Seasonal variability of epibenthic communities in different areas of the southern North Sea

Henning Reiss and Ingrid Kröncke

Between November 2000 and May 2002, epibenthos was sampled monthly with a 2-m beam trawl at three stations along a transect from the southern German Bight towards the northeastern part of the Dogger Bank (North Sea) in order to investigate the seasonal variability of the epibenthic communities. The stations were chosen to reflect a gradient in the hydrographic regime, organic matter supply, and fishing effort. The epibenthic community of the southern German Bight was characterized by high biomass and abundance, dominated by Asterias rubens and Ophiura albida. In contrast, at the northern stations in the Oyster Ground and at the Dogger Bank, epibenthic biomass and abundance were substantially lower and the dominant species were mainly crustaceans such as Corystes cassivelaunus, Liocarcinus holsatus, and Pagurus bernhardus. In terms of seasonal variability, mean abundance and biomass in the southern German Bight showed highest values in the summer months and lowest values in the winter months. A similar pattern, but less distinct, was observed in the Oyster Ground. But at the Dogger Bank the pattern was different, with highest abundance and biomass values in the winter months. The differences in spatial and temporal patterns are discussed in relation to differences in temperature, thermal stratification and fishing effort at the three study sites.

Keywords: Dogger Bank, epibenthos, fishing effort, German Bight, migration, Oyster Ground, temporal variability.

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Introduction

The North Sea has been studied intensively in the past decades and benthic subjects were the focus of many of these investigations (Salzwedel et al., 1985; Künitzer et al., 1992; Kröncke, 1995; Craeymeersch et al., 1997). After the classical studies of Petersen (1914, 1918), the main interest focused on quantitative aspects of endobenthos, whereas quantitative studies of epibenthos are rare until recently.

Since larger macrobenthos form a significant proportion of the by-catch in trawl fisheries, initial studies of the epibenthos of the North Sea relied on an examination of the invertebrates caught as by-catch during fishery surveys (Dyer et al., 1982, 1983). Semi-quantitative investigations with a smaller gear (2-m beam trawl) were performed first by Frauenheim et al. (1989) and continued by Jennings et al. (1999a), Zühlke et al. (2001), and Callaway et al. (2002) for the whole North Sea. The description of the large-scale distribution and structure of the epibenthic communities in connection with important environmental factors were the main result of these investigations. The observed differences between northern and southern North Sea assemblages were best explained by temperature variation (Jennings et al., 1999a) and by the influence of different water masses (Frauenheim et al., 1989).

As a shelf sea in temperate regions, the North Sea, particularly the relatively shallow German Bight, is characterized by strong seasonal fluctuations of temperature and salinity (Otto et al., 1990; Becker et al., 1992). Also primary production and, thus, the food supply for the benthic fauna is determined by annual cycles of temperature, nutrient input, and light availability (Colijn and Cadée, 2003). Overall, temperature is believed to be a main factor to trigger spatial as well as temporal changes in benthic communities (Duineveld et al., 1991; Callaway et al., 2002).

Thus, a detailed knowledge of the short-term spatial and temporal variability of the epifauna is essential to assess long-term changes in epibenthic communities, but these
information are lacking for the North Sea. Frauenheim et al. (1989) broadly compared the spatial distribution of epibenthos between summer and winter in the whole North Sea, as did Hinz et al. (2004) for the southern German Bight over a three-year period.

In this study, the seasonal variability of epibenthic communities in the southern North Sea was investigated from November 2000 until May 2002 at three stations along a transect from the southern German Bight towards the northeastern part of the Dogger Bank. The transect reflects a gradient in temperature, salinity, food supply, and fishing effort. Since so little is known about the ecology and biology of many epibenthic species in the North Sea, these data provide valuable information on the seasonal patterns of several epibenthic species. The purpose of this study was to (I) describe the seasonal variability in species number, abundance, and biomass of the epibenthos at three stations in the southern North Sea and (II) to discuss environmental parameters which are in accordance with faunal patterns.

Material and methods

Study sites

Three study sites, located along a transect from the southern German Bight towards the northeastern Dogger Bank (North Sea, Germany), were sampled monthly from November 2000 to May 2002 (Figure 1). Some months are missing due to bad weather conditions. Coordinates of the stations are given in Table 1. Samples were taken from an area of about 0.5 nm around the station. The sample sites were chosen to reflect gradients in temperature and salinity (Otto et al., 1990; Becker et al., 1992), organic matter supply (Riegman et al., 1990), and hydrographical conditions (Otto et al., 1990; Becker et al., 1992; Kröncke and Knust, 1995).

The depth ranged from 30 m at the shallowest Station DB9 at the Dogger Bank to 37 m and 41 m at Stations GB5 and OG7 in the German Bight and the Oyster Ground, respectively.

Sampling and sample treatment

Most samples were obtained with RV “Senckenberg”. In May 2001/2002 and January 2001/2002 samples were taken with RV “Gauss” and FRV “Walther Herwig III”, respectively. All samples were taken with a 2-m beam trawl with a chainmat attached. The mesh size of the net was 20 mm and a liner of 4 mm knotless mesh was fitted inside the codend. Details about the equipment are given in Jennings et al. (1999a). After contact with the sea bottom the beam trawl was towed at approximately 1 knot for 5 min. To estimate the towing distance and thus the sampled area, the position at the beginning and at the end of towing was recorded by the GPS of the vessels. The average length of tow was 290 ± 130 m.

