussion and Conclusions**

A main division of the macrozoobenthos in the North Sea between its deeper northern and shallower southern parts is obvious in the results of the NSBP 2000 survey, which was also shown for the survey of 1986 (Künitzer et al., 1992; Heip et al., 1992). This division is well seen in the separation of assemblages along the Frisian Front at about 30 m depth and at the northern lower slope margin of the Dogger Bank. The latter occurs at about 50–60 m depth according to the outcome of cluster analysis (Figure 6).

Large-scale changes in comparison with earlier descriptions (especially from 1986) are discussed by I. Kröncke et al. (A:06; see also Section 5.2. of CRR 288). Here, we highlight changes in the community of the submerged Pleistocene Elbe valley (*Amphiura filiformis* with *Spiophanes bombyx*), which is also found at the outer margins of the Dogger Bank. Such changes and the spreading of *Acrocnida (Amphiura)*
*brachiata* towards the inner German Bight and on the Dogger Bank are discussed in the contribution of J.D. Eggleton et al. (A: 20; see also Section 5.4 in the above mentioned CRR 288).

The relationship between spatial patterns in the infauna, epifauna, and fish are described by H. Reiss et al. (A: 1, see Section 6.1 CRR 288). It is also interesting to note similarities in the distribution of the infauna and the plankton, namely a division between southern and northern communities with a transitional zone to the North of the Dogger Bank area. The northern community is especially influenced by the degree of north Atlantic inflow, while a third zone in the SW North Sea is additionally characterized by stronger coastal-water influences (MAFF, 1981). Fransz *et al.* (1991) similarly highlighted the dominant effect of north Atlantic inflow on copepod species composition and abundance in stratified waters, in contrast to coastal mixed waters to the SE where communities are more locally variable in character (see also Adams, 1987).

General latitudinal trends of increases in diversity and (less clearly) density from south to north as described for the 1986 data (Heip *et al.*, 1992) were again shown in 2000. They are at the same time related to water depths, which follows the same general trend. These depth-related zonations were also identified in early work by Spårek (1935), Remane (1940) and Jones (1950). Glémarec (1973) stressed the importance of increasing stability in the water temperature regime with increasing depths, which he defined in terms of zones (or “étages”). Such depth zonations are well known from shelf seas, e.g. the Bay of Biscay (Glémarec, 1973) or the Eurasian Arctic seas (Sirenko, 1998). Other stress factors such as wind- and current-induced turbulence also decrease with depths. Stations in the Norwegian Skagerrak do not follow this rule, presumably because they are exceptionally deep and, thus, subject to reduced food inputs.

Lowest diversities were found in nearshore waters along the whole southern and southeastern North Sea (Figure 9). This may be related not only to the reduced salinities there, but also to the high climatic and hydrological variability and disturbing human influences, including pollution and eutrophication. The west-to-east trends shown with univariate methods (Figure 3) indicate that the eastern North Sea (especially a large part of the German Bight in the southeast) is generally impoverished in diversity. This part of the North Sea is most remote and biogeographically apart from the species-rich Atlantic Ocean and most strongly under the disturbing natural and anthropogenic “continental” (mainland) influences.
While some northern and central parts of the North Sea were poorly covered by sampling stations by 2000, the nearshore areas along the eastern English Channel and the French and Belgian North Sea coasts were sampled with very high spatial resolution. The groups identified there by clustering may be regarded as local sub-associations of larger communities (e.g. the well known *Macoma* or the *Goniadella-Spisula* communities) reflecting the high spatial variability of environmental conditions in such waters.

Compared with the wider North Sea, these local variants appear to be of minor importance but, because inshore waters surrounding heavily-populated areas are commonly subject to a wide range of human influences and are the target of several environmental or nature protection measures. They have been intensively studied (e.g. Degraer *et al.*, 2003, 2006; Van Hoey *et al.* 2004; Daan and Mulder, 2005; Rachor and Nehmer, 2003; Rachor, 2006; see also Rees and Eleftheriou, 1989, and Kröncke and Bergfeld, 2003). Nevertheless, as for the wider North Sea, distinctions between these variants can also be explained by responses to natural variation in sediment conditions, water depths and longitude (see Figure 6).

While the more offshore fine to medium sand areas in the Dutch and German waters as well as the higher Dogger Bank appear inhabited by a relatively homogenous community of the *Tellina fabula* type, areas off the English east coast (with water depths of less than about 30 m) are less uniform in substratum type and, accordingly, inhabited by different assemblages.

North of the “Frisian Front” with very muddy sediments at about 30 m depth, the Oyster Ground with mixed fine substrates up to the southern margin of the Dogger Bank is inhabited by the *Amphiura filiformis*
community with *Corbula gibba*, partly extending across the Pleistocene Elbe valley in the East. This influence is more strongly expressed in the TWINSPLAN results (Figure 5), while the clustering identifies a stronger relationship with the central North Sea *Myriochele* community in the depression east of the Dogger Bank Tail End. Thus, differences between clustering and TWINSPLAN outputs are mainly related to the above transitional areas.

A discussion on whether the few more substantial changes between 2000 and 1986 are related to warming of the North Sea and/or more stable conditions in the years preceding 2000 is given by in Section 5.2.

**Acknowledgements**

The author acknowledges the support of all contributors of data to the SGNSBP. He is also thankful for the support given by the German Federal Agency for Nature Protection (BfN) for the work in the southeastern North Sea.

**References**

The results of the North Sea benthos survey 2000 are fully presented in CRR 288:


Other citations:


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