Whenever possible three replicates were taken at each station (Table 1). Because of differences in the diurnal activity of some epibenthic species, sampling took place only during daylight.

The samples were sieved over a 5-mm mesh and organisms collected. The majority of species were identified on board, counted, and weighed wet with a motion compensated marine scale. Modular organisms were only noted as present/absent and were not mentioned in the quantitative analysis. If the identification of species was not possible on board, specimens were fixed in 4% buffered formalin for identification in the laboratory.

Despite the relatively short towing distance, subsampling was necessary at Station GB5 during the summer months, due to a high abundance of Ophiura albida. In this case, large macrofauna were removed from the catch and the remains were subsampled to determine the abundance and biomass of O. albida and other small specimens such as small crustacean or bivalve species.

Temperature and salinity

The temperature and salinity of the water column could only be measured occasionally during the cruises. In June, July, and October 2001, these parameters were measured using a Hydrobios temperature/salinity probe. The data of January 2002 were provided by the Federal Research Centre for Fisheries, Hamburg. Weekly sea surface temperature data (SST) were obtained from the Federal Maritime and Hydrographic Agency of Germany, Hamburg.

Sediment characteristics

Sediment samples were taken with a 0.1-m² box corer. Three replicates were taken at each station during each month. The upper 0.5 cm of the sample was used for the analyses of total organic carbon (TOC) contents and the upper 2 cm was used to determine sediment structure and phytotpigment content.

The organic carbon contents of the sampled sediments were analysed using a Heraeus C/N analyser. Fresh sediment was frozen at −20°C and freeze-dried. Samples were finely powdered and homogenized. An aliquot of 20–90 mg was combusted at 1010°C following acidification of the samples with concentrated HCl in a desiccator to remove inorganic carbonates.

Analyses of sediment mud content were determined on dried samples that had been sieved with a 500-μm sieve to remove large shell particles.

An aliquot of each sample was filled in a Laser Particle Sizer “Analysette 22 Economy” (Fritsch Germany) and was automatically homogenized by a stirrer and by ultrasonication. The grain size fraction <63 μm was considered as mud content of the sediment.

Analyses of sediment mud content were determined on dried samples that had been sieved with a 500-μm sieve to remove large shell particles.
Figure 1. Area of investigation with sampling sites.
Table 1. General characteristics of the study sites. Sediment parameters are given as means over the whole study period. Trawl numbers are given in brackets (− = no sampling because of bad weather conditions).

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<thead>
<tr>
<th></th>
<th>GB5</th>
<th>OG7</th>
<th>DG9</th>
</tr>
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<tbody>
<tr>
<td>Latitude</td>
<td>54°06.5’N</td>
<td>54°50’N</td>
<td>55°30’N</td>
</tr>
<tr>
<td>Longitude</td>
<td>07°24’E</td>
<td>05°35’E</td>
<td>04°10’E</td>
</tr>
<tr>
<td>Depth</td>
<td>37 m</td>
<td>41 m</td>
<td>30 m</td>
</tr>
<tr>
<td>Mud content</td>
<td>38.6% &lt;63 μm</td>
<td>20.0% &lt;63 μm</td>
<td>1.9% &lt;63 μm</td>
</tr>
<tr>
<td>Median grain</td>
<td>75.6 μm</td>
<td>129.9 μm</td>
<td>242.9 μm</td>
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<tr>
<td>TOC (% sed. dry wt)</td>
<td>0.32</td>
<td>0.19</td>
<td>0.07</td>
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<tr>
<td>Chlorophyll a</td>
<td>1.49 μg g⁻¹</td>
<td>1.33 μg g⁻¹</td>
<td>1.23 μg g⁻¹</td>
</tr>
<tr>
<td>Date of sampling</td>
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<td>(3) Dec 2000</td>
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Chlorophyll $a$ was extracted from 5 g frozen sediment with 5 ml 90% acetone. After incubation for 1 h at 4°C in darkness it was mixed for 1 min, followed by an ultrasonication in a water bath for 3 min. To remove particles the suspension was centrifuged for 25 min at 1,745 × g at 0°C. Chlorophyll $a$ was analysed in the supernatant by high performance liquid chromatography (HPLC) as described by Wallerstein and Liebezeit (1999). Standards (Sigma, Germany) were used for the quantification of chlorophyll $a$.

Fishing effort data

Fishing effort data were provided by S. Ehrich from the “Federal Research Centre for Fisheries of Germany”, Hamburg. Unfortunately, only data of the German fishing fleet were available, but temporal and spatial variability will be similar to fishing activities of other countries. Therefore, patterns can be compared. For the period of investigation, all data were recorded monthly as hours fishing per ICES rectangle, where our stations were located.

Data processing

Prior to data analysis, abundance and biomass data were standardized to a sampled area of 500 m² (towing distance 250 m). Because no correspondence between species numbers and tow length was found at the sampled spatial scale, the species number is given per catch.

Fish species were excluded from the analysis because of the high mobility of many species, which makes a quantitative sampling by a small and slow moving beam trawl unreliable.

Multivariate data analysis was performed using the Primer statistical package (Plymoth Marine Laboratory, Primer v5.1). Non-metric multidimensional scaling (MDS) was used on fourth root transformed abundance data to detect seasonal changes in the community structure. Similarities were calculated using the Bray—Curtis similarity index (Bray and Curtis, 1957) and SIMPER of the Primer statistical package was used to identify characteristic species of the communities.

The Spearman Rank correlation was applied to calculate the correlation between two variables.

The feeding modes of taxa were determined according to information in literature (Hartnoll, 1972; Britton and Morton, 1994; Hayward and Ryland, 1995; Oh et al., 2001).

Results

Environmental data

Sea surface temperatures showed a similar seasonal pattern at all three stations with minimum values in March 2001 and maximum values in August 2001 (Figure 2a). Temperatures during the summer months followed a clear decreasing gradient from the southern Station GB5 with maximum temperature of 18.4°C to the more northern Stations OG7 and DG9 with 17.4°C and 16.1°C, respectively. In contrast, highest values of winter temperatures were measured at Station OG7 with 5.3°C compared to 4.8°C at Station DG9 and 4.3°C at Station GB5, most likely due to the inflow of warmer water masses from the Atlantic.

Thermal stratification occurred at Stations OG7 and DG9 in June and July 2001, whereas no stratification could be observed at Station GB5 (Figure 2b).

Salinity was relatively constant throughout the water column at all stations with exception of Station GB5 in June 2001, where the salinity of the surface water was reduced to 30.5 in contrast to 31.4 below 5-m water depth. In general, salinity increased from Station GB5 towards Station DG9 (Figure 2b).

Strong seasonal fluctuations in salinity were only detected at Station GB5, with an increase from 30.5 in
Figure 2. Sea surface temperature (a) and profiles of temperature and salinity of the water column (b) at the sampling sites.
General community structure

A total of 115 epifaunal species was found, of which 25 fish species as well as 20 species of modular organisms (e.g. bryozoa, cnidaria) were excluded from further analysis.

Mean abundance and biomass were highest at the southern Station GB5 in the German Bight with over 6616 individuals and 3467 g wet wt 500 m⁻², respectively. At Stations OG7 in the Oyster Ground and DG9 at the Dogger Bank lower abundances and biomasses were found with 101 individuals and 545 g wet wt 500 m⁻² and the common starfish Asterias rubens (155 ind. 500 m⁻²/1163 g wet wt 500 m⁻²), and the swimming crab Liocarcinus holsatus (12 ind. 500 m⁻²/74 g wet wt 500 m⁻²) were mainly found at Station DG9 (Table 2).

Seasonal variability in community structure

Species number, abundance, and biomass

At Station GB5 in the German Bight, mean abundance and biomass showed a clear seasonal pattern with highest values in the summer months with up to 15 600 ind. 500 m⁻² (September 2001) and 8550 g wet wt 500 m⁻² (July 2001). Lowest values could be observed during winter and spring (Figure 3).

The opposite pattern was found at the Dogger Bank (DG9) with lowest abundance in the summer months (May until August 2001) from 56 to 68 ind. 500 m⁻² and for a lesser amount by the common starfish Asterias rubens (155 ind. 500 m⁻²/1163 g wet wt 500 m⁻²; Table 2). Also Station OG7 was mainly dominated by echinoderms, but species differed, such as A. rubens (22 ind. 500 m⁻²/204 g wet wt 500 m⁻²), the sand star Astropecten irregularis (18 ind. 500 m⁻²/53 g wet wt 500 m⁻²) and the common heart urchin Echinocardium cordatum (4 ind. 500 m⁻²/86 g wet wt 500 m⁻²).

In contrast, crustacean species such as the hermit crab Pagurus bernhardus (15 ind. 500 m⁻²/113 g wet wt 500 m⁻²), the masked crab Corystes cassivelaunus (10 ind. 500 m⁻²/80 g wet wt 500 m⁻²), and the swimming crab Liocarcinus holsatus (12 ind. 500 m⁻²/74 g wet wt 500 m⁻²) were mainly found at Station DG9 (Table 2).
and highest values in autumn and winter with up to 144 ind. 500 m$^{-2}$ (November 2001). Biomass was relatively constant during most of the study period and varied between 250 and 450 g wet wt 500 m$^{-2}$. Large peaks in biomass could be detected for December 2001 and April 2002 with 586 g and 826 g wet wt 500 m$^{-2}$, respectively.

At Station OG7 in the Oyster Ground highest mean abundances $>100$ ind. 500 m$^{-2}$ were found in early summer (June and July 2001) and autumn (November 2000). Also the biomass showed a peak with values $>700$ g wet wt 500 m$^{-2}$ in early summer (June 2001 and May 2002) and in November 2000.

Mean species numbers and Shannon–Wiener diversity index fluctuated rather irregularly throughout the study period and varied between 8 and 19 species per haul and between 1.5 and 3.8 $H'$ (Figure 4). Nevertheless, lowest species numbers were found in early summer at all stations.

Figure 3. Mean abundance (ind. 500 m$^{-2}$) and mean biomass (g wet wt 500 m$^{-2}$) during the study period.
Taxonomic groups and feeding modes

Seasonal changes of the epibenthic community structure were analysed regarding feeding modes and taxonomical groups (Figures 5 and 6). The dominant omnivore brittle star *Ophiura albida* at Station GB5 was excluded from the analyses, because its high abundance at this station would mask possible indications.

A clear dominance of predators and predators, which also feed as scavengers such as shrimp species (*Crangon* spp., *Processa* spp.), *C. cassivelaunus*, *L. holsatus*, and *A. rubens*, were found at Stations GB5 and OG7, with relatively constant ratios during the study period. High abundances of predatory shrimp species at Station GB5 led to the highest proportion of predators in October 2001 (Figure 5). Pronounced seasonal changes from spring towards autumn in terms of feeding modes occurred at Station DG9, with a decrease of predators such as *C. cassivelaunus* and *Philoceras trispinosus* and an increase

![Graphs showing species number and Shannon diversity index (H') over time for GB5, OG7, and DG9](https://academic.oup.com/icesjms/article-abstract/61/6/882/677440)

*Figure 4. Mean species number per haul and Shannon diversity Index (H') during the study period.*
of omnivores which also feed as scavengers such as *P. bernhardus* (Figure 5).

The ratios of the different taxonomic groups at Station DG9, clearly dominated by crustaceans, remained relatively stable during the study period (Figure 6). However, highest proportions of echinoderms, mainly *A. rubens* and *A. irregularis*, were observed during the summer months.

At Stations GB5 and OG7 echinoderms dominated, such as *A. rubens* and *A. irregularis*, especially during winter and spring. Proportions of crustacean, mainly shrimp species such as *C. crangon* and *C. allmanni* and the
swimming crab *L. holsatus* increased considerably from spring towards autumn (Figure 6).

**Multivariate analysis**

The results of the multidimensional scaling (MDS) based on fourth root transformed abundance data revealed two separate clusters at all stations, dividing the autumn and winter communities from the spring and summer communities (Figure 7). Samples taken in May, June, July, August, and September were grouped together at all stations. Additionally, samples from April 2002 at Stations OG7 and DG9 and from October 2001 at Station DG9 were grouped together with the spring/summer cluster.

Species responsible for the discrimination between these two clusters are listed in Table 3. At Station GB5 the brittle

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**Figure 6.** Relative abundance for taxonomical groups excluding *Ophiura albida.*
Figure 7. MDS ordination of √ transformed abundance data.
star Ophiura albida, the masked crab Corystes cassivelaunus (Figure 8), and the swimming crab Liocarcinus holsatus (Figure 9) showed highest abundances during the spring and summer period. In contrast, the common shrimp Crangon crangon (Figure 11) and the related shrimp species Processa nouveli holthuisi (Figure 10) occurred at Station GB5 nearly exclusively during the autumn/winter period, particularly in late autumn (October and November 2001).

Similar to Station GB5, the crab C. cassivelaunus characterized the spring/summer period also at the other Stations OG7 and DG9 (Table 3), but L. holsatus showed an opposite seasonal distribution pattern at Stations OG7 and DG9, with highest abundances during the autumn/winter period. Additionally, the shrimp species Crangon allmanni (Figure 11) was found to be a discriminating species at Stations OG7 and DG9, mainly found in autumn and winter. The shrimp species Philoceras trispinosus occurred in low abundances during the whole study period at Station DG9 and occasionally at Station GB5. This species might be underrepresented in these samples because of their small size. Nevertheless, during winter and early spring large individuals, mainly females with eggs, could be found in high abundances at Station DG9 (Figure 10). The sand star Astropecten irregularis characterized the spring/summer cluster at Station OG7.

For the dominant species, the hermit crab Pagurus bernhardus and the common starfish Asterias rubens, no clear seasonal distribution patterns could be found in terms of biomass and abundance. However, lowest abundances of both species were found in the winter months at Stations GB5 and OG7 (Figures 12 and 13).

### Epibenthos and environmental parameters

#### Temperature, TOC, and chlorophyll a contents

Sea surface temperature was found to correlate significantly with most of the faunal data at Station GB5 like mean abundance and mean biomass of all epibenthic species and mean abundance of crustacean, echinoderms, omnivores, omnivores/scavengers, and predators/scavengers.

At Station OG7, mean abundance of crustacean and omnivores/scavengers, predators/scavengers and, additionally, mean species number were positively correlated, and at Station DG9 mean abundance of predators was negatively correlated to the sea surface temperature (Table 4).

Chlorophyll a contents did not correlate with any epibenthos parameter and also TOC contents only correlated positively with echinoderms at Station GB5 and negatively with predators at Station DG9.

#### Fishing effort

The fishing effort was highest near Station GB5 where mainly beam trawling was carried out. Otter trawling effort increased towards the northern stations and was nearly exclusively carried out near Station DG9 (Figure 14). Despite the high fishing effort near Station GB5, mainly due to beam trawling, epibenthic parameters did not correlate with fishing effort (Table 4). The only exception that occurred was a correlation between otter trawling and mean abundance of surface deposit feeders. In contrast, at Station DG9 like mean species numbers, mean abundance of crustacean, predators and predators/scavengers were negatively correlated with otter trawling effort. At Station OG7 mean species number, mean abundance of crustacean and

| Table 3. Seasonal occurrence of characteristic epibenthic species. Discriminating species indicated by SIMPER between spring/summer and autumn/winter clusters for the Stations (a) GB5, (b) WB7, and (c) DG9. |
| Mean abundance || GB5 | OG7 | DG9 |
| Mainly autumn/summer | (autumn/winter–spring/summer) | (autumn/winter–spring/summer) | (autumn/winter–spring/summer) |
| Crangon crangon | 68.8 | 1.9 | — | — | — | — |
| Crangon allmanni | 75.2 | 21.3 | 14.5 | 0.3 | 1.8 | 0.1 |
| Processa nouveli holthuisi | 62.8 | 0.4 | 15.3 | — | — | — |
| Philoceras trispinosus | 2.2 | 0.4 | — | — | 17.6 | 3.8 |
| Mainly spring/summer | Ophiura albida | 4 494.3 | 8 207.7 | 3.0 | 2.3 | — | — |
| Corystes cassivelaunus | 10.8 | 30.3 | 4.1 | 13.4 | 3.2 | 13.6 |
| All year | Asterias rubens | 138.3 | 175.4 | 20.7 | 23.8 | 4.5 | 5.2 |
| Pagurus bernhardus | 2.7 | 5.8 | 3.6 | 3.0 | 15.3 | 15.0 |
| Difference between stations | Astropecten irregularis | 3.8 | 3.5 | 6.5 | 31.9 | 5.2 | 5.1 |
| Liocarcinus holsatus | 16.6 | 23.9 | 5.9 | 0.3 | 23.5 | 4.7 |

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Discussion
Spatial community structure
Most investigations of spatial distribution patterns of epibenthic communities in the North Sea revealed rather similar patterns separating the southern North Sea from the central and northern North Sea (Dyer et al., 1983; Frauenheim et al., 1989; Jennings et al., 1999a; Zühlke et al., 2001; Callaway et al., 2002). The most conspicuous boundaries were the 50-m depth contour, as well as the 100-m and 200-m depth contours. This agrees with the concept of the three endobenthic étages of Glémarec (1973).

A separation of the southern community, where our study sites were situated, into different epibenthic communities

omnivores/scavengers were positively and mean abundance of echinoderms were negatively correlated with fishing effort.

Figure 8. Mean abundance (ind. 500 m$^{-2}$) and mean biomass (g wet wt 500 m$^{-2}$) of Corystes cassivelaunus.

GB5

OG7

DG9
was found by several authors (Duineveld et al., 1991; Zühlke et al., 2001; Callaway et al., 2002). Zühlke et al. (2001) described an epibenthic community inhabiting the shallow parts of the continental coast with high abundance and biomass of echinoderms such as the brittle stars *Ophiura ophiura*, *O. albida*, and the common starfish *Asterias rubens*, and the crustacean *Liocarcinus holsatus*. Towards the central North Sea the starfish *Astropecten irregularis* and the hermit crab *Pagurus bernhardus* were found to be the dominant species. Also Duineveld et al. (1991) separated a biomass-rich epibenthic community situated along the continental coast from an offshore community. This agrees well with our results, with high total abundance and biomass at Station GB5 in the southern German Bight, mainly due to the dominance of *O. albida* and *A. rubens* (Table 2). In contrast, total abundance and biomass at the Dogger Bank Station DG9 was low and dominant species were mainly crustaceans such as
P. bernhardus, the masked crab Corystes cassivelaunus and L. holsatus. The station in the Oyster Ground (OG7) provided an intermediate state between the northern and the southern stations dominated by A. rubens, A. irregularis, and C. cassivelaunus, with a similar total abundance and biomass as at Station DG9 (Table 2). Nevertheless, most dominant species occurred at each of the three stations but at different abundances.

Spatial differences in the epibenthic community structure may be linked to several factors. Local differences in depth, sediment characteristics, hydrographical conditions such as stratification of the water column and circulation patterns, temperature, and primary production are known to be closely related to benthic community patterns (Duineveld et al., 1991; Rees et al., 1999; Callaway et al., 2002).

The relationship with depth is not expected to be causal and could not be responsible for the observed differences between the stations investigated in this study, since the depth is similar at all stations (Table 1). However, the observed boundary separating northern and southern epibenthic communities along the 50-m depth contour described above coincides with the large-scale distribution

![Graphs showing mean abundance of Processa nouveli holthuisi and Philoceras trispinosus at different stations](image)

Figure 10. Mean abundance (ind. 500 m$^{-3}$) of Processa nouveli holthuisi and Philoceras trispinosus.
of water masses in the North Sea. The northern North Sea is mainly influenced by the influx of deep Atlantic water, whereas the southern part is affected by the influx of water from the English Channel. Frauenheim et al. (1989) found a shift in epibenthic community patterns from the general north/south division in summer to an east/west division in winter, which was caused by an enhanced inflow of deep Atlantic water into southern regions along the English coast in winter. But the shift in distribution patterns was restricted to rare species, while the distribution patterns of abundant species were seasonally constant. Thus, variations in the circulation patterns might partly influence the faunal distribution, but can neither explain the rather constant large-scale patterns, nor the differences at our stations in the southern North Sea, where water mainly originates from the English Channel, only slightly mixing in the south with coastal waters (GB5) and in the north (DG9) possibly with deep Atlantic waters (Becker et al., 1992).

Jennings et al. (1999a) found that annual variation in bottom-water temperatures was most likely to be responsible for the distinctive boundary between epibenthic communities found south and north of the 50-m contour,

Figure 11. Mean abundance (ind. 500 m$^{-2}$) of Crangon crangon and Crangon allmanni.
with higher seasonal temperature fluctuations in the southern than in the northern North Sea, due to differences in stratification and vertical mixing of the water column. Also our results indicate that temperature causes the observed spatial differences between the three stations investigated. The northern Stations OG7 and DG9 showed a stratified water column in the summer months, whereas the southern station (GB5) was mixed throughout the year, resulting in higher seasonal temperature variation at this station compared to the northern ones (Figure 2).

In terms of sediment parameters, Rees et al. (1999) found that substratum type appeared to be the main structuring force for epibenthic communities, whereas other investigations found it difficult to relate bottom type and epibenthic community patterns (Basford et al., 1990; Duineveld and van Noort, 1990; Duineveld et al., 1991). In areas with a wide range of different substrate types,
including gravel and rocks, like those studied by Rees et al. (1999), the relationship between epibenthic communities and substrate seems to be clearer, due to an enhanced diversity of sessile species on coarser ground. In contrast, in areas where mainly sandy or muddy sediments dominate, like in most parts of the North Sea, the relationship between sediment structure and epibenthos seems to be of minor importance (Basford et al., 1990).

Organic content in the sediment as an indicator of food supply for benthic organisms might also affect the faunal distribution patterns (Rees et al., 1999). The high biomass at Station GB5 in the southern German Bight might be caused by an enhanced food supply from the water column. The strong riverine input results in high levels of inorganic nutrients which, together with a relatively long residence time of the water masses due to the anticlockwise circulation pattern, result in intense algal blooms and a high input of organic matter into the sediment (Dippner, 1993; Dauwe et al., 1998; Stoeck and Kröncke, 2001). High TOC and to a lesser extent chlorophyll $a$ contents at

![Figure 13. Mean abundance (ind. 500 m$^{-2}$) and mean biomass (g wet wt 500 m$^{-2}$) of Pagurus bernhardus.](image-url)
Station GB5 in contrast to the northern Stations WB7 and DG9 reflect the comparatively high organic input (Table 1). The dominance of the brittle star *Ophiura albida* at Station GB5, at least partly feeding on detritus, supports this suggestion, representing over 90% of total abundance and over 50% of total biomass (Table 2). However, differences in the composition of feeding modes between the three investigated sites indicate differences in

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<th>Surface water temperature</th>
<th>TOC</th>
<th>Chlorophyll a</th>
<th>Fishing effort (beam trawling)</th>
<th>Fishing effort (otter trawling)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GB5</td>
<td>OG7</td>
<td>DG9</td>
<td>GB5</td>
<td>OG7</td>
</tr>
<tr>
<td>Mean abundance</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean biomass</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Mean species number</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Crustacea</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Echinodermata</td>
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<td>+</td>
<td></td>
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</tr>
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<td>+</td>
<td></td>
<td>+</td>
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<tr>
<td>Omnivores</td>
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<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Omnivores/scavengers</td>
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<td>+</td>
<td></td>
<td>+</td>
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<tr>
<td>Predators</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Predators/scavengers</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Surface deposit feeder</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
</tbody>
</table>

Table 4. Positive (+) or negative (−) correlations between environmental parameters and the epibenthos. (+ (−) p < 0.05; + + (−) p < 0.01; <sup>a</sup> significant only with accumulation of both parameters (beam trawling and otter trawling); <sup>b</sup> referring to the fisheries data one month before sampling.

Figure 14. Fishing effort given as hours fishing per ICES rectangle 37 F7 (GB5), 38 F5 (OG7), and 39 F4 (DG9) for beam trawling (a) and otter trawling (b).
the foodweb structure of the epibenthic communities (Figure 5).

Bottom trawling was found to affect epibenthic communities too (Bergmann et al., 1990; Ramsay et al., 1998; Frid and Hall, 1999; Kaiser et al., 2000). In the southern German Bight, where mainly beam trawling is carried out, fishing effort is substantially higher than in the northern regions (Rijnsdorp et al., 1998; Jennings et al., 1999b; Zühlke et al., 2001). Fishing effort at Station GB5 in the southern German Bight is about five times higher than at the northern Stations OG7 and DG9 (Figure 14).

Changes in the epibenthic community attributable to fishing could be caused either by an enhanced food supply of discards for scavenging species (Fonds, 1994a; Kaiser and Spencer, 1994; Groenewold and Fonds, 2000) or by increased mortality of the epifauna itself (Fonds, 1994b; van Santbrink and Bergman, 1994). Mortality rates of discard species are lowest for echinoderms such as Asterias rubens, Astropecten irregularis, or ophiuroids due to their relatively flexible exoskeleton and their ability to regenerate limbs (Kaiser and Spencer, 1995; Kaiser, 1996; Ruppert and Barnes, 1996). Additionally, the relatively small species Ophiura albida will mostly pass through the meshes of the commercial fishing gear with a mesh size of about 8 cm (stretched) (Bergman et al., 1990; Fonds, 1994a; Duplisea et al., 2002).

The dominance of echinoderm species at Station GB5 might partly be caused by this high resilience of most echinoderms to the effects of trawling, like suggested for other heavily fished areas in the North Sea (Lindley et al., 1995; Tuck et al., 1998; Rumohr and Kujawski, 2000).

Seasonal variability of epibenthic communities

In contrast to the large-scale spatial distribution pattern of epibenthos in the North Sea, almost no information is available for the short-term temporal or seasonal pattern and the underlying factors. The epibenthic communities of the three sites in the southern North Sea studied during this investigation showed different seasonal patterns in terms of mean abundance and biomass of epibenthos at the different sites. In the southern German Bight (GB5) a clear seasonal cycle with maximum abundance and biomass in summer was found. In the Oyster Ground (OG7) this seasonal pattern was less distinct, and at the Dogger Bank (DG9) an opposite pattern was found with highest values in winter (Figure 3).

These seasonal patterns were mainly related to variability in the abundance of the main species. Migration of new species into the study sites seasonally is less important. This is indicated by the relative constant species numbers during the study period.

However, the question arises of what causes both the differences in seasonal variability between the sites and the variability within the sites?

Primary production and hence food availability for the benthos follows a distinct seasonal cycle, due to differences in light availability and nutrient concentration (Colijn and Cadée, 2003). Hyperbenthic species are known to migrate actively into areas of high primary production (Hamerlynck and Mees, 1991). However, fluctuations in sediment characteristics like TOC and chlorophyll a contents as a marker of food quantity and quality in the sediment were not significantly correlated to seasonal variability of epibenthic communities. Thus, primary production seems to have no effect on the epifaunal structure, since these communities mainly consist of predators and scavengers which do not directly profit from the organic material bound to the sediment.

As discussed above, variations in bottom-water temperature are most likely responsible for large-scale spatial differences in the North Sea. But also the seasonal variability of epibenthic community structure seems to be affected by the variability of water temperature. Stratification of the water column was found during this study at Station OG7 in the Oyster Ground and at Station DG9 on the Dogger Bank during summer months. At Station GB5 the water column was well mixed throughout the year, which caused stronger seasonal fluctuations in temperature in the southern German Bight compared to the northern sites (Otto et al., 1990; Becker et al., 1992). Significant correlations between surface water temperature and most epibenthic community parameters could be observed at Station GB5 and to a lesser extent at Station OG7 (Table 4). Also Krönncke et al. (1998, 2001) found that the seawater surface temperature (SST) was significantly correlated to benthic community patterns in a well mixed area off the island of Norderney, indicating the direct effect of temperature on benthic communities in coastal areas. In contrast, at Station DG9 only the abundance of predators were correlated to water temperature. This might be due to the temperature effect on the reproduction of C. cassivelaunus (as described below).

Mortality attributable to low winter temperatures, and the resulting decrease in abundance and biomass seems to be of minor importance for the seasonal variability in the epibenthic communities investigated during this study. The populations of most species found with increased abundance in the summer months mainly consisted of adult organisms and not of juveniles due to recruitment. This is also reflected by the seasonal pattern of biomass, which showed the same pattern as abundance (Figure 3).

Thus, migration is supposed to be the most important process in epibenthic communities mediating between temperature and seasonal density fluctuations, since migration is triggered mostly by changes in temperature (Boddeke, 1976; Oh et al., 1999; Freeman et al., 2001; Temming and Damm, 2002). Species known or supposed to be migratory are most responsible for the increase in abundance during autumn at the Stations GB5 and OG7, whereas at Station DG9 these species were absent or were
found with highest abundance only during winter (e.g. *L. holsatus, C. allmanni*). Even fluctuations in the abundance of less mobile species such as *O. albida* and *A. rubens* seem to be caused more likely by migration than by mortality. Also Hinz et al. (2004) found an increase in abundance and biomass of *O. albida* and *A. rubens* from winter to summer in the southern German Bight, and related this finding mainly to adults moving into the area during summer. Winter migration was also detected for *A. irregularis* by Freeman et al. (2001).

At the Dogger Bank Station DG9, the minimum abundance and biomass during the summer months May to August 2001 corresponds with the highest fishing effort in that area. Therefore, fishing might also affect the short-term temporal distribution patterns of epibenthos. Short-term impacts of fishing might be due to the direct removal of epibenthic animals or due to the attraction of scavenging species to the dumped discarded and dead animals remaining in the trawl track. To estimate this short-term impact, we correlated the epibenthos data with available monthly data on fishing effort for the ICES rectangles covering the study sites. Surprisingly, the correlation revealed that fishing effort seems to have no effect on the short-term epibenthos pattern in the heavily fished area of the southern German Bight (GB5). However, possible effects may be masked by the strong effect of seasonal variability in temperature at that station as discussed above. Another explanation might be that the epibenthic community in this area has undergone a long-term change due to the intense fishing impact over decades, and only those species tolerant to fishing, such as echinoderms, have survived. Therefore, the community structure at GB5 might be a result of long-term fishing effort. In contrast, at Station DG9, where fishing effort was comparatively low, species numbers and abundance of crustaceans, predators and predators/scavengers were negatively correlated with the otter trawling effort, indicating a direct effect of fishing on the epibenthic communities. Although total abundance decreased during the summer months with highest fishing effort, the relative proportion of scavengers increased. Those species might benefit from an enhanced food supply. Nevertheless, it has to be taken into account that trawling effort is very patchily distributed and effort data per ICES rectangle can only give an approximate estimation of the frequency and locality of trawling in our area (Rijnsdorp et al., 1998; Jennings et al., 1999b). A detailed knowledge at the small-scale distribution of fishing effort is essential to sufficiently address the impact of fishing on benthic communities on a temporal and a spatial scale.

**Migration of species**

Despite the observed spatial differences in the seasonal epibenthic community, the multivariate analysis revealed small-scale seasonal differences at the three stations and separate autumn/winter communities and spring/summer communities (Figure 7). Species characterizing the autumn/winter community were mainly shrimp species, most likely due to migratory movements.

Seasonal migration is a well-known phenomenon in the common shrimp *Crangon crangon*, which characterized the autumn/winter community at Station GB5 in terms of abundance (Boddeke, 1976; Henderson and Holmes, 1987). This species migrates during autumn after water temperature reaches its maximum from the shallow areas of the Wadden Sea towards the German Bight and vice versa during early spring (Boddeke, 1976). The offshore migration is reflected during this study by a peak in abundance of *C. crangon* at Station GB5 in October and by its contrasting absence from May until September (Figure 10). The inshore spring migration could not be observed, likely due to the lack of data in early spring time.

In contrast to the occurrence of *C. crangon*, which was restricted to Station GB5, the related species *C. allmanni* characterized the autumn/winter community of the northern Stations OG7 and DG9. Concerning migratory patterns, Allen (1960) assumed a seasonal inshore migration of *C. allmanni* at the Northumberland coast during winter and offshore during summer, i.e. inversely to the migration pattern of *C. crangon*. However, Creutzberg and van Leeuwen (1980) found no indication for migration of *C. allmanni* in the southwestern North Sea and attributed the decline in abundance, they had found, to mortality during the summer. The highest abundance of *C. allmanni* at Station GB5 in October, and at Station OG7 one month later, would indicate an offshore migration of *C. allmanni* during autumn, especially as *C. allmanni* was only found in winter samples at the northern Station DG9. These shrimps might originate partly from the Helgoland Trench, where Blahudka and Türkay (2002) found the only reproducing population of *C. allmanni* in the German Bight.

Another shrimp species characterizing the autumn/winter community at Station GB5 was *Processa nouveli holthuisi*. Adults of this species were first found in the German Bight in 1985 (Wehrtmann, 1986) and have only been found occasionally since then (Neudecker, 2001). This absence might be caused, at least in part, by diurnal migration (Gruner et al., 1993), because *P. n. holthuisi* larvae make up over 50% of the non-crangonid shrimp larvae in the German Bight (Wehrtmann and Greve, 1995). In the course of this study, an abundance of up to 337 ind./500 m² were found at Station GB5 in October (Figure 10), which might also be due to migration in order to avoid low temperatures in the southern German Bight. This hypothesis is confirmed by records of this species north of Helgoland in January 1999 and 2000 by Neudecker (2001).

An opposite seasonal distribution pattern with highest abundances during spring and summer was detected for the brittle star *Ophiura albida* characterizing the spring/summer community at Station GB5 and the masked crab *Corystes cassivelaunus* characterizing the spring/summer community at all three stations (Figure 8). The seasonal
pattern of the latter species can be explained by the burrowing life mode of this crab described by Hartnoll (1972). The specimen remains buried throughout the year, with the exception of mature crabs, which leave the sediment during the breeding season from April to June. This behaviour is reflected in our results (Figure 8).

*O. albida* dominated the epibenthic community at Station GB5 and abundance and biomass increased during summer. Nevertheless, the abundance and biomass of *O. albida* were highly variable in the summer months. This could not be explained by problems with sampling, e.g. a jumping beam trawl, because high fluctuations were only observed in the abundance and biomass of *O. albida* and not simultaneously of other species (Figure 3). Additionally, H. Neumann (pers. comm.) also found highly variable abundances of *O. albida* in an area in the southern German Bight, usually dominated by *O. albida*, in winter 2003. He found 0 to 35 ind. 500 m\(^{-2}\) for the most parts of a sampling area of 10 × 10 nm. Only at one station at the edge of the area an abundance of about 3000 ind. 500 m\(^{-2}\) was found. A patchy distribution pattern and aggregation was previously observed for *O. albida* but mainly on a small scale (replicates of grab samples and aquarium) probably due to food availability (Dahm, 1991). The patchy distribution in time and space observed during this study and by Neumann may indicate a migration of large parts of the population of *O. albida* at the study sites, possibly as a reaction to unfavourable environmental conditions like low winter temperatures or fluctuating food supply (summer). Thus, future studies using acoustic seabed classification systems like QTC might be useful to map the distribution patterns in time and space of *O. albida* beds over a large scale.

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References